

**USING MIGRATION MONITORING DATA TO ASSESS BIRD POPULATION STATUS  
AND BEHAVIOR IN A CHANGING ENVIRONMENT**

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A DISSERTATION

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By Evan M. Adams

Dissertation Advisor: Dr. Brian Olsen

A Lay Abstract of the Thesis Presented

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Across the world, researchers use migration banding stations to document bird migration and study the phenomenon. In this dissertation, I focus on ways of analyzing bird migration banding data and the utility migrating birds as indicators of ecosystem health that make these monitoring efforts more useful to answering ecological questions and managing migratory species. In Chapter 1, we provide background on hierarchical modeling and an overview of our findings. In Chapter 2, we developed and validated new methods to estimate daily changes in migratory population size while controlling for changes in detectability due to environmental conditions. In Chapter 3, this modeling technique was then employed to evaluate the continental-scale and the local-scale determinants of migratory population size for ten species of migrants using a Key Biscayne, FL site for migratory stopover in the fall. Species showed diverse relationships between abundance and local weather conditions. Wet conditions on the breeding grounds consistently increased migratory onset and dry conditions on the non-breeding grounds from the previous winter consistently reduced population size across all species. In Chapter 4, we looked at how daily changes in migrant density influenced the stopover behavior of seven

songbirds at the Key Biscayne stopover site. Density-dependence had positive and negative effects on mass gain across species, the chance of that effect being negative increased with the average daily stopover population size of the species. Density-dependence was hypothesized to be a function of overall migrant abundance at the site, with only highly abundance species showing negative effects. Finally, in Chapter 5 migrating birds are used to tell us about contaminant exposure in their breeding and non-breeding environments. We found higher amount of mercury in fall than the spring and there was evidence that fall mercury exposure was altering migratory behavior. These patterns provide the first evidence that Hg exposure alters migratory physiology in songbirds. Overall, this dissertation suggests that migration monitoring is useful for both basic and applied research and provide a tool for understanding the complicated life cycles of migratory animals.

## **DEDICATION**

This is for Kate. Thank you for supporting me through it all.

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## CHAPTER 1: INTRODUCTION

Migratory bird banding stations are useful for elucidating regional migration patterns and assessing population status for many passerines and near-passerines (e.g., Lloyd-Evans and Atwood 2004). Traditionally these data have been analyzed with statistical models of catch per unit effort. This method leaves many survey biases inestimable, particularly detection probability, one of the largest sources of bias in ecological surveys (Sauer and Link 2004). Studies of closed populations on the breeding grounds suggest that detection probabilities likely vary with year, day, season, habitat, species, and other variables. More traditional methods for modeling variation in detection probability are not suitable for migratory populations due to their irregular openness and large (order of magnitude) daily changes in abundance. Recent quantitative advances in this area, however, will allow for inferences about these types of populations. In the chapters that follow, we use these new modeling advances to estimate the abundance of migratory populations and to explore environmental conditions on birds' breeding, wintering, and migratory stopover habitats.

The primary quantitative tool used to disentangle detection probability from observed abundance is the hierarchical model. Occupancy models are the most widely used hierarchical model, and they serve as an illustrative example of how hierarchical models work in general (MacKenzie et al. 2002). Hierarchical models simultaneously model nested functions. The two general functions of primary import to ecology describe A) the relationship of environmental conditions or other factors to organismal abundance (the "process" model) and B) the bias associated with gathering ecological data (the "observation" model). For example, many ecological surveys use some standardized methodology to count the number of individuals. These counts can be summarized as naïve abundance estimates (naïve because they assume that all animals that could be counted, were counted). To measure true abundance, naïve abundance must be corrected with some estimate of observation error. Basic detection probability models

use variation in the count data itself to estimate how likely it is for an organism to be counted and thus, how likely it is that organisms were present but went uncounted during a given survey (observation error). Hierarchical models are useful tools because they estimate observation error in tandem with a process model that explains variation in true abundance. This allows error to be properly propagated throughout the model and allows researchers to elucidate complex relationships within ecological data sets (e.g., Chandler and King 2011, Chandler et al. 2011).

In this dissertation, we explore analytical methods for bird migration banding data and, more broadly, the utility of migrating birds as indicators of ecosystem processes. Our migration monitoring data come from Key Biscayne in South Florida, where migration monitoring has been ongoing for over ten years. In Chapter 2, we develop a hierarchical model to estimate the abundance of migratory birds on stopover and explore covariates of both the process and observation models. We employed the recently developed, Dail-Madsen model in a novel usage to estimate daily changes in the migratory population size of black-throated blue warblers, controlling for variation in detectability. We found that daily changes in weather affected both detection probability and rates of immigration and emigration. Aside from survey effort, the most important factors affecting detectability included precipitation, wind speed, and wind direction (during both the banding session and during the previous night). Together, these environmental factors accounted for 30% more variation in detection probability than effort alone. Our study suggests that hierarchical modeling efforts are effective at estimating migratory population size, and future studies attempting to understand the population dynamics of migrating animals should consider similar techniques.

In Chapters 3 and 4 we use this new modeling technique to explore covariates of migratory population abundances and migratory stopover behavior, respectively. For Chapter 3, we disentangle the effects of broad-scale climate change on total migratory population size with the effects of changing local weather on the day-to-day changes in stopover population size. Using the hierarchical N-mixture modeling techniques from Chapter 2, we quantified the effects



of the summer (breeding season) North Atlantic Oscillation (NAO), winter (non-breeding season) El Niño Southern Oscillation (ENSO), and winter Madden-Julian Oscillation (MJO) on the subsequent autumnal migratory population. For each of these climate indices, we tested for relationships with migratory timing and population size across ten songbird species. Over the ten-year period of observation, we found negative trends in overall abundance in five of the ten species and positive trends in none. Increasing breeding-season NAO (wetter summers) predicted earlier migratory timing (10/10 species) and increased population size for some species (6/10 species). Increasing ENSO and MJO (drier winters) had consistently negative effects (9/10 and 8/10 species, respectively) on total annual migratory population size. We show that fall migration is significantly impacted by events on the previous breeding and non-breeding seasons, and, on the whole, conditions from the previous winter had a consistently stronger effect on migratory populations than did effects from the previous breeding season.

In Chapter 4, we explore how the number of migrants at the stopover location influenced refueling rates at Key Biscayne. We measured stopover refueling rates (the rate of change in mass over the course of the banding day on average across the population) in seven songbird species during fall migration to test for density dependence in refueling rate across multiple temporal scales (current day, previous day, previous week and previous two weeks) and two population scales (conspecific and all migrants). We used 10 years of migration banding data to analyze stopover mass gain in a generalized linear mixed model framework. Our top model for daily mass gain included the effects of age, physiological condition, and daily conspecific abundance. The density-dependent effects varied with species; some responded positively to daily conspecific density and others negatively. Across species, the magnitude of negative response to conspecific population size increased with the average stopover population size. Given the diversity of species-level response to conspecific density, density-dependence is either highly context dependent (by species, stopover site, flock-foraging community) or a general

phenomenon where response is dependent on the overall magnitude of conspecific stopover abundance. Species with low conspecific densities may not experience enough competition to impede fuel acquisition, and at low overall numbers, increases in density may confer foraging advantages due to flocking.

Finally, in Chapter 5 we invert the paradigm from the previous chapters and ask what migratory birds can tell us about their environment (rather than the effect that environment has on the birds). Using two fall and three spring migration seasons, we collected blood and feather samples from a subset of the individuals and quantified the amount of mercury in the tissues. We then compared Hg concentrations on tissues during migration with those collected on the breeding ground and tested for correlations between migratory Hg level and environmental conditions, energy stores, and mass gain during both fall (with feather tissue) and spring migration (with blood tissue). In spring, blood-Hg concentrations were most dependent on species, year, and the time of day the bird was captured. In fall, feather Hg was negatively correlated to species, year, quantity of fat stores, and also size-controlled mass and refueling rate at the stopover site for some species. These patterns provide the first evidence that Hg exposure alters migratory physiology in songbirds, and further they suggest that Hg exposure on the breeding grounds is large enough to lead to interactions with fitness during migration. We suggest that migration monitoring efforts could be useful for determining broad-scale Hg exposure, particularly in light of planned Hg emission reductions across the United States and globally.

In conclusion, we developed and applied new models for estimating stopover abundance for migratory species and found that weather and climate on the breeding and non-breeding grounds were important to predicting daily and annual abundance of these species. There was a diversity of responses to climate and weather among our study species, suggesting that different migratory strategies and life histories were successfully modeled in our framework. Given the

consequences for daily variation in migrant abundance and the ability for migration monitoring stations to be used to measure changes in other kinds of population status (e.g., contaminant exposure), we think that such monitoring efforts have incredible utility for both basic and applied research and give conservation practitioners a powerful tool for understanding the complicated life cycles of migratory animals.

## CHAPTER 2: USING A HIERARCHICAL MODELING FRAMEWORK TO ESTIMATE ABUNDANCE AND DETECTION BIAS IN SURVEYS OF MIGRATING ANIMALS

### 2.1. Introduction

Migration—an important driver of animal population dynamics and limitation—has been difficult to understand at the population level because migratory abundance is inestimable using traditional survey methods (Sauer and Link 2004, Hochachka and Fiedler 2008). This is primarily because surveys of moving animals rarely meet the assumptions of current ecological abundance modeling frameworks (e.g., population closure). Despite this, constant effort surveys along migratory routes have been used across a variety of taxa to understand migratory behaviors and habitat use (Moore et al. 1990, Meitner et al. 2004, Rimmer et al. 2004, Olsen et al. *In Press*), migratory habitat quality (Moore et al. 1990, Kitorov 2008), migration routes (Moore et al. 1990, Norris et al. 1999, Olson et al. 2009) and migratory population sizes or trends (Perryman et al. 1999, Findlay and Best 2006, Dunn et al. 1997, Kahurananga and Silkiluwasha 1997, Lloyd-Evans and Atwood 2004, Peterson et al. 2008, Osenkowski et al. 2012). Because these efforts have been unable to account for detection bias, they have been limited to quantifying changes in relative abundance for migratory populations—a metric that is prone to error and can lead to inaccurate estimation of population size and changes (Sauer and Link 2004, Kéry et al. 2010, Guillera-Arriota et al. 2014). Here, we propose an analytical framework for surveys of migratory animals that quantifies observation bias and more accurately estimates migrating population size. We apply this framework to ten years of passerine banding data from southern Florida as a case study, and compare our estimates of abundance to relative abundance estimates obtained via traditional methods.

Myriad factors influence detectability in surveys of wildlife, including individual behaviors (e.g., trap shyness, Nichols et al. 1984), habitat (Chandler et al. 2011, Ballard et al. 2003, Mallory

et al. 2004), environmental conditions (Dunn and Hussell 1995, Dunn et al. 1997, Hussell et al. 2004, Simons et al. 2007) and time of year (Royle et al. 2005). Often, mark-recapture methods are employed to estimate population size or migratory behaviors while estimating detection bias, but in the open populations created by migration such methods can introduce their own biases (Winker et al. 1992). Techniques have been used to deal with transients moving through a resident population but, to this point, work has focused on a way of removing them from analysis rather than quantifying them directly (Hines et al. 2003). There is no reason to think that surveys of migrants lack similar issues of detectability that sedentary populations exhibit. To make surveys of migrants more useful as a means for monitoring populations and for answering basic ecological questions about migratory behaviors requires a broadly applicable method of estimating detection bias.

Here we employ a hierarchical model (Dail and Madsen 2011) that disentangles changes in population size with changes in detectability in open populations. The Dail-Madsen model has improved our estimates of sedentary populations (e.g., Chandler and King 2012, Chandler et al. 2011) but has not been yet applied to surveys of unmarked migrating animals. Here, we use counts of black-throated blue warbler (*Setophaga caerulescens*) captured and recaptured during migratory stopover at the Cape Florida Bird Observatory on Key Biscayne, FL to test this modeling framework and provide a basis for estimating stopover abundance and detectability in migrating animals. The objectives of this study are to: (1) formulate and validate a hierarchical model that can estimate detectability in migrating vertebrates, (2) use this model to determine if there are environmental correlates of detection probability for one species at a long-term monitoring station, and (3) determine if models that estimate detectability provide different estimates of migratory abundance for this species over traditional methods. This study is the first to our knowledge to decouple changes in detectability with changes in abundance for surveys of

migrating animals and provides a framework useful to a variety of different monitoring methods and taxa.

## **2.2. Methods**

### **2.2.1. Data Collection**

Songbird migration was monitored at Bill Baggs Cape Florida State Park on Key Biscayne, FL (25.674355°N, 80.161166°W) from 2002 to 2011 using a standardized protocol for migration monitoring with mist nets and banding (Ralph et al. 1993). Nets were opened at least 5 days a week at dawn for a minimum of 6 hours a day, weather permitting. New net locations were added to the station over the course of the study, so both daily net effort and number of nets varied by year. Nets were checked once every 15-30 minutes, and birds were extracted and banded with a uniquely numbered USGS aluminum band, noting species, age, and sex (Ralph et al. 1993). Numbers of total captures of black-throated blue warblers—selected because it was the highest abundance species during fall migration at the station—were summarized every day the station was operated. Net-hours (the number of 12-m nets multiplied by the number of hours left open), was calculated and summarized for each day. We examined 102 monitoring days per year over 10 years, with migratory sampling periods starting on August 9 of each year.

All weather data used in this study were collected from Miami International Airport, 15 km northwest of the study site, using the National Climatic Data Center ([www.ncda.noaa.gov](http://www.ncda.noaa.gov)). Data were compiled hourly and included temperature, humidity, wind speed, wind direction, amount of precipitation, and sea-level air pressure. For use in our modeling framework, we calculated means (or sums in the case of precipitation) for each variable in three time intervals: the hours of 0000-0500 (morning), 0600-1800 (daytime), and 1800-2300 (evening). Wind direction was decomposed into its northerly and easterly components and averaged for each time

period. All covariates were normalized before inclusion into the model using the “scale” function in R.

### **2.2.2. Objective 1: Creating and Validating a Hierarchical Model**

In this analysis we wanted to estimate stopover population size as accurately as possible for black-throated blue warblers with an approach that would be generally applicable to the widest variety of migratory species. To do this we used the total number of captures each day at the station to estimate the daily stopover population size without breaking up the sampling period into subperiods or use our knowledge of individual capture history. To estimate true daily abundance we used the Dail-Madsen variation of the Royle N-mixture model (Dail and Madsen 2011, Royle 2004) in the “pcountOpen” function in package “unmarked” (Fiske and Chandler 2011) within the R statistical computing environment (R Core Team 2014). The intended use of this model to estimate true population size across sites by estimating detectability for each sampling event, while relaxing the assumption of population closure among sampling periods. Population closure is difficult to assume even at small temporal scales in migrating animals; movements of individual birds within each sampling period (Aborn and Moore 1997, Taylor et al. 2011, Cohen et al. 2012) cause high population turnover throughout the day, and makes sub-sampling within days unrealistic.

The model assumes that detections are independent events (i.e., individuals are making migratory decisions independently from one another) and calculates detection probability for an aggregate of sampling locations (nets, in our case study). The first assumption appears rational in the case of black-throated blue warblers, as flock membership is not stable across multiple migratory flights in songbirds generally, and individuals appear to make migratory decisions based on their own condition in addition to local weather conditions and time of year (Schmaljohann and Dierschke 2005). Other species may not make migratory decisions

independently (particularly species with stable family or group membership during migration, such as some waterfowl, ungulates and marine mammals), and for these cases a multinomial formulation of the detection model would be more appropriate.

As for the second assumption, an aggregate estimate of detection probability across a group of nets is not problematic so long as the relative differences in detection probability among those nets are consistent through time. The most likely exception to this assumption would be the unequal distribution of netting time among nets throughout a given monitoring season. At our site, the capture effort at any individual net was significantly correlated with overall net effort at the site (linear regression,  $p < 0.001$ ). Thus, while micro-habitat differences among nets could lead to consistent differences in net-specific detection rates, all the nets were consistently opened and closed together during this study, and the effects of estimating detection probability as a site-wide aggregate are likely small to nonexistent. And while nets were added over the course of the study, we did not find an effect of year of first inclusion on capture rates ( $r^2 = 0.01$ ) so we considered total net effort a consistent proxy for survey effort across all years.

Typically, Dail-Madsen models use variation in counts of animals over  $i$  sites and  $t$  survey periods, but in this case we lacked the spatial replication of sites and instead substituted the independent replication of survey years for sites. This replacement of sampling years for sampling sites offers some unique advantages for migratory populations and many opportunities to explore migratory behaviors within a given migratory season. The overall hierarchical modeling structure (and mathematical structure) remains the same here as it has in past Dail-Madsen models:

$$N_{it} \sim \text{NB}(\lambda)$$

$$G_{it} \sim \text{NB}(\gamma)$$



$$S_{it} \sim \text{Binomial}(N_{it-1}, \omega)$$

$$N_{it+1} = G_{it} + S_{it}$$

$$y_{it} \sim \text{Binomial}(N_{it}, p)$$

In our analysis,  $N_{it}$  is the number of individuals present at year  $i$  and survey day  $t$ ,  $G_{it}$  is the number of individuals recruited during year  $i$  at survey period  $t$  (immigration to the site in a migratory population),  $S_{it}$  is the probability of an individual persisting from primary survey period  $t-1$  to the day  $t$  within year  $i$  (i.e., that an individual remains on “stopover”; the converse,  $1 - S_{it}$ , is the probability of departure from the site), and  $y_{it}$  is the number of individuals observed during year  $i$  and period  $t$  (the daily count of observations). The four parameters this model directly estimates are initial population size at the beginning of each migration season ( $\lambda$ ), daily immigration into the migratory site (traditionally “recruitment”:  $\gamma$ ), the daily probability of persisting at the migratory site (traditionally “apparent survival”:  $\omega$ ), and detection probability ( $p$ ). We used the negative binomial distribution as opposed to the traditional Poisson because of over-dispersed count data in our study.

In the original version of the Dail-Madsen model, sites are considered to be independent sampling events that change across sampling periods over time. Migratory monitoring stations often lack independent spatial replication. In the case of songbirds, for instance, mist nets are often placed close together and fundamentally measure the same daily migratory phenomenon. Any model that assumed that the capture rates of individual nets were independent would produce very biased estimates in the traditional approach to songbird migration monitoring. Through our formulation, we instead assume that captures across years are independent, not nets. Time and space have been substituted for each other in the way before in hierarchical population modeling. Yamaura et al. (2011) effectively estimated breeding and wintering animal population size at a

single site. While the modeling structures are different between the current study and Yamaura et al. (2011), the assumption of independence of among years is similar in both and there is clear precedence for successful estimation while making this assumption. If our assumption of independence is inaccurate, we would expect our estimates of population size to remain accurate, but variance estimates would be biased low.

Density-dependence, seasonal interactions, and other demographic processes, however, make it possible for migratory population size to be dependent between subsequent years (Norris and Marra 2007). While this is possible, the number of processes influencing bird abundance and movements from year to year is high and highly variable, so we assume that in aggregate the migratory population size in any given day of any given year is not dependent on the migratory population size in any given day of any other year. Lastly, this assumption of independence can be an advantage for estimating trends in population size, as there is no mathematical dependence among years which leads to clear population trend estimates.

While we had individual recapture data and we use both the initial capture and recapture data to estimate daily population size, we did not use an individual based analysis. Often the numbers of captures or recaptures are not high enough to precisely estimate population size and thus ineffective for many types of migratory surveys (Ballard et al. 2004, Kendall et al. 2004). Additionally, the subset of the migrating population that is recaptured tends to be individuals that are in poor condition on their first capture (Winker et al. 1992, Hochachka and Fiedler 2008, Ktitorov et al. 2008). Thus recaptures are not a random subset of the entire migratory population, making inferences about abundance using recapture rates biased.

To test whether the Dail-Madsen model could accurately estimate population size across ten independent years each with 102 primary sampling periods, we simulated a data set with similar properties to the black-throated blue warbler data. The purpose of the simulation study

was not to evaluate all the assumptions we made during this analysis but to determine if “pcountOpen” would be effective in producing unbiased results if our assumptions were reasonable. We generated 100 data sets based on the same parameters: for 10 years we started at an initial value ( $\lambda$ ) then added constant new recruits to the population ( $\gamma$ , a Poisson process) and allowed individuals with the population to persist at the site ( $\omega$ , a binomial process). Lastly, we allowed each individual a probability of being detected during the survey ( $p$ , a binomial process) at each of the 102 steps. Using a null model with no covariates, unmarked estimated parameter values of  $\lambda = 2.9$ ,  $\gamma = 3.9$ ,  $\omega = 0.95$  and  $p = 0.07$  for the Black-throated Blue Warbler data set. We then used these values as estimates of central tendency for the data set simulation process. After each data set was generated we used the “pcountOpen” function in program unmarked, we then estimated  $\lambda$ ,  $\gamma$ ,  $\omega$  and  $p$  for each randomly generated data set and compiled these data to look at average bias from the original parameter estimate and the variance that surrounds those estimates. In three cases, the model did not properly converge and those models were removed from the analysis.

### **2.2.3. Objective 2: Environmental Correlates to Detection**

We tested the hypothesis that  $\gamma$ ,  $\omega$  and  $p$  were dependent on local weather conditions by using Akaike’s Information Criterion (AIC) to select the top model of a candidate set (Anderson and Burnham 2002). The integration limit ( $K$ ) of the daily population size was determined by testing multiple values and set to 500 for each candidate model (following Fiske and Chandler 2011). Thirteen candidate models were selected based on *a priori* predictions in a modular fashion, where all potential covariates for a given parameter group were either completely included or completely excluded. We used the negative binomial distribution for the  $\lambda$  and  $\gamma$  parameters in all of our models and no relationship was implied between  $\gamma$  and  $\omega$  (i.e., the “constant” dynamics scenario in “pcountOpen”).

Our groups of modular covariates were A) weather effects on immigration, B) calendar effects on immigration, C) weather effects on emigration, D) weather effects on detection, and E) net-effort effects on detection. We included no covariates for initial population size, assuming that our surveys started early enough each year (August 9<sup>th</sup>) to avoid interannual differences in initial population size due to migratory phenology variation (i.e., the initial population size should be close to zero for all years). Immigration ( $\gamma$ ) covariates included the quadratic term of calendar date, morning wind speed, morning wind direction, and the interaction of the latter two terms. We used evening atmospheric pressure at sea level and evening wind direction as potential correlates to persistence ( $\omega$ ; emigration probability would be  $1-\omega$ ). Lastly, we modeled detection probability ( $p$ ) as a function of net effort, daytime temperature, daytime wind speed, daytime wind direction, daytime rainfall, early morning wind speed, and early morning wind direction. In the case of these last two variables, we wanted to test if nighttime migratory conditions and conditions inducing landing at the site influenced detectability during the subsequent banding day (e.g., was the activity and therefore detectability of birds forced to land due to poor weather different from those landing for other reasons).

#### **2.2.4. Objective 3: Model Comparison**

We evaluated the top model selected in Objective 2 by comparing its estimated trends in abundance at the migration monitoring station with those estimated by two more traditional approaches. The first of these approaches was the historical standard for migratory bird data, where the seasonal number of captures is simply divided by the total amount of net effort (Ralph et al. 1993). This approach does not include any daily covariates in the modeling structure.

The second approach to which we compared our top hierarchical model was a generalized linear mixed model with multiple covariates for detection rate, which is a more contemporary and robust modeling framework that has been used to evaluate trends in migratory banding data (e.g.,

Osenkowski et al. 2012). While this model can successfully model count data with multiple covariates, it cannot distinguish between the variation in the response due to observation bias and that due to ecological process. We included all the same covariates and interactions in this mixed model as were present in the top hierarchical model. Year and calendar day were assigned as random variables, while all other explanatory variables were considered fixed effects. In this model we related the evening wind speed covariate to the subsequent day of capture (as evening weather conditions cannot affect capture rates earlier in the day in this structure). Daily captures were modeled using a Poisson error distribution with a logarithmic link function. The generalized linear modeling was conducted in package “lme4” in the R statistical computing environment. Relative abundance estimates from these two approaches for each year were compared to the estimates of true abundance from the hierarchical model for each year with Pearson correlation.

## **2.3. Results**

### **2.3.1. Objective 1: Validating the Hierarchical Model**

The hierarchical modeling framework successfully estimated known rates of emigration and detection probability from our simulated data. Standardized differences in the average estimates for  $\omega$  and  $p$  from the known parameter value were 0.7% for emigration and 2.7% for detection probability. There was also high precision in these estimates (Coefficients of Variation were 3.7% and 11% for  $\omega$  and  $p$ , respectively; Fig. 1). Our mean, standardized estimate of  $\gamma$  was 60% higher (more immigrants) than the known value, although the precision (CV = 24.4%) was such that zero was included within one standard error of the mean estimate (Fig. 1). The accuracy of  $\lambda$  (-30% fewer individuals) was also less than  $\omega$  and  $p$ , though the standard error

again included zero. Estimates for  $\lambda$  were over an order of magnitude less precise relative to that of the other parameters (CV = 159.5%).

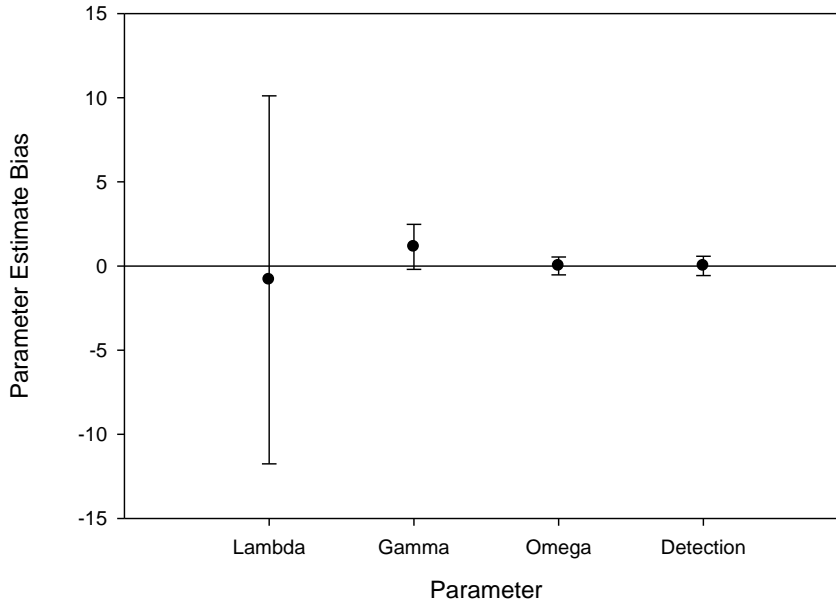


Figure 2.1. Estimates of standardized parameter estimate bias in our modeling framework using mean parameter estimates and their standard errors from 100 model runs. Before we calculated bias, each parameter was standardized (dividing by the known parameter value used to create the simulated database) to make our estimates of bias directly comparable across parameters. Initial abundance is lambda ( $\lambda$ ), immigration is gamma ( $\gamma$ ), persistence is omega ( $\omega$ ; emigration is  $1 - \omega$ ) and detection is p.

### 2.3.2. Objective 2: Environmental Correlates to Detection

The model that received the most  $AIC_c$  weight ( $> 0.999\%$ ) was the most complex model we tested. It strongly out-performed the next ranked model, which dropped the calendar date term in the immigration parameter ( $\Delta AIC_c = 51.4$ ). Because of this overwhelming support, we only consider this model in subsequent analyses. Estimates of initial population size were low ( $\mu$  [lower 95% confidence limit, upper 95% confidence limit]: 12.5 [9.3, 16.9]; Table 1). Overall, immigration varied non-linearly with calendar date, independent of other conditions (with a peak

recruitment date in the middle of each migration season). Controlling for this basic phenological pattern, immigration was highest when winds were strong and from the north in the early morning. Emigration rates were highest when atmospheric pressure was high and winds were from the north in the evening. On average, the immigration rate across all days and years was 10 individuals per day [9.21, 10.9] and the daily emigration probability was low overall but with high variability: 0.08 [0.06, 0.72].

Table 2.1. Parameter estimates for the top model. All variables are standardized before modeling so parameter estimates can be directly compared to determine relative effect size. Initial population size and immigration rate parameter estimates are log-transformed, and emigration and detection probability parameters are logit-transformed. For wind direction N and E are positive in the variable space. P-values are determined by a Z-test.

Model	Term	Parameter Estimate	Standard Error	P-value
Initial Population Size	Intercept	2.53	1.29	0.05
Immigration Rate	Intercept	1.197	0.08	<0.001
	Morning Wind Direction (N/S)	-0.11	0.10	0.3
	Morning Wind Speed	0.12	0.08	0.13
	Calendar Day <sup>2</sup>	0.48	0.06	<0.001
	Morning Wind Direction (N/S)*Morning Wind Speed	0.62	0.10	<0.001
Persistence Probability	Intercept	6.51	0.49	<0.001
	Atmospheric Pressure	-1.58	0.21	<0.001
	Evening Wind Direction (N/S)	-2.44	0.35	<0.001
Detectability	Intercept	-3.69	0.05	<0.001
	Daily Temperature	0.09	0.03	0.003
	Daily Precipitation	0.29	0.02	<0.001
	Net Effort	1.03	0.03	<0.001
	Daily Wind Speed	0.16	0.03	<0.001
	Daily Wind Direction (N/S)	0.28	0.03	<0.001
	Daily Wind Direction (E/W)	0.11	0.02	<0.001
	Morning Wind Direction (N/S)	-0.27	0.03	<0.001
	Morning Wind Speed	0.14	0.04	<0.001
Dispersion	Intercept	-2.8	0.832	<0.001



Average detectability across all conditions at the site was 0.13 [0.13, 0.14], but many environmental variables affected this parameter on a day-to-day basis. Net effort was the strongest single effect, and detection probability increased with effort. Daily temperature, precipitation, and wind speed also had positive effects on detectability. Northerly and easterly winds during the banding session increased detectability. Lastly, environmental conditions from the previous night that increased immigration rate (particularly strong northerly winds) were opposite those that increased bird detectability once they landed (strong, southerly, evening winds). Environmental conditions collectively explained more than 30% of the daily variation in detection probability than net effort alone.

### **2.3.3. Objective 3: Model Comparison**

When comparing estimates of relative abundance between the hierarchical Dail-Madsen and catch-per-unit-effort models, we found little correlation (Pearson  $r = 0.16$ ; Fig. 2). The generalized linear mixed model and the hierarchical model showed a stronger, but still weak, Pearson correlation coefficient ( $r = 0.40$ ). The catch-per-unit-effort model and the generalized linear model had the highest Pearson correlation ( $r = 0.65$ ). While correlation coefficients over 0.30 are often considered ecologically relevant, all three of our models used the exact same data set, and the different models still consistently disagreed in their annual estimates of migratory abundance (Fig. 3). Dail-Madsen estimates in 2002 appear to be an outlier in our ten years of data with an unusually high estimate with high standard error. If this year is removed from the correlation analysis, the Pearson correlation improves to 0.56 with the GLMM and 0.39 with the catch-per-unit-effort model.

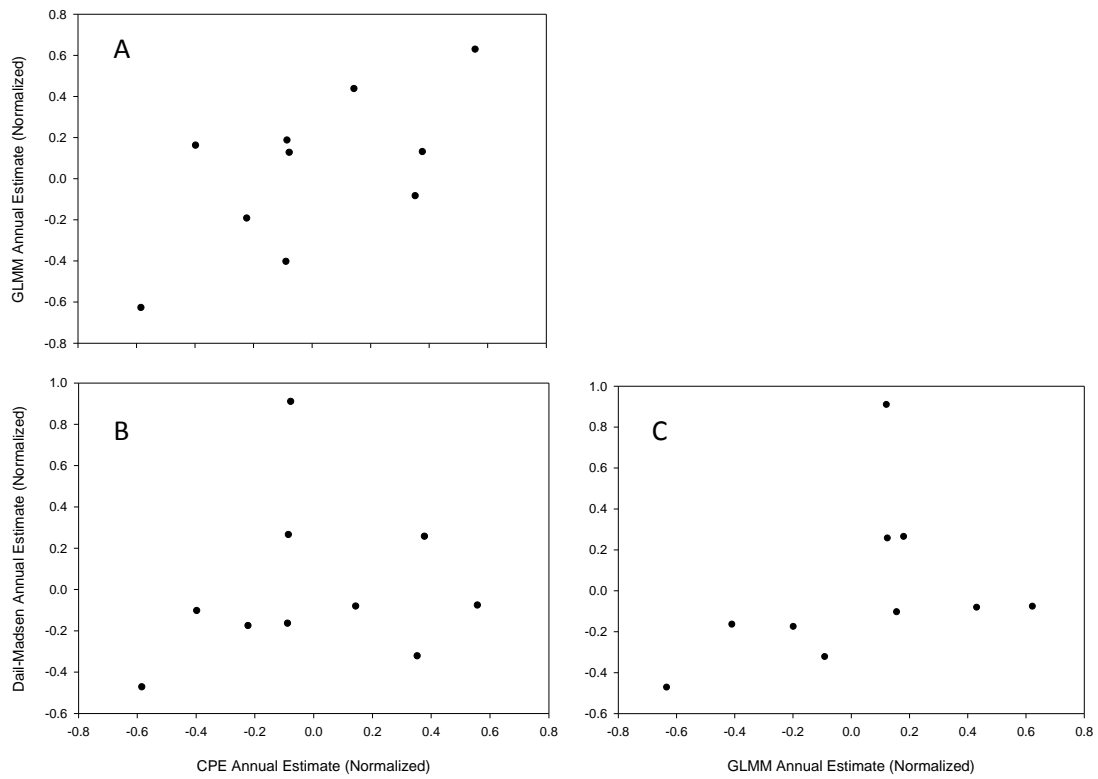


Figure 2.2. Comparison of annual population size estimates among the three modeling techniques. (A) Scatterplot between normalized catch per effort (CPE) and generalized linear mixed model (GLMM) estimates of annual abundance ( $r=0.60$ ). (B) Scatterplot between CPE and Dail-Madsen detection-corrected estimates of annual abundance ( $r=0.07$ ). (C) Scatterplot of GLMM and Dail-Madsen estimates of annual abundance ( $r=0.37$ ).

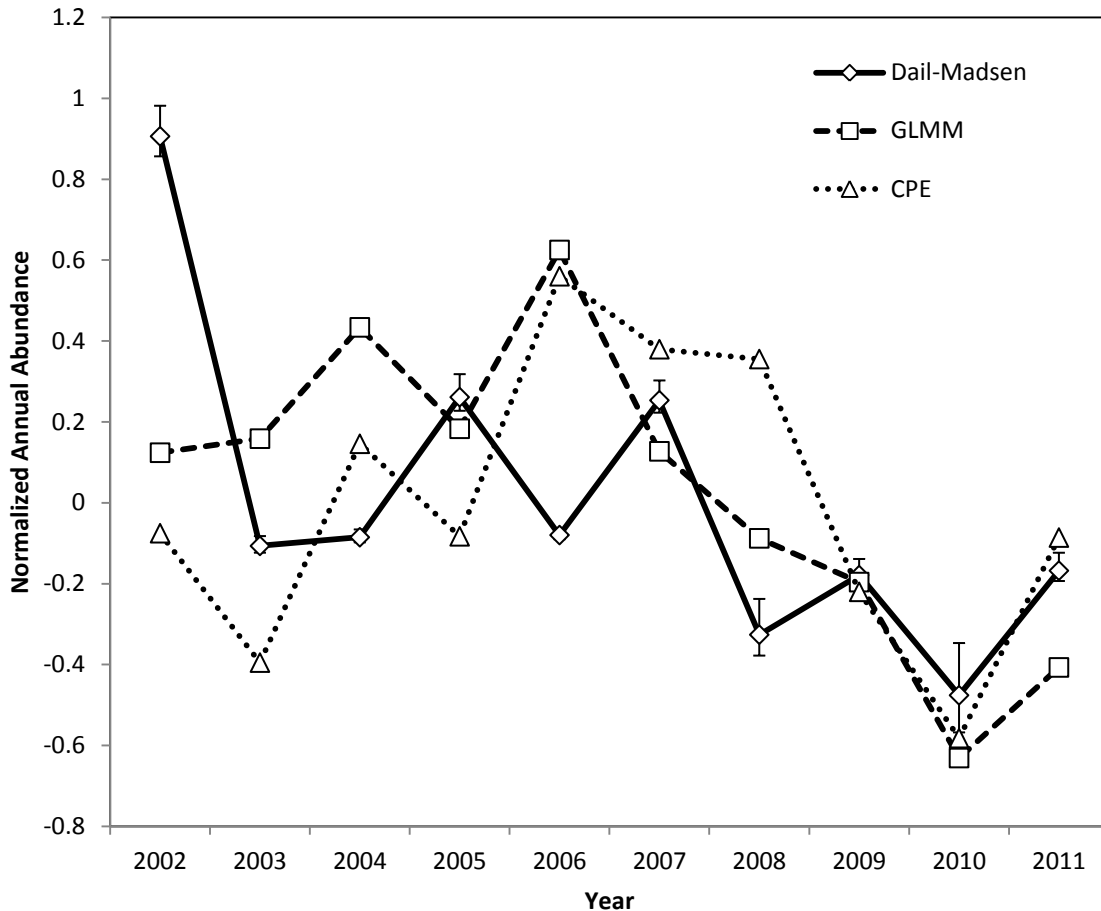


Figure 2.3. Annual trend estimates from the Dail-Madsen hierarchical model, generalized linear mixed model, and catch per effort model. Error bars represent upper and lower 95% confidence intervals for the Dail-Madsen estimates.

## 2.4. Discussion

Hierarchical models were effective in modeling simulated migratory abundance data and provided estimates of abundance that did not agree with more traditional model estimation methods for migrating populations. By allowing us to estimate detection bias directly for bird capture data at a migration banding station, this technique presents a clear advantage over previous methods by disentangling observation error from ecological process. The demonstrated effects of environmental covariates on relative abundance estimates by previous work (Olsen et

al. in press, Osenkowski et al. 2012, Jenni and Schaub 2003, Schmaljohann and Dierschke 2005) increases our confidence in the need for estimating ecological process cleanly. Our study identified and quantified many sources of detection bias. Given (A) the ability of this modeling framework to estimate detection bias in a simulated dataset accurately, and (B) the large daily variance in detection bias, it seems likely that our hierarchical approach is a more effective method for estimating trends in migratory abundance at long-term banding stations than traditional methods.

#### **2.4.1. A Validated Approach**

Overall, our simulation analysis suggests that our top model accurately estimates the population parameters of migrating animals. There was no significant bias in our estimates of immigration, emigration, and detection probability. Immigration tended to be more positively biased than the other parameters and we have a small chance of overestimating the number of individuals entering the population each day. Initial population size was likewise unbiased, although its estimate showed a high degree of variance. This is likely due to the lack of secondary sampling periods in our design and thus only ten opportunities (i.e., years) to estimate initial population size in our data set. This imprecision likely has limited impact on the overall accuracy of the model in this specific case, as the start of our sampling seasons were early enough to minimize interannual variability in initial population size (i.e., they were all close to zero). The model would be less accurate for studies where migration observations begin well after the initiation of migration at a site, especially for sites with relatively few years of observations.

#### **2.4.2. Environmental Correlates of Abundance and Detection**

Our reported relationships between immigration and emigration and local covariates are supported by previous work, which increases our confidence that this hierarchical approach indeed identified significant variance in detection probability. Quadratic time of year was a

strong predictor of migrant immigration rate, as seen in other studies (Olsen et al. in press, Osenkowski et al. 2012). Fall immigration rates were also positively correlated with northerly evening winds (tailwinds during fall migration). This finding is strongly supported by the observational and experimental literature (Jenni and Schaub 2003, Schmaljohann and Dierschke 2005). Emigration was highly correlated with barometric pressure and favorable winds, which is similar to what Erni et al. (2002) found in European radar studies. While estimating population size was our primary goal, this model also appears useful for describing migratory behavior at the daily scale.

Unsurprisingly, the largest variation in detectability was explained by net effort, but environmental covariates also had significant effects. Temperature and precipitation during the survey period increased detectability within the range of those variables' during station operation. Foraging movements can increase under warm and wet conditions, thus exposing birds to nets more often (Smith et al. 2004), or birds could be making longer diurnal movements during colder weather reducing detectability (Chernetsov 2005). The model does not separately parameterize detectability and availability so explanations for our results (as above and below) could include both processes.

Wind direction during the banding period affected detection probability, increasing detection most when winds came from the north and east. If birds immigrating to Key Biscayne are more likely to stopover on the lee side of the island, northeasterly winds would increase detection probability (as the banding station is located on the southwest side of the island). Additionally, our model estimated that northeasterly winds also increase emigration if they are maintained into the early evening. Therefore, birds may forage more actively in preparation for departure under these conditions, increasing detection by our nets. These hypotheses are not mutually exclusive.

Wind conditions before the banding station opened, particularly strong southerlies, significantly increased the detectability of the birds once the station opened. Those kinds of conditions are typically associated with migratory “fallouts”, where the majority of migrating individuals are forced to land due to weather that dramatically increases the costs of migration (e.g., strong precipitation or headwinds). During such events, bird activity on the ground may increase relative to the average behavior under non-fallout conditions, when birds have stopped due to lower individual energetic condition (Jenni and Schaub 2003) rather than increased costs of flight for all birds. Birds in high energetic condition roam more broadly over a stopover site, while birds in low energetic condition (i.e., those that stop for reasons other than for deteriorating weather conditions) are more likely to defend specific foraging areas and move less (Moore et al. 1990; Rappole and Warner 1976), both these behaviors could explain the differences in detectability we report here.

### **2.4.3. Comparison with Traditional Methods**

The annual abundance estimates of the Dail-Madsen model were never more related than a Pearson coefficient of 0.56 with the more traditional methods. While it is impossible to know the true daily migratory population size of the field data, the differences in predicted results are large for a study on the same data set and presents strong evidence that detection bias affects migrating animal surveys. Thus, we suggest hierarchical modeling is not only possible but likely necessary for quantifying the movements of migrating animals. While there are factors that we do not address in this model that could still bias the results (e.g., habitat change: Mallory et al. 2004; herd behavior: Olson et al. 2009; time of day: Simons et al. 2004), this modeling technique is flexible enough to handle many additions to the current framework.

#### **2.4.4. Conclusions**

We have demonstrated that our formulation of a Dail-Madsen model is useful for understanding the population sizes and dynamics of single site surveys of a migrating animal, when independent migratory decision-making can be reasonably assumed. We strongly suggest that future efforts to analyze abundance or trends in migrating animals use a similar hierarchical-modeling approach. This approach does present limitations (mostly in the amount of data required), but the advantages are many: more accurate estimates of annual population size, daily estimates of migrating population size, independent estimates of detection bias, and proper error propagation throughout the model. Vast amounts of migration monitoring data (e.g., USGS Bird Banding Laboratory, US National Oceanographic and Atmospheric Administration) can be used to describe variation in migratory populations on seasonal and yearly time scales with our methods. This kind of modeling could be useful for not only more accurately describing patterns of past abundance but accurately predicting changes to future abundance in migratory populations.

**CHAPTER 3: DEMONSTRATED CARRY-OVER EFFECTS FROM PRIOR BREEDING  
AND NON-BREEDING PERIODS ON THE FALL MIGRATORY  
POPULATIONS OF TEN SONGBIRD SPECIES**

**3.1. Introduction**

Weather at both short and long time scales (i.e., climate) interacts with habitat to affect population size of migratory animals across the annual cycle (Sillett et al. 2000, Holmes and Sherry 2001, Saether et al. 2000, Newton 1998, Nolet et al. 2013, Warren et al. 2001, Post and Stenseth 1999). Abundance during any particular season is controlled by short, local-scale interactions through direct impacts on survival and movement or by longer and larger scale interactions via carryover effects from previous seasons and distant locales. During migration these interactions manifest in two ways: abundance at a given site during migration is dictated by behavioral responses to local weather and habitat (Jenni and Schaub 2003), and large-scale climate patterns that influenced the population vital rates in a previous life stage that determine each year's total migratory population size available to use a given stopover site (Sillett et al. 2000).

Migratory bird monitoring stations have long taken advantage of these local and continental interactions to track large- and long-scale processes like changes in migratory phenology (Marra et al. 2006, Jenni and Kery 2003, Moller et al. 2008, Hüppop and Hüppop 2003) and migratory population size (Dunn and Hussell 1995). It is important to note, however, that simply tracking captures rates confounds processes at the large (carryover abundance) and small (local decision making) scales along with not dealing with the effects of observer bias. In this study we use hierarchical modeling methods to understand how the abundance of songbird populations on migratory stopover is affected by changes in climate and stopover habitat on annual temporal scale and changes in weather on daily temporal scale.



Climate impacts migratory bird populations in many ways. Large-scale climate indices correlate with migratory onset (Cotton 2003, Moller et al. 2008, Hüppop and Hüppop 2003, Marra et al. 2005), and changes in migratory schedule can then affect population dynamics (Both and Visser 2001). Climate can have density-independent effects at any point in the annual cycle (Newton 1988) and can also cause density-dependent effects on reproductive success (Sillett et al. 2000, Rodenhouse et al. 2003, Nagy and Holmes 2005, Homes 2007) and breeding and non-breeding survival (Studds and Marra 2005, Sherry and Holmes 1996, Holmes et al. 1996, Saether et al. 2008, Holmes 2007). Further, because impacts on individuals or populations in one season can be long-lasting (Marra et al. 1998, Norris et al. 2004, Bearhop et al. 2004, Studds and Marra 2007, Saino et al. 2007), changes in climate during one aspect of the life cycle can influence fitness or population size in another (Norris et al. 2004).

The abundance of birds at a stopover site will also be driven by local conditions. During migration, both weather and habitat are cues for migratory decisions and constraints on when and where birds stop en route (Jenni and Schaub 2003). Weather (particularly wind speed, wind direction, rainfall and barometric pressure) affects departure and landing decisions by altering the energetic efficiency of migratory flight (Chapter 1, Jenni and Schaub 2003, Alerstam 2003, Nisbet and Drury 1968). Habitat, meanwhile, affects migratory decision-making (Chernetsov 2006), refueling efficiency during stopover (Smith and McWilliams 2010) and the risk from predation while doing so (Ktitorov et al. 2008). Thus, in a local context, weather conditions and habitat quality constrain the proportion of the migratory population found within any stopover habitat.

For migration monitoring stations to track the population trends of migrating birds, we must be able to disentangle these regional and local processes. To complicate analysis further, however, our ability to detect the net effects of both processes is constrained by our own sampling methods. Weather can influence the detectability of birds that are present at a stopover

site while also influencing bird abundance and behavior (Chapter 1). Without accounting for these issues, changes in migratory population size or phenology could be confounded by changes in local environmental conditions. Recent advances in open-population, hierarchical-modeling techniques provide an effective tool to estimate daily changes in measured population size due to variation in detection probability and local weather conditions (Dail and Madsen 2011, Chapter 1). By using this technique, we can control for local processes and estimate the total migratory population sizes that use the stopover site.

In this study we use migration-monitoring data from a songbird banding station on Key Biscayne, FL to quantify the effects of local weather and habitat on bird abundance during stopover and the effects of large-scale climate on total migratory population size. For a suite of 10 Atlantic-flyway passerine species that winter in the Caribbean basin, we used hierarchical modeling techniques to: (1) estimate total stopover population size and the temporal trend over ten years, (2) describe how local-scale weather and habitat quality predicts daily stopover abundance, (3) quantify how broad-scale climate indices from the sedentary periods predict fall migratory population size and timing, while controlling for daily changes in stopover population. By successfully disentangling local processes from broad-scale drivers of migratory abundance, we can use migratory survey data to understand how migratory populations are limited at a large scale.

## **3.2. Methods**

### **3.2.1. Migration Surveys**

Songbird migration was monitored at Bill Baggs Cape Florida State Park on Key Biscayne, FL (25.674°N, 80.161°W) from 2002 to 2011 using standardized mist-netting banding station methods (Ralph et al. 1993) in a two-hectare area. Nets were opened at least five days a week at dawn, and for a minimum of six hours a day, weather permitting. Nets were checked

once every 15-30 minutes, and captured birds were extracted, banded with a uniquely numbered aluminum band, and identified to species. Each day the station was operated, we summarized the number of total captured birds. To quantify capture effort, we calculated net-hours (the number of 12-m nets multiplied by the number of hours left open) for each day. This study includes captures from 102 monitoring days each year over ten years, with each annual migratory sampling period starting on August 9.

We examined the capture abundances of the ten most common species captured during fall migration for this analysis: American redstart (*Setophaga ruticilla*), black-and-white warbler (*Mniotilta varia*), black-throated blue warbler (*S. caerulescens*), common yellowthroat (*Geothlypis trichas*), gray catbird (*Dumetella carolinensis*), northern parula (*S. americana*), ovenbird (*Seiurus aurocapilla*), Swainson's thrush (*Catharus ustulatus*), Swainson's warbler (*Limnothlypis swainsonii*) and worm-eating warbler (*Helmitheros vermivorum*).

### **3.2.2. Climate, Weather, and Habitat Variables**

Habitat data were collected using remote imagery from the Landsat 4 satellite Thematic Mapper (TM). One satellite image was acquired from each year from 2002 to 2011 and TM bands 4 and 5 were extracted to calculate Normalized Difference Vegetation Index (NDVI, sensu Anderson 1993). We selected the image with the highest quality and fewest clouds from August to December of each year (a period where leaf color is stable in South Florida) using the USGS Global Visualization Viewer ([glovis.usgs.gov](http://glovis.usgs.gov)). We then delineated the banding station and an additional 52 areas throughout South Florida to conduct radiometric normalization (sensu McCullough et al. 2013). These additional areas were selected in deep open water or areas with consistent light-colored reflective surfaces (e.g., the tops of buildings and airports). After radiometric normalization of TM bands 4 and 5 to the clearest of the ten images, using principal

components analysis in the R statistical computing environment package “stats” (R Core Team 2014), we calculated the NDVI values for the banding station for each year.

All local weather data used in this study were collected from Miami International Airport, 15 km northwest of the study site, using the National Climatic Data Center ([www.ncda.noaa.gov](http://www.ncda.noaa.gov)). Data were summarized hourly and included average temperature, wind direction, amount of precipitation, and air pressure at sea level in three time intervals: the hours of 0000-0500h (early morning), 0600-1800h (daytime), and 1800-2300h (evening). Wind direction was decomposed into northerly and easterly components. All covariates were normalized before inclusion into the model using the “scale” function in R package “stats”.

In addition to the local weather covariates, we also compiled data from three large-scale climate indices: North Atlantic Oscillation (NAO), El Niño Southern Oscillation (ENSO), and Madden-Julian Oscillation (MJO) from the NOAA Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/>). We averaged the NAO during the boreal summer months (June-August) prior to each fall migration season as a general indicator for summer breeding conditions. We averaged the ENSO and MJO for the boreal winter months (January-March) prior to each fall migration season as an index of conditions at the tropical wintering grounds for our study species. In the summer, positive NAO is correlated with cool and wet conditions in eastern North American (Ottersen et al. 2001). During the winter months both ENSO and MJO are correlated positively with dry conditions, though MJO is more correlated with dry conditions when ENSO is neutral (Jury et al. 2007, Martin and Schumacher 2011).

### **3.2.3. Modeling Techniques**

We used a modified formulation of the Dail-Madsen hierarchical N-mixture model to estimate daily and yearly migratory population size at the stopover site (see Chapter 1 for additional details). Briefly, this model considers our different sampling years as the independent

sampling sites in traditional N-mixture models. Further, because there is no reproduction at these sites, the conventional recruitment parameter ( $\gamma$ ) can be interpreted as immigration into the stopover site and the conventional apparent survival parameter can be interpreted as the inverse of emigration from the site ( $1 - \omega$ ). Using this framework, we can estimate changes in daily and annual migratory population size at a migratory stopover site. Further, we can estimate yearly variation in migratory phenology through the initial population size parameter ( $\lambda$ ). In years of earlier migration, the initial population is larger because initial sampling is closer to the peak of migration for the year. The hierarchical structure of this analysis is expressed as:

$$N_{it} \sim \text{Poisson}(\lambda)$$

$$G_{it} \sim \text{Poisson}(\gamma)$$

$$S_{it} \sim \text{Binomial}(N_{it-1}, \omega)$$

$$N_{it+1} = G_{it} + S_{it}$$

$$y_{it} \sim \text{Binomial}(N_{it}, p)$$

where  $N_{it}$  is the number of individuals present in year  $i$  and survey day  $t$ ,  $G_{it}$  is the number of individuals immigrating to the stopover site in year  $i$  at survey day  $t$ ,  $S_{it}$  is the probability of an individual persisting at the stopover site in year  $i$  from primary survey period  $t-1$  to the period  $t$  ( $1 - S_{it}$  is the probability of emigration from the stopover site), and  $y_{it}$  is the number of individuals observed in year  $i$ , during survey day  $t$ . In our model we will directly estimate annual starting population size ( $\lambda$ ), daily immigration to the stopover site ( $\gamma$ ), emigration from the stopover site ( $1 - \omega$ ) and detection probability ( $p$ ).

We tested one model for each species that included both daily and annual covariates of each parameter (Table 1). We used the same set of local weather covariates indicated during model selection in a previous study of the black-throated blue warbler stopover abundance using

the same dataset (Chapter 1) then we added the three climate indices and the single habitat index into the analysis. We tested a different family of variables for each parameter (Table 1). We included NAO on the summer prior to the migration season as a predictor of initial population size ( $\lambda$ ), to capture how variance in summer conditions predicted variance in migratory onset. We included all of our climate indices as predictors of immigration to the site ( $\gamma$ ), hypothesizing that these conditions could influence the number of birds available for stopover during migration (i.e., total migratory population size). We also included early morning wind northerly and easterly wind component and the quadratic of calendar day as covariates of this parameter. Lastly, we tested for the impact of evening atmospheric pressure, northerly wind component, and an annual index of habitat (NDVI) on emigration ( $\omega$ ) and net effort, daily rainfall, wind direction during the day, wind direction during the morning and stopover habitat influence detection ( $p$ ). In both cases we are anticipating an effect of weather and habitat influencing migratory behavior after arrival at the site.

Table 3.1. The ecological interpretations of environmental covariates for each of the four parameters estimated in the Dail-Madsen N-mixture model.

Parameter	Factor	Scale	Interpretation
Lambda ( $\lambda$ )	Summer NAO	Annual/Continental	Annual change in migratory timing
Gamma ( $\gamma$ )	Summer NAO	Annual/Continental	Annual change migratory population size
	Winter ENSO	Annual/Continental	Annual change migratory population size
	Winter MJO	Annual/Continental	Annual change migratory population size
	Early morning N/S Wind	Daily/Local	Daily change in immigration to the stopover site
	Early morning E/W Wind	Daily/Local	Daily change in immigration to the stopover site
	Julian day <sup>2</sup>	Daily	Daily change in immigration to the stopover site
	Omega ( $\omega$ )	Evening SLP	Daily/Local
Evening N/S Wind		Daily/Local	Daily change in emigration from the stopover site
NDVI		Annual/Local	Annual change in emigration from the stopover site
p	Daytime Temperature	Daily/Local	Daily change in detection probability
	Daytime Precipitation	Daily/Local	Daily change in detection probability
	Daily Net Effort	Daily/Local	Daily change in detection probability
	NDVI	Annual/Local	Annual change in detection probability
	Daytime N/S Wind	Daily/Local	Daily change in detection probability
	Daytime E/W Wind	Daily/Local	Daily change in detection probability
	Early morning N/S Wind	Previous Day/Local	Daily change in detection probability
	Early morning E/W Wind	Previous Day/Local	Daily change in detection probability

#### 2.2.4. Comparing Trends Over Time and Across Species

We estimated daily stopover population size using the empirical Bayes method with package ‘unmarked’ and package ‘ranef’ in Program R (Fiske and Chandler 2011). The approach

combines model-predicted results with observed data to estimate the distribution of true daily abundances. We then summed the mean estimate of daily stopover abundance for each year to calculate annual migratory population size. We also report the summed estimates of the 2.5% and 97.5% quantiles for each species to estimate variance on our modal predictions (the 95% credible interval of the daily estimates). We ran post-hoc ANOVAs between annual population size and year for each species to determine if significant trends were present.

To test for the general strength of climate versus local weather and habitat on migratory populations, we aggregated parameter estimates from each species' model. We used two-way Ward hierarchical clustering analysis (biclustering) on two sets of species variables: (1) local weather and habitat variables that affect changes in daily and annual migratory abundance, respectively, and (2) large-scale climate indices that affect annual migratory population size and timing. We set alpha for all statistical tests to 0.05 *a priori*. Program JMP v. 9.03 (SAS Institute, Cary, NC) was used for the two way clustering analysis while the R Statistical Computing Environment (R Core Team 2014) was used for all other analyses.

### **3.3. Results**

#### **3.3.1. Estimates of Migratory Population Size**

Annual stopover population size was highly variable across our ten study species. Mean estimates of annual abundance for the species ranged from an average of 12,209 black-throated blue warblers (95% credible interval: 10,669 to 13,762) to 183 Swainson's thrush (53 to 417) (Fig. 1). Five of the ten species we tested exhibited significant negative trends in annual stopover population size over the ten-year study period (black-throated blue warbler, black-and-white warbler, ovenbird, Swainson's thrush, and worm-eating warbler) and there were no significantly positive population trends (*Post hoc* ANOVA, Table 2). American redstart showed a near



significant decline over the study period ( $p=0.12$ ). Common yellowthroat, gray catbird, northern parula, and Swainson's warbler had relatively stable abundance through the study period. We should note that species detectability varied widely with environmental variables, and this analytical technique allows us to compare abundances among species while controlling for these differences (Table 3).

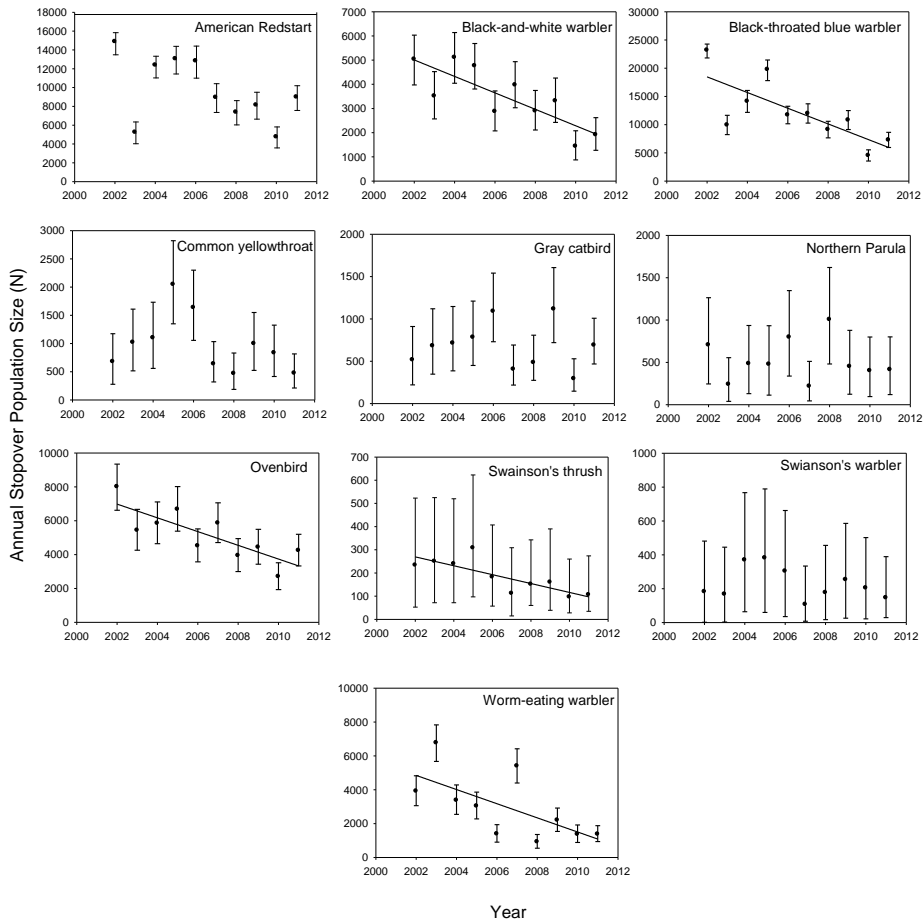


Figure 3.1. Migratory population size estimates for each species over the study period. Error bars represent credible intervals of the mean Bayesian empirical estimate. A line indicates a significant relationship ( $p < 0.05$ ) using linear regression.

Table 3.2. Estimated change in annual migratory populations of species at Key Biscayne.

Species	Yearly Population Change (individuals)	SE	p-value
American Redstart	-597	345	0.12
Black-and-white Warbler	-339	85	<0.01
Black-throated Blue Warbler	-1389	430	0.01
Common Yellowthroat	-56	55	0.034
Gray Catbird	-4	31	0.89
Northern Parula	-4	29	0.89
Ovenbird	-405	104	<0.01
Swainson's Thrush	-19	5	<0.01
Swainson's Warbler	-9	11	0.43
Worm-eating Warbler	-471	189	0.04

Table 3.3. List of parameter estimates for environmental covariates for each species modeled.

Species	Lambda		Immigration					Emigration					Detection																				
	Summer.NAO	Summer.NAO	Summer.NAO	Winter.ENSO	Winter.MJO	EW.EA	NS.EA	JULIAN	SLP.EVE	NS.EVE	NDVI	Temp.66	Precip.66	Effort	NDVI	EW.66	NS.66	EW.EA	NS.EA														
American Redstart	0.59	*	-1.12	*	-0.43	*	-0.05	*	0.71	0.07	-0.45	-1.41	*	-4.94	*	-0.29	*	0.03	0.13	*	1.14	*	0.00	-0.02	0.05	0.00	0.00						
Black-and-white Warbler	0.68	*	0.17		-0.08		-0.44	*	0.83	*	0.84	*	-1.17	*	-0.40		-1.07	*	0.06	-0.10		0.12	*	0.99	*	-0.07	0.06	0.00	0.06	0.00			
Black-throated Blue Warbler	1.41	*	0.12	*	-0.36	*	-0.26	*	0.84	*	0.73	*	0.60	*	-2.27	*	-1.68	*	-0.17	0.01		0.28	*	1.09	*	-0.07	0.14	*	0.29	*	0.15	*	-0.22
Common Yellowthroat	1.65	*	-0.19	*	-0.12		-0.55	*	0.00		-0.49	*	0.43	*	-1.08	*	0.33		-0.21	0.15	*	0.12	*	1.10	*	0.33	-0.16	*	0.26	*	-0.11	*	-0.16
Gray Catbird	1.80		0.06		-0.43	*	-0.23	*	-0.31	*	-0.45	*	1.41	*	-0.78	*	-0.24		-0.56	-0.39	*	0.52	*	1.07	*	0.08	0.16	*	0.11	0.25	*	0.10	
Northern Parula	1.95		-0.18	*	-0.12	*	-0.24	*	0.23	*	-0.16	*	0.06		0.20		0.13		0.98	*	-0.09		0.10		1.27	*	-0.67	*	0.21	*	0.04	-0.14	-0.17
Ovenbird	1.00	*	0.14	*	-0.01		0.06		-0.03		0.19		-0.91	*	0.15	*	-0.98	*	-0.01	-0.07		0.00		0.74	*	-0.05	0.04	0.01	0.07	*	0.04		
Swainson's Thrush	1.76		0.18		-0.15		-0.20		0.09		-0.80	*	0.65	*	-1.65	*	0.62		-0.09	0.02		0.33	*	1.02	*	0.15	-0.04	-0.04	0.13	-0.29			
Swainson's Warbler	0.44		-0.05		-0.14		-0.46	*	0.07		-0.09		0.05		-0.26		0.51		0.03	0.42		0.06		0.95	*	0.03	-0.01	-0.13	0.13	0.04			
Worm-eating Warbler	1.03		0.32	*	0.16	*	0.15	*	0.58		0.65	*	-1.74	*	0.21	*	-0.82	*	-0.13	-0.29	*	-0.06		0.88	*	0.46	*	0.24	*	0.14	*	0.02	0.05
<b>Median</b>	<b>1.22</b>		<b>0.09</b>		<b>-0.13</b>		<b>-0.23</b>		<b>0.16</b>		<b>-0.01</b>		<b>0.05</b>		<b>-0.59</b>		<b>-0.53</b>		<b>-0.11</b>	<b>-0.03</b>		<b>0.12</b>		<b>1.04</b>		<b>0.02</b>	<b>0.05</b>	<b>0.04</b>	<b>0.06</b>	<b>0.00</b>			

\*Indicates a parameter estimate with a p-value less than 0.05

### **3.3.2. Effects of Local Weather and Habitat Change on Migratory Dynamics**

Early morning (0000 – 0500h, prior to the sampling period) easterly winds showed a consistent positive effect on abundance across species while northerly winds showed a neutral effect (Table 2). The easterly component of wind (from the Atlantic Ocean) was a significant effect in four of the ten species, and winds blowing from the west (the Gulf of Mexico) increased immigration in one of those case. The north/south component of local winds was a significant effect in seven of the ten species, although the direction of the effect was highly variable among these cases. Barometric pressure and the north/south wind component were consistent predictors of emigration from the site (Table 3, Fig. 2). High pressure systems and northerly winds during the evening (1800 – 2300h) significantly increased the probability of emigration from the stopover site for seven and five species, respectively. An index of primary productivity on the site (NDVI) only influenced emigration rate for two species (positive for northern parula and negative for American redstart) and detectability for two species (negative for northern parula and positive for worm-eating warbler). Only Swainson’s warbler showed no significant relationship with any local-scale predictor.

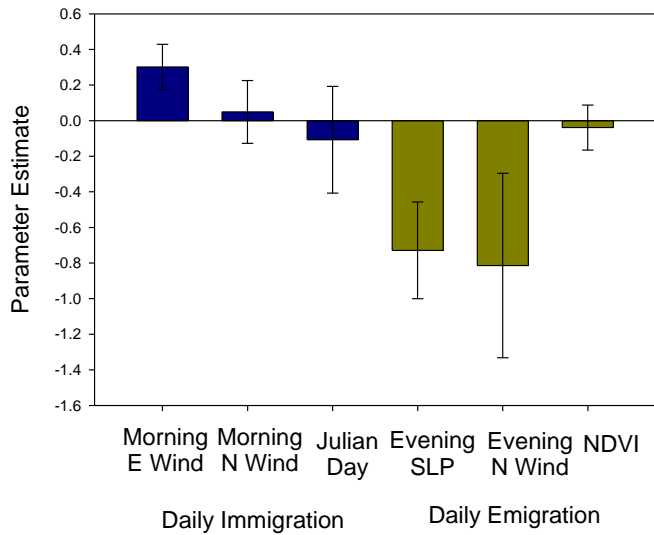


Figure 3.2. Average effect of local weather and habitat on daily immigration and emigration at the stopover site across all ten study species. Error bars represent standard error of the mean.

Hierarchical clustering emphasized four main migratory responses to local weather conditions (Fig. 3). Those that were strongly associated with arriving on northerly and easterly wind and leaving during high pressure (American redstart and black-throated blue warblers), those that arrived on northerlies/easterlies but were more neutral in their response to high pressure (black-and-white warbler and worm-eating warbler), those with arrival patterns not strongly related to tailwinds and departed under more low pressure conditions (northern parula, ovenbird, Swainson’s warbler) and those that arrived during southerly winds and departed with high pressure (common yellowthroat, Swainson’s thrush, gray catbird).

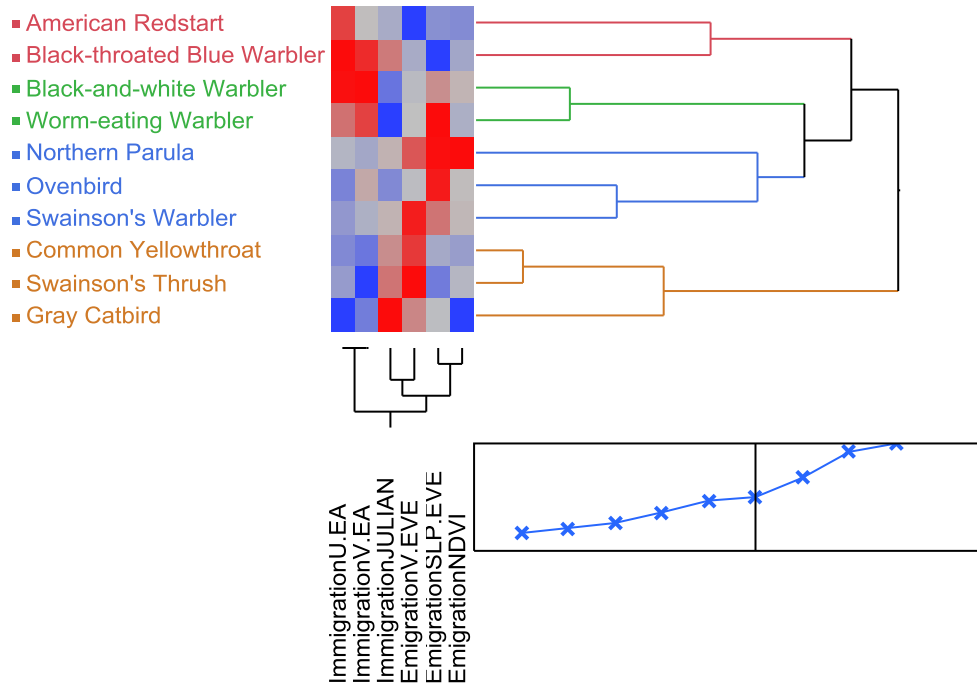


Figure 3.3. Biclustering analysis of species variation in response to local weather and habitat variables. Warm colors represent relatively positive and cool colors represent relatively negative correlations with each explanatory variable. Species are colored by group and the group was selected using the broken stick in the bottom right.

### 3.3.3. Effects of Broader Scale Climate on Annual Abundance and Migration Timing

On the community level, there was a positive relationship between migratory onset and summer NAO, a negative relationship between total migratory population size and both winter ENSO and winter MJO, and no relationship between total migratory population size and summer NAO (Fig. 4). The relationship between NAO and migratory timing was significantly positive in five species and the parameter estimate was positive in all others (Table 3). The relationship between total migratory population size and winter ENSO was significantly negative in four and significantly positive in one (worm-eating warbler). Winter MJO was significantly related to

migratory population size in seven species, and significantly positively related in only one (worm-eating warbler again). Total migratory population size and NAO exhibited a more variable relationship; three species were significantly positively related and three were significantly negatively related. This variance led summer NAO to have a smaller average parameter estimate and appear less important on the community level (Fig. 4).

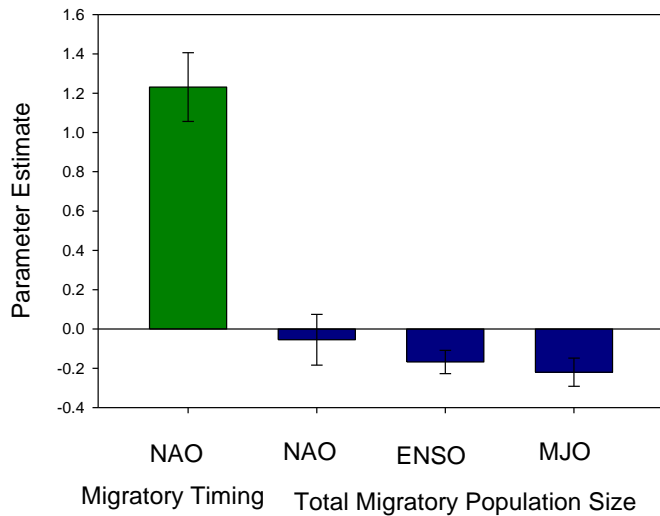


Figure 3.4. Average effect of large-scale climate indicates on migration onset and annual migratory population size across all ten study species. Error bars represent standard error of the mean.

On the species level, we found four major response types to climate indices (Fig. 5). Note that while warmer colors are more positive and cooler colors are more negative, they are all relative to the central tendency of each parameter estimate. For example, while some species can be shown to have a relatively positive relationship with MJO compared to other species, that relationship is still negative in the absolute sense because species tended to respond negatively to MJO. First, American redstarts whose migratory onset was not strongly affected by NAO but showed highly negative responses to both wet summers and dry winters. Second, a group where



migratory onset was not affected strongly by NAO or winter ENSO but were negatively affected by winter MJO (black-and-white warbler and Swainson's warbler). Third, a group that showed strong positive responses in migratory onset with NAO and relatively neutral (though still overall negative) response to dry winter (black-throated blue warbler, gray catbird, common yellowthroat, northern parula). And fourth, a group with a migratory onset moderately affected by NAO, strongly affected by wet summers and weakly affected by dry winters (ovenbird and worm-eating warbler). Notably, species that declined significantly were a part of three of the four groups and that each of the species that declined showed a strong positive relationship with summer NAO.

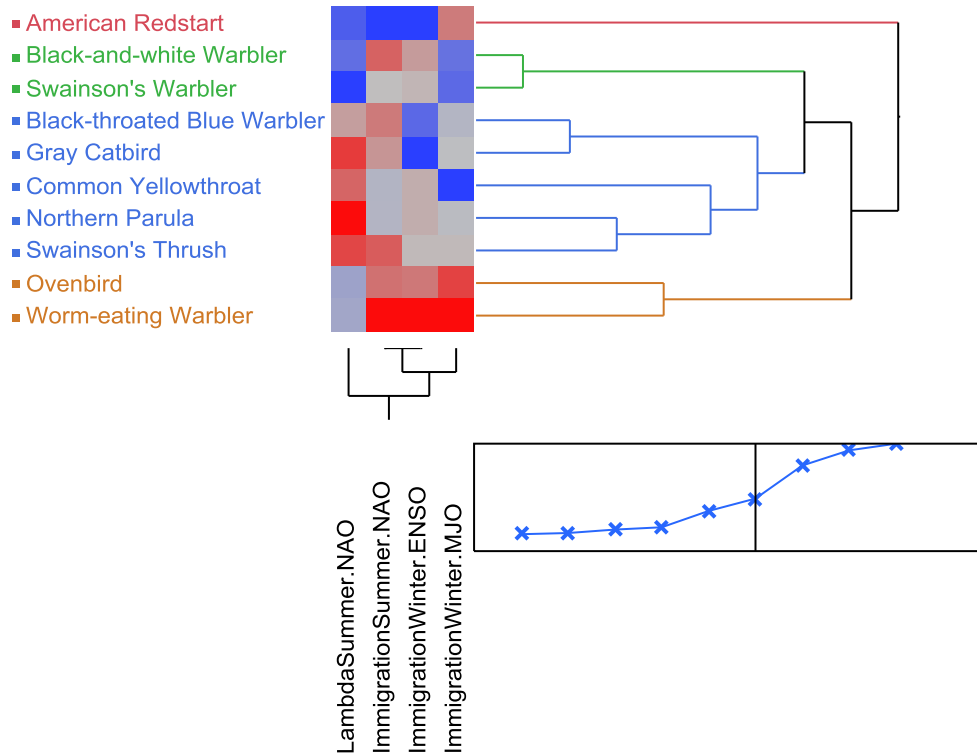


Figure 3.5. Biclustering analysis of species variation in response to large-scale climate indices. Warm colors represent relatively positive and cool colors represent relatively negative correlations with each explanatory variable. Species are colored by group and the group was selected using the broken stick in the bottom right.

### 3.4. Discussion

Using recent developments in hierarchical modeling, we documented detection-corrected trends in annual stopover abundance in songbirds over a ten-year period in South Florida. Once we controlled for detectability, we were able to elucidate general and species-specific migratory stopover behaviors due to local conditions. Across ten species, birds were more likely to land at the site when there were winds coming in from the open ocean, and they were more likely to leave the site when there was a tailwind or high barometric pressure. Controlling for these local

processes, we were able to describe population trends and large-scale controls on both migratory timing and the abundance of migratory populations. Half of the species we examined showed declines in migratory population abundance over the sampling period, and none increased. The species that declined were those that showed the strongest positive correlations between summer NAO and annual population size. Across all the species, migratory timing was consistently influenced by wet conditions on the previous summer (a positive NAO), while annual migratory population size was strongly influenced by dry conditions during the previous non-breeding season (a positive ENSO and MJO). These overall patterns, however, also varied by species.

### **3.4.1. Local Weather and Habitat Effects on Stopover Populations**

Many of the species showed responses we considered typical in migratory behavior to local weather conditions: that is, high immigration rates and emigration rates during favorable tailwinds (Jenni and Schaub 2003). The species that did not show these behaviors (like Swainson's thrush, common yellowthroat and gray catbird) could be using the site for non-stopover purposes (i.e., overwintering for the yellowthroat and the catbird) or arriving at the site using smaller scale local movements that are not as weather dependent as migratory flights (Cohen et al. 2012). Variability in the responses among species to local weather could be due to general differences in migratory strategies, i.e., whether they consistently make overwater flights (Delingat et al. 2008). Most species showed an increase in stopover abundance after easterly early morning winds. Given the geographic position of Key Biscayne, strong easterly winds push birds departing from further up the coast back toward the mainland via wind drift (Bingman et al. 1982).

Only two species responded to habitat change: American redstarts by leaving the stopover site sooner and northern parula by staying longer. This suggests that redstarts stay longer in earlier succession migratory habitat while parulas stay longer in later succession.

Deppe and Rotenberry (2008) showed redstarts have higher relative stopover abundance in habitat with a high canopy and parulas as having little relationships with habitat, so our result is at odds with previous research. Two explanations are possible: first, relative abundance (measured previously) and emigration probability (measured in this study) are not the same response variable and we are measuring bird behavior more directly, and second, NDVI was a poor index of succession stage at the stopover site. More broadly, the overall lack of importance of NDVI to emigration rates probability suggest that habitat change is decoupled from intrinsic habitat quality at the stage of succession at this site or our measurement of habitat change with NDVI was ineffective. A similar pattern was seen in the relationship between NDVI and detectability: only two species showed a significant relationship. As trees grow and more structure is available for birds (e.g., northern parula) above the nets, detection rates could drop for species that forage higher in trees. Likewise, undergrowth could grow large enough to attract low foraging species (e.g., common yellowthroat and worm-eating warbler) to areas around the nets. NDVI can be a useful measurement of succession in forested landscapes (Rey-Benayas et al. 2010), and we were able to detect known tropical storm damage in 2004 using this metric, so we suggest that detecting habitat change is possible using NDVI. Intra-annual variation in NDVI, however, could be high, and the metric might not be useful for assessing dynamic migratory behavior (Olsen et al. in press).

### **3.4.2. Effects of Climate on Migratory Timing and Population Size**

Once we controlled for daily changes in stopover population size and species-specific detectability, we found that large-scale climate indices of the prior breeding and non-breeding periods predicted migratory timing and total migratory population size. Only one of our ten species (Swainson's thrush) did not show significant carry-over effects from either the previous breeding or non-breeding season or from both. Breeding season conditions (NAO) showed a consistent relationship with earlier migration which suggests a shorter breeding season under

these conditions for most species. Seven of these species are confirmed double-brooders, behavior that is more frequent during warm springs (Townsend et al. 2013) or less common in cool, wet breeding seasons (Jacobs et al. 2013). An early end to the breeding season could facilitate an early molt that accelerates migration timing (Stutchbury et al. 2011), or it could present cues to prepare for migration earlier. Similar effects with NAO and migration timing have been found in other studies from Europe (Hüppop and Hüppop 2003), but studies in North American migrants have not found a relationship between NAO and migratory timing (Marra et al. 2006). We suspect differences among North American studies may arise from the migratory flyway, species sampled, or the ability of our modeling techniques to control for factors that are confounded with more traditional methods.

Given what we know about seasonal interactions in songbirds (Norris and Marra 2007), our overall finding, that conditions at the breeding and non-breeding grounds affect the subsequent autumnal migratory population in some species, is not surprising. Climate on the grounds of the stationary periods is a clear driver of reproductive success and population size in both that season and subsequent seasons (Sillett et al. 2000, Nott et al. 2002, Norris et al. 2004). In the non-breeding season, birds that responded negatively to ENSO also did the same with MJO. This lends more evidence to the idea that Caribbean-wintering songbird populations are consistently negatively affected by dry winters than wet summers. What is surprising in our results is the extent to which we found seasonal interactions to be prevalent among these species and our ability to identify them using only migration banding station data.

Our ten species were organized into four groups. Most groups were defined by the degree to which migratory timing was positive associated with NAO and the degree to which population size was negatively associated with ENSO or MJO (the two strongest patterns in our data). Birds that responded positively in migratory onset to summer NAO (black-throated blue warbler, gray catbird, common yellowthroat, northern parula) tend to use secondary forest, scrub

or wetlands (excepting the parula) and are well-known double-brooders. Wet summers could have particular strong effects on those kinds of habitats and influence the timing and amount of productivity. Some species that tended to be resilient to dry winters (ovenbirds and worm-eating warblers) forage in dry leaf litter, which is probably a more stable strategy than flycatching or gleaning when rainfall is low and insect populations are reduced. Overall, our knowledge of life history can only give us a small insight into why these patterns occur. We suspect that a greater understanding of the geographic distributions and life histories of core non-breeding populations will shed light on the mechanism behind these distinct responses.

The species that showed significant declines were all species that had a strong positive correlation between NAO and population size. The NAO declined significantly over the course of the study, so this suggests that for our study period, birds that responded positively to wet breeding conditions had decreased migratory populations. On the non-breeding grounds all species that responded significantly to the ENSO responded similarly to the MJO. We expect that winter rainfall is the primary driving factor for these patterns, and that ENSO and MJO correlate with rainfall patterns in different regions (Jury et al. 2007). Thus, their importance for a particular species is dependent on the non-breeding range and non-breeding habitat use of the migratory populations passing through Cape Florida.

Our findings for the American redstart are validated by past work showing strong relationships between winter rainfall and population dynamics (Sherry and Holmes 2005, Studds and Marra 2007). For this species at least, we were able to detect population drivers previously identified on the breeding and non-breeding grounds using data from a single migratory stopover site. Similar non-breeding data from other species is lacking, but many of the species in this study use seasonally dry forests and scrub habitat in the non-breeding season that is strongly affected by winter rainfall. Given the generally strong effects of dry winters on subsequently

lower fall migration population size, perhaps we have quantified a common population limiting mechanism for Caribbean wintering migratory songbirds breeding in eastern North America.

### **3.4.3. Limitations of the Modeling Effort**

While our modeling effort represents one of the most robust estimates of annual migratory population size to date (due to hierarchical detection estimation and the control for daily stopover behaviors), the modeling framework still has limitations. First, species with the lowest abundances often had fewer significant correlations with predictor variables than those with higher abundances. Thus, a lack of statistical power may explain the lack of significant parameter estimates for less abundant species. Second, we know from previous work that this modeling approach is relatively imprecise (although not biased) in its prediction of  $\lambda$  relative to the other parameters (Chapter 1), so it is possible that our estimates for this parameter are more imprecise than the others. We would expect this modeling weakness to decrease our power to detect significant correlates of migratory timing. In this analysis, however,  $\lambda$  was significantly correlated with NAO for five of the ten species, suggesting a strong effect of the variable. Third, some species exhibited relatively high  $\lambda$  in our model. If accurate, this means our survey effort appears to have missed the beginning of their migration at Cape Florida, and could be causing us to underestimate migratory population size for early migrants.

### **3.4.4. Predictions for the Future of Migrants in South Florida**

Currently, the NAO is predicted to increase with global warming and the northeastern United States is supposed to get wetter in the summer (Monahan et al. 2000). It is likely that this will result in many species arriving at southern Florida earlier in the migratory season. The effect of an increasing NAO will have a much more varied effect on annual migratory population sizes in Florida. Species like American redstart and common yellowthroat should see the largest

decreases while black-and-white warbler and worm-eating warbler should see the largest increases.

Under current climate models, there is a roughly equal chance of climate change increasing the amplitude of ENSO as eliminating the pattern altogether (Latif and Kennlyside 2008). While this uncertainty makes it difficult to predict directional changes in bird populations, the first scenario would cause a subset of our study species (e.g., American redstart and gray catbird) to experience either greater variability in migratory populations or higher annual migratory population sizes. While it is unclear what global effect a diminishing ENSO would have, the MJO could become an even more significant driver of tropical rainfall. In such a case, we could expect migratory population size for Caribbean migrants to match that index even more than they currently do.

### **3.4.5. Conclusions**

This study is the first to quantify correlations between migratory timing and total migratory population size while controlling for both changes in daily migration behaviors and variation in detection probability. Over our ten-year sampling period many species decreased their annual stopover population size and none showed an increase. Across all ten species, climate conditions on the breeding grounds positively influenced migratory onset, while dry conditions on the non-breeding grounds decreased annual migratory abundance. Breeding ground conditions were an overall neutral factor on the community level but all the species that showed a decline over the study had positive relationship with summer NAO. As our ten species were almost exclusively Caribbean wintering migrants, this suggests the potential for a region-wide, climate-driven conservation issue. More life history information is needed for this group of species, particularly on the non-breeding grounds, to confirm these patterns and give us a better understanding of why species response to climate in this way. Future studies of climate



adaptation in migratory songbirds should note, however, that taxonomically similar migratory species showed diverse responses to climate and weather, suggesting that a “model species” approach to climate responses in this group is unlikely to be effective. Lastly, we suggest that population studies of animal responses to climate more generally should control for responses to smaller scale changes in weather and habitat to avoid confounding these mechanisms of population change.

**CHAPTER 4: CONSPECIFIC DENSITY AFFECTS MIGRATORY STOPOVER  
REFUELING RATES BOTH POSITIVELY AND NEGATIVELY  
ACROSS SEVEN SONGBIRD SPECIES**

**4.1. Introduction**

Migration is energetically demanding, often requiring periods of exceptionally rapid energy gain (Hedenstrom and Alerstam 1997, Alerstam 2003). Conditions during migration affect stopover mass gain, altering migratory decision-making and survival probabilities. Changes in migratory survival could limit the populations of many migratory birds (Sillett and Holmes 2002, Newton 2006); thus high quality migratory stopover habitat is crucial to the conservation of migratory songbirds (Moore et al. 1995, Petit 2000, Buler and Dawson 2012). However, the ability of individual birds to rest safely and refuel quickly at stopover is spatially and temporally variable (Cohen et al. 2012; Olsen et al. *in press*). This variance in habitat quality is dependent on intrinsic qualities—based solely on the resources held within the habitat—and extrinsic qualities—based on factors outside of the habitat like geographic position or surrounding weather patterns (Buler and Moore 2011). Moreover, actual refueling rates can change on a daily basis depending on the density of stopover migrants at the site (Kelly et al. 2002), providing a link between extrinsic and intrinsic components of stopover habitat quality. In this study, we tested for the influence of migrant density on realized stopover habitat quality (as shown by songbird refueling rates) over multiple temporal and population scales.

Extrinsic components of migratory stopover habitat quality determine whether migrants have an opportunity to rest and refuel at the stopover site. These include weather patterns that influence individual landing decisions (Jenni and Schaub 2003), the location of the stopover site within the flyway (Buler and Dawson 2012), and the surrounding landscape (Ktitorov et al.

2008). Intrinsic factors of stopover habitat quality determine refueling rate and stopover duration once an individual has landed. Two of the most important factors are cover from predators and food resources (Lindstrom 1990, Petit 2000, Moore and Aborn 2000, Ydenberg et al. 2002). These traits can vary spatially and temporally within the migratory season (Prop 1991; Olsen et al. *in press*). Importantly, a stopover site does not need both extrinsic and intrinsic qualities to increase the survival probability of individuals. A barren island in the right location can be crucial to a successful migration, and a patch of high-quality forest habitat without ideal geographic position can be useful to migrants (Mehlman et al. 2005).

Extrinsic and intrinsic factors are linked through density-dependent processes during migration. Sites with high extrinsic value support higher migrant densities, which can alter the quality of the habitat in multiple ways. High densities of birds can deplete local food resources, so that birds arriving later cannot gain energy as quickly (Moore and Wong 1991, Kelly et al. 2002). Migrant density can also directly interfere with the foraging efficiency of conspecifics or heterospecifics (Carpenter et al. 1993). Prey depletion can occur on multiple temporal scales from minutes to weeks (Greenberg 2000, Newton 2006), while interference competition requires coincident individuals. Alternatively, higher migrant density could make foraging safer and more efficient via flocking behavior. Flocks can increase foraging efficiency and reduce predation risk (reviewed in Greenberg 2000). During migration flocks are common, because foraging efficiency is important for completing migrations quickly (King 1972); birds lack information about local food resources; migratory species have broader foraging niches (Martin and Karr 1990, Parrish 2000); predation risk is high (Silllett and Holmes 2002, Alerstam et al. 2003, Schmaljohann and Dierschke 2005); and flocking partners are abundant and available. Flocking behaviors are also condition dependent—individuals in good energetic condition are more willing to join flocks, whereas poor-condition individuals are not (Rappole and Warner 1976). Because the advantages and disadvantages of flock-joining are both resource and condition dependent, we expect that the

relative benefits and costs of density-dependence can be variable among species and temporal scale.

We explore how migrant densities on multiple temporal scales affect songbird refueling rates at a migratory stopover site in southern Florida. Seven songbird species common to the site were used in this study to understand the effects of songbird abundance across taxa with variable life history and migratory strategies. We use population-level changes in size-controlled body mass—a technique commonly used in other migration monitoring studies as an estimate of stopover habitat quality (Winker et al. 1992, Moore and Kerlinger 1987, Dunn 2002, Bonter et al. 2007)—to quantify daily stopover habitat quality over 10 years of migration monitoring. We examine the effect of estimated migrant density on mass gained per minute for birds around the monitoring station for the current day (the negative effects of co-incident interference competition and/or the positive effects of flocking facilitation) as well as the effect of migrant density over the previous days and weeks (the negative effects of resource depletion). Estimates of migrant density were derived from a previous study on climate and weather effects on migratory birds with the same database as this study that controlled for detection bias (Chapter 2). While the issue of migrant density and foraging rates has been examined before (see Newton 2006 for a review), our treatment of the issue provides the first long-term assessment of the importance of migrant density (on a daily scale) with detection-probability corrected estimates of migrant density and adds the important piece of temporal scaling of density-dependence to test hypotheses.

## 4.2. Methods

### 4.2.1. Data Collection

Songbird migration was monitored at Bill Baggs Cape Florida State Park on Key Biscayne, FL (25.67°N, 80.16°W) from 2002 to 2011 using a standardized migration monitoring protocol (Ralph et al. 1993). The site is a restored tropical hardwood hammock with consistent sources of food and cover from strangler figs (*Ficus* spp.) and buttonwood mangrove (*Conocarpus erectus*). Mist nets were opened at least 5 days a week at dawn and for a minimum of 6 hours a day, weather permitting. Nets were checked once every 15-30 minutes and birds extracted and banded with a uniquely numbered USGS aluminum band, noting species, age, sex, unflattened wing chord, fat reserves (an estimate of furcular fat with 0 as none and 5 as excessive amounts), the amount of pectoral muscle (an estimate of pectoral muscle mass with 1 as minimal and 5 as a robust amount), and body mass (Ralph et al. 1993). For purposes of this study, we examined 102 monitoring days per year over 10 years, with migratory sampling periods starting on August 9 of each year.

We examined the effect of migrant abundance for each of the seven most common species captured at the banding site: American redstart (*Setophaga ruticilla*), black-and-white warbler (*Mniotilta varia*), black-throated blue warbler (*Setophaga caerulescens*), common yellowthroat (*Geothlypis trichas*), gray catbird (*Dumetella carolinensis*), ovenbird (*Seiurus aurocapilla*), and worm-eating warbler (*Helmitheros vermivorum*).

Daily estimates of migrant abundance were collected from a previous study at this stopover site (Chapter 2). In this study, we used hierarchical Dail-Madsen N-mixture models to estimate daily migrant abundance for the species examined for the present study at the same stopover site and the same 10 years as this study. This model used large-scale climate and local-scale weather covariates to predict the daily abundance of migrants at the site while correcting for

detection bias using empirical Bayes methods in package “unmarked” in the R Statistical Computing Environment. Daily abundance estimates were calculated for each of the seven study species. For the current study we summarized daily migrant abundance in five ways: (1) the summed abundance of the 15 most common migratory species, (including cape may warbler, *Setophaga tigrina*, northern parula, *Setophaga americana*, northern waterthrush, *Parkesia noveboracensis*, ovenbird *Seiurus aurocapilla*, painted bunting, *Passerina ciris*, prairie warbler, *Setophaga discolor*, red-eyed vireo, *Vireo olivaceus*, Swainson’s thrush, *Catharus ustulatus*, and Swainson’s warbler, *Limnothlypis swainsonii*, in addition to the seven species described here), (2) the estimated daily abundance of conspecifics for each of the seven focal species, (3) the summed abundance of the 15 most common migratory species during the previous day, (4) the summed abundance of all 15 species over the past 6 days (the previous week), and (5) the summed abundance of all 15 species over the past 13 days (the previous two weeks).

#### **4.2.2. Statistical Analysis**

General linear mixed models (GLMMs) were used to test for the fixed effects of species, migrant density (using all five metrics described above), age, body size and condition, and time of day on the body mass of stopover migrants at the banding site. We set year and sampling day as random variables to account for annual and daily variation in mass gain via weather patterns, seasonal phenology, and interannual plant community changes.

We tested a candidate set of 70 GLMMs, which all included a base set of fixed effects in addition to the random effects of day and year: time of capture and the square of time of capture (to quantify changes in mass over each day as a proxy for refueling rate), species, wing chord length nested within species (as a proxy for body size variation within species), age of individual, fat score and pectoral score (as proxies for physiological condition and energetic demand), the interaction of age and time of capture (to allow for differential mass gain through the banding day

by age), and the interactions between time of capture and both fat score and pectoral score (to allow mass gain to vary by initial physiological condition). These terms were included in all models (including a null model), because past studies indicate their importance for predicting mass change, and we wanted to control for them before estimating the effect of density. We then constructed A) 5 models that tested for the base effect of each of the density effects without an interaction with time of day, B) 15 models that tested each of the possible additive combinations of the five migrant-density variables nested within time of day each (to allow the rate of mass change to vary with migrant abundance), C) 15 models that tested these same combinations nested within time of capture but also nested within species (to allow for variation in the effect of density-dependent mass gain among species), D) each of the previous 30 models with the addition of two, three-way interactions (fat score by species by time and pectoral score by species by time) to allow species to gain mass at different rates depending on their initial physiological condition. Optimization was done via maximum likelihood methods to allow for direct comparison among models, and the final model was selected using Akaike's Information Criterion (AIC).

A third of the full data set (3317 data points) was withheld from initial model parameterization to validate the top model. The actual and predicted response variables were compared with linear regression and  $r^2$  to assess model performance and global goodness of fit. Further, to illustrate the effects of important interactions in the top model, we predicted mean mass change for each species over the course of a typical banding day (0600-1200) under differing conditions of fat stores, pectoral muscle mass migrant abundance during that day (the 2.5<sup>th</sup>, 50<sup>th</sup>, and 97.5<sup>th</sup> percentiles of the range in our initial dataset), holding all other covariates constant. The R Statistical Computing Environment with packages "lme4" (Bates et al. 2012) and "stats" (R Core Team 2014) were used for all analyses.

### **4.3. Results**

#### **4.3.1. Model Selection**

The top model included daily conspecific abundance nested within both time of capture and species but no other measures of conspecific abundance. It also included the two, three-way interactions between physiological condition (mass or pectoral score), time, and species. This top model was strongly supported in our AIC model selection (model weight = 0.82;  $\Delta\text{AIC} = 5.0$  from the next best model; Table 1) and is the only model discussed further. Variation of random effects made up 7.0% of the total variance in the model, with sampling day accounting for 5.1% of the variance and year accounting for 1.9%.



Table 4.1. Top eight models ordered by Akaike’s Information Criterion (AIC) along with the global null model for comparison. All models in this list have a base component that includes the random effect of date, species, time of capture, pectoral score, fat score, wing chord nested within species, calendar date, the interaction of date with itself, age, the interaction with age and time, the interactions of pectoral score by time by species, and fat score by time by species. Both conspecific abundance on the day of capture (“Conspecific Abundance” below) and total migratory community abundance (15 species) during the two weeks prior to the day of capture (“Two-Week Abundance” below) are nested with time of capture and species (denoted with the “/” symbol). The time of capture is abbreviated as “Time”.

Model	K	ΔAIC	AIC	Likelihood	AIC weight	Deviance
Time x Species x Conspecific Abundance	66	0	23562	1.00	0.82	23430
Time x Species x Daily Abundance/ Time x Species x Two-week Abundance	73	5.5	23567	0.08	0.07	23421
Time x Species x Daily Abundance/ Time x Species x Two Week Abundance/ Time x Species x Conspecific Abundance	80	4.6	23567	0.08	0.07	23421
Time x Species x Daily Abundance/ Time x Species x Conspecific Abundance	66	8.1	23570	0.02	0.01	23424
Base	59	8.4	23570	0.02	0.01	23452
Time x Two Week Abundance	60	9.3	23571	0.01	0.01	23451
Two Week Abundance	60	8.9	23571	0.01	0.01	23451
Null	1	31150.1	54712	0.00	0.00	54706

The top model predicted bird mass well in the validation data set ( $r^2$  between actual and predicted y-values was 0.96, root mean squared error=1.77). The slope of the linear relationship between actual and predicted response was 0.94. These values indicated that the predicted y-values were highly correlated with the actual values and that there is little bias in the relationship.

Taken together with AIC selection, this result indicated that our top model has a strong global goodness of fit and is relatively the best model among those that we tested.

#### 4.3.2. Important Determinants of the Rate of Stopover Mass Gain

Younger birds (hatch years, HYs) gained more mass over time than older birds (after hatch years, AHYs;  $\beta=0.0002\pm0.0001$  grams per minute; Fig. 1). Our dataset did include a small percentage of unknown aged birds (1.2% of all captures), but there was no significantly different relationship with mass or mass gain between these birds and unknown age birds and were not shown in the figure ( $\beta=-0.54\pm0.692$ ).

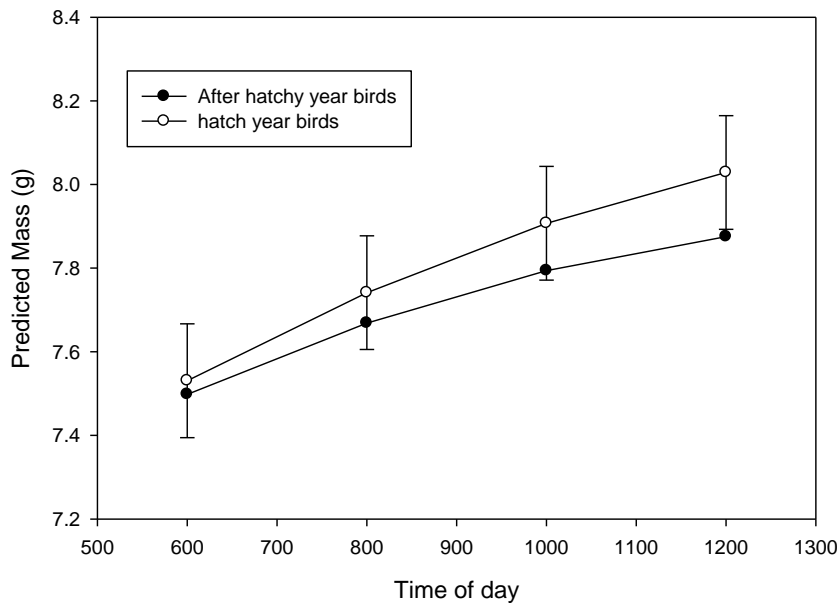


Figure 4.1. Model-predicted effect of age for American redstarts. Age behaved similarly for all species so this one was selected for example purposes. The solid line is AHY birds and the dotted line is HY birds. The error bar is the summed standard error of the mean for the age and age x time parameter estimates of HY birds from the final model.

Overall, birds with higher than average pectoral scores showed increased mass gain over time ( $\beta=0.0008\pm0.0003$  grams per minute) while birds with higher than average fat scores

showed decreased mass gain over time ( $\beta=0.0003\pm 0.0001$  grams per minute). However, there was variation in these effects among species. American redstarts and black-and-white warblers with above average pectoral scores showed higher daily mass gains, while gray catbirds, ovenbirds, and worm-eating warblers with above average pectoral scores showed a decreased mass gain (Fig. 2). Fat score also showed a variable pattern of mass gain with initial physiological condition among species (Fig. 3). American redstarts and gray catbirds showed strong decreases in mass when they possessed higher fat scores, while the other species maintained similar levels of mass gain regardless of fat scores.

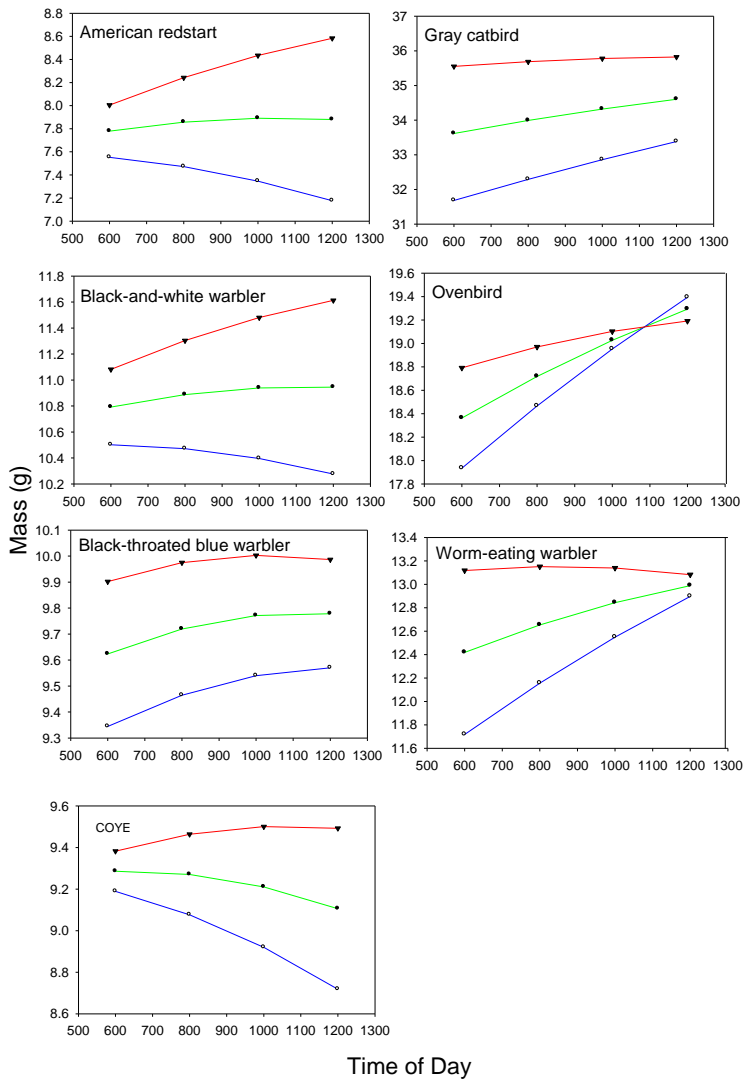


Figure 4.2. Predicted effect of pectoral muscle mass on mass changes during morning monitoring activity. Blue lines are bird with a pectoral score of three (below average muscle), green is a score of 4 (a typically robust muscle) and red is a score of 5 (the maximum score).

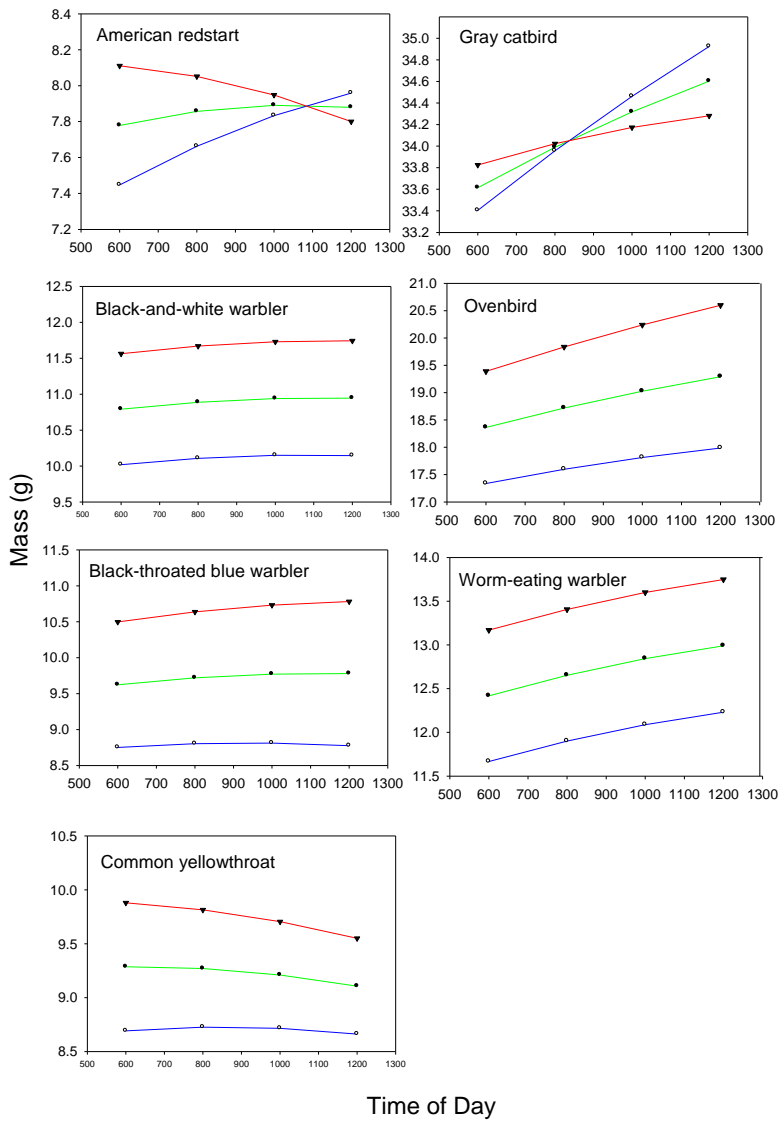


Figure 4.3. Predicted effect of fat store on mass changes during morning monitoring activity. Blue lines are bird with a pectoral score of 0 (no fat), green is a score of 2 (furcular is half full of fat) and red is a score of 4 (furcular is full and bulging with fat).

Daily stopover abundance varied among species, ranging from the estimates for black-throated blue warblers ( $\mu \pm SE = 160 \pm 1$ ) to common yellowthroat ( $19 \pm 2$ ). American redstarts, black-and-white warblers, common yellowthroats, and gray catbirds showed an overall positive relationship between abundance of conspecifics on the day of capture and mass gain, while black-throated blue warblers, ovenbirds, and worm-eating warblers showed a negative relationship (Table 2; Fig. 4). In a post-hoc test, we found a negative relationship (Pearson correlation coefficient = 0.33; Fig. 5) between absolute conspecific abundance and the relationship between conspecific abundance and mass gain, such that species with higher conspecific abundances on average during stopover also exhibited lower mass gains on days with the highest conspecific densities. Additionally, while six of the seven species showed an average increase in mass over time, we found that common yellowthroats consistently lost mass over time under all abundance conditions tested.

Table 4.2. Beta estimates of the nested conspecific abundance x time terms for each of the species.

Species	Nested estimate of Conspecific Abundance x Time	SE	t-value
American redstart	1.37E-06	8.39E-07	1.631
Black-and-white warbler	2.99E-06	2.41E-06	1.239
Black-throated blue warbler	-3.30E-07	4.27E-07	-0.773
Common yellowthroat	3.39E-06	4.81E-06	0.706
Gray catbird	6.27E-06	2.59E-06	2.424
Ovenbird	-4.51E-06	1.56E-06	-2.89
Worm-eating warbler	-1.17E-06	1.76E-06	-0.666

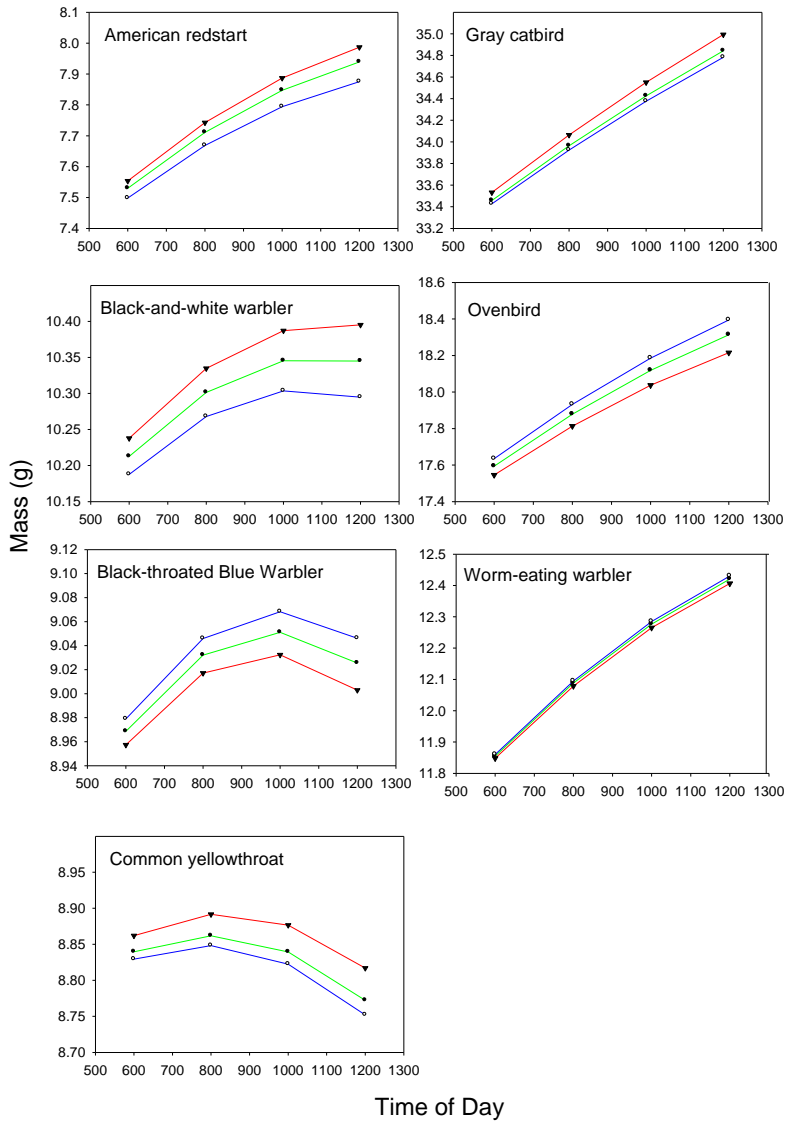


Figure 4.4. Predicted mass changes over time of day for the seven species as conspecific abundance varies from the 25<sup>th</sup> quantile, median and 75<sup>th</sup> quantile.

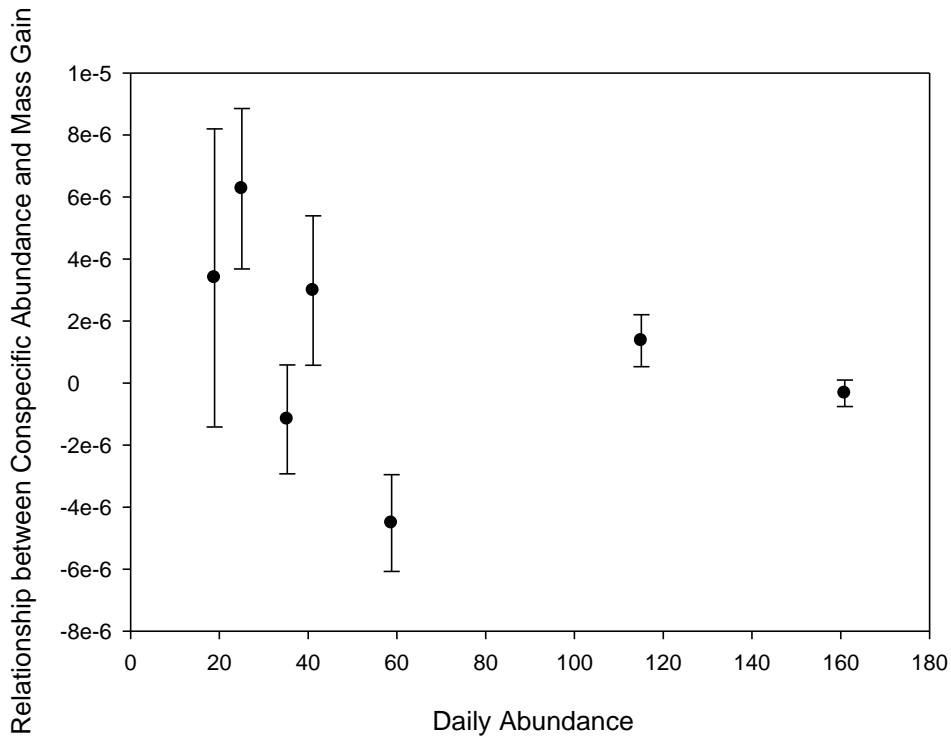


Figure 4.5. The relationship between species abundance and the effect of that abundance on stopover mass gain for all species. Error bars represent standard error of the parameter estimate. The Pearson correlation coefficient for this relationship is 0.33.

#### 4.4. Discussion

Age, physiological condition, and daily conspecific abundance were most important for predicting stopover mass change among migrants. Hatch-year birds arrived at the site with similar mass as AHYs and showed increased mass gain compared to AHYs. Physiological condition could have both positive and negative effects on mass gain depending on species. Conspecific abundance at the stopover site influenced mass gain with both strong positive and negative effects, also depending on species. The species-level effects of conspecific density were negatively correlated with average species abundance, suggesting that some species may not have



had high enough abundances to reach the threshold where competition from conspecifics outweighed the advantages of flocking. For black-and-white warbler and black-throated blue warbler, daily conspecific abundance changed the predicted final mass at which individuals stabilized during stopover.

#### **4.4.1. The Effect of Inexperienced Migrants**

Young birds gained mass more rapidly than AHYs, and ended each day with higher levels of mass on average. This result is dissimilar to past work where young birds were found to have lower overall energetic conditions compared to older birds (Woodrey and Moore 1997, Jones et al. 2002). Our data suggest that younger birds either spend more time foraging or are more efficient foragers during migration. We find the second explanation unlikely, as young of the year are migrating for the first time and relying on social or genetically ingrained cues to migrate successfully (Pulido 2007). Increased foraging rates could be adaptive, because young birds may have higher energetic requirements during migration due to more inefficient flight mechanics or poor migratory decisions. Stopover perhaps provides them an opportunity to “catch up” with more efficient adults; however, the increased body mass or the decreased vigilance associated with higher foraging rates could also put them at higher risk of predation (Burns and Ydenberg 2002, Brown 1999).

#### **4.4.2. Condition-based Stopover Decision-making**

Energetic condition is a primary decision-making tool for songbirds during stopover migration (Rappole and Warner 1976, Jenni and Schaub 2003). Birds in high enough condition to continue with migration are less likely to increase their exposure to predation in order to increase their energetic stores (Ydenberg et al. 2002). Here we show that fat stores and pectoral muscle mass make up different proportions of total body mass of different species, and that species are making different stopover fueling decisions based on their physiological condition as

assessed by these two indicators. The rates of mass gain dependent upon fat stores and pectoral muscle mass also varied among species. Particularly, American redstarts showed lower than average mass gain with high fat and higher than average mass gain with a lower pectoral score, and gray catbirds showed lower than average mass gain with high fat and high pectoral score. These differences suggest redstarts and catbirds have different migratory strategies than other species and they could value the importance of fat and muscle mass differently than other species (e.g., they may catabolize muscle tissues more readily or be willing to depart with less fat than other species). Overall, the diversity of responses to current energetic condition suggests variability in migratory strategy and the relative value that some species place on fat stores (or the interspecies variation in our ability to assess fat during migration).

#### **4.4.3. Density-dependent Effects on Stopover Mass Gain**

Conspecific density during stopover influenced mass gain, increasing or decreasing refueling rates depending on the species. We hypothesize that increased rates of mass gain are due to increases in foraging efficiency by joining mixed-species flocks (Greenberg 2000). Those species that experienced negative impacts on refueling due to conspecific abundance are likely experiencing interference competition (Carpenter et al. 1993) or short-term local resource depletion (Moore and Yong 1991). Moore and Yong (1991) and Kelly et al. (2002) both reported decreases in mass gain during stopover with high abundance of songbirds. While the present study found similar negative effects of density on stopover mass gain in songbirds, we also found positive effects that have not been previously demonstrated. We suspect that differences in migrant densities, stopover habitat quality, and bird community dynamics were responsible for the differences between the present study and past work.

Migratory songbirds often form mixed-species foraging flocks, and while total migrant density was not an important factor in the final model, multiple migrants of the same species

could be flocking with resident species. So species that gain mass faster during stopover in high conspecific density conditions could be those that have the least overlap in foraging niche with resident species (Greenberg 2000) or partition effective foraging niches within the flock (Sridhar et al. 2009). Species that gain mass faster with higher amounts of conspecifics could simply experience limited intraspecific interference competition but still receive the benefits from reduced predation risk in relatively higher densities. Alternatively, realized stopover mass gain may drive local abundance. Individuals may make decisions regarding local movements or stopover length based on their mass gain. This is easy to imagine for species where high abundances were associated with high mass gain or for species where there was no strong pattern overall, but it is difficult to imagine a scenario where emigration from a site is depressed when mass gain is low.

Densities over the past week to two weeks were not included in the top model and did not appear to have a strong effect on stopover mass gain. This is likely because foraging habits of migrant songbirds are generalist enough to buffer them from variability in prey availability. Warbler species (six of the seven focus species in this study) show plasticity in foraging behaviors during migration (Parrish 2000, Martin and Karr 1990), which could expand their foraging niches and prevent food resource depletion from having a strong effect on refueling rate. Niche expansion during migration could also reduce interference competition and perhaps could facilitate the positive relationships detected with daily conspecific abundance. Stopover habitat quality could also influence the lack of depletion effects seen in the top model. Key Biscayne has a high number of *Ficus* spp. in the area, providing consistent fruit all through the migratory season, and insect-dense scrub that could prevent depletion effects from occurring locally. Migrants may also time their migration to match peak food abundance at stopover sites to defray the effects of depletion (Olsen et al. *in press*).

The effect that conspecific density had upon refueling rates was loosely correlated with the average abundance of the species at the stopover site. While certainly not conclusive, this pattern suggests that species could have a stopover density threshold where additional conspecifics no longer increase the benefits of flocking but continue to increase the costs of interference competition. Under this scenario, our data do not show species-specific reactions to conspecific density but rather species responding to different points along the continuum of a common density-dependent mechanism across all species.

#### **4.4.4. Incongruities and Issues**

We detected a peculiar pattern of mass change in common yellowthroats. They were the only species predicted to lose mass over average conditions experienced at the stopover site. There are two primary possibilities for such a pattern: common yellowthroats are wintering at or around the site, and they are not trying to add mass to continue their migratory journey further into the Caribbean; or the stopover site lacks the necessary forage for them to refuel efficiently. We suspect the former explanation is the most accurate as there are probably both resident and migratory yellowthroat populations at the site (Guzy and Richison 1999).

#### **4.4.5. Conclusions and Implications**

In this study we found strong and variable effects of density-dependence on migratory refueling rate across species. Intrinsic and extrinsic components to habitat quality appear to be linked via density-dependence in a way that could change the realized habitat quality on the species at daily scales. We also suspect that site and community composition play roles in how density-dependence is expressed during migration. The responses that species have to density could influence where birds are willing to stop and which species they are willing to share the site with. Species with sensitivity to density may be more likely to time migratory movements to match resource phenology and interference competition along the migration route. It remains to

be seen whether interference competition selects for migratory route, timing, or stopover behaviors though the effects seen in this study would make such an effect plausible.

## **CHAPTER 5: MERCURY EXPOSURE ACROSS THE ANNUAL CYCLE IN MIGRATORY SONGBIRDS AND IMPLICATIONS FOR MIGRATORY BEHAVIOR**

### **5.1. Introduction**

Long-distance migratory animals are uniquely vulnerable to global pollutants like mercury (Hg), as they can be exposed at a wide range of geographic locations and exposure has the potential to disrupt migratory behaviors require the complex coordination of physiological systems under high energetic demand. As a result, migrants can act as sentinels of ecosystem health in areas that are difficult to access or assess directly, and they can integrate signals over a broad spatial scale (Piersma and Linstrom 2004). Migrants could also be adversely affected by such exposure and reduce their fitness during migration. In this study, we explored the potential of Neotropical-Nearctic migratory songbirds to act as sentinels of remote mercury exposure risk, and examined how that exposure influences migratory decision-making and physiology.

The global distribution of mercury is a function of: (1) Hg release into the atmosphere by anthropogenic sources (e.g. coal-fired power plants and small-scale gold mining) or natural sources (e.g., volcano eruptions), (2) atmospheric transport on prevailing winds, and (3) deposition into habitats (primarily in wetland soils) where micro-organisms convert inorganic mercury into the more biologically toxic and environmentally persistent methylmercury (MeHg; Ullrich et al. 2001). Methylmercury is environmentally persistent thus MeHg can be stored in for long times (e.g., in the ocean) and reemerge into the atmosphere for redeposition. As a result of this process, Hg is distributed globally and is found in ecosystems where there are no local sources, though local sources can represent a significant proportion of total exposure (Driscoll et al. 2007, Pacyna et al. 2010). On the North American breeding grounds of Neotropical-Nearctic

songbirds, atmospheric Hg deposition has increased by a factor of two to four since the beginning of the industrial period (Lindberg et al. 2007) and global Hg emission have been increasing from 2005-10 (UNEP 2013). Point-source exposure to Hg on the non-breeding grounds in Central and South America has also increased due to artisanal small-scale gold mining, which is currently the single largest source of Hg emissions on the globe (Telmer and Veiga 2009, Beal et al. 2013). Amazonia and the boreal forests of North America are vast, remote, and present considerable challenges for wide-spread monitoring of fauna. Migratory songbirds could be useful for describing Hg (Hg will be used as shorthand for MeHg from here on as MeHg the primary form of Hg in songbirds) availability in these regions because of their movements between the sites.

While migrating birds could be good indicators of Hg levels at their breeding and non-breeding grounds, any patterns could be difficult to interpret because Hg exposure could influence migratory behaviors directly. The seasonal movement of individuals to different habitats and locations is a complex behavioral and physiological process. Migratory birds must minimize the time spent during migration (where mortality rates are high: Sillett and Holmes 2002) while maximizing their energy stores (primarily in the form of subcutaneous fat) needed to fuel long-distance flights (Jenni and Jenni-Eiermann 1998). As a result, migratory behaviors catabolize contaminant-storing body tissues (e.g., digestive organs, muscle and fat; McWilliams et al. 2004, McWilliams et al. 2005) where much of the MeHg body burden is sequestered (mostly muscle and digestive tissues; Spalding et al. 2000a) placing these species at a presently unquantified risk of Hg exposure.

Mobilized Hg has the potential to disrupt migratory behaviors via its neurotoxic and endocrine-disrupting effects. Birds in particular appear susceptible to MeHg effects (Heinz et al. 2009), including endocrine and immune system disruption (Heath and Frederick 2005, Hawley et al. 2009, Adams et al. 2009), neurological impairment (Spalding et al. 2000b), migratory performance (Carlson et al. 2014), reproductive impairment (Evers et al. 2008; Jackson et al.

2011a; Frederick and Jayasena 2011), territorial behavior (Hallinger et al. 2010) and reduced body mass (Ackerman et al. 2012). As both migratory and non-migratory insectivorous songbirds are at high risk of exposure due to their trophic position, this could place migratory songbirds at high risk for adverse effects (Evers et al. 2005; Cristol et al. 2008; Jackson et al. 2011b).

There are many potential pathways by which Hg could affect bird migration, few of which have been tested in free-living populations. Although Seewagen (2013) found Hg levels in a single songbird species were not high enough to affect migratory refueling rates, there are other potential pathways by which MeHg could affect migratory fitness. Altered levels of corticosterone — a reported effect of mercury exposure in birds (Adams et al. 2009, Frederick and Jayasena 2011) — could influence rates of foraging, catabolism, and anabolism during migration. Testosterone plays a role in migratory timing in addition to reproductive development in males (Tonra et al. 2013), and the effect of Hg on this steroid or its hormonal precursors could have a complex effect on migratory performance (Tartu et al. 2013). Lastly, Hg alters coordination, motivation, and learning behaviors in birds, which could alter flight efficiency, navigation and foraging rates during migration (Scheuhammer 2007).

To explore the relationships between Hg and migration, we assessed migrating songbirds in South Florida for three spring seasons (2009-11) and two fall seasons (2010-11) for Hg exposure using blood and tail feathers, respectively. Blood sampled during the spring should be representative of Hg exposure on the non-breeding grounds that the birds have just left, while fall tail feathers are grown immediately post-breeding and represent breeding ground Hg exposure. Additionally, blood is metabolically active and in dynamic equilibrium with the total body Hg burden, unlike feathers which become metabolically inert after growth. Blood Hg concentrations will thus likely change over the course of migration, as fats and proteins are catabolized and



anabolized. Blood Hg concentrations, therefore, are a product of both current physiological state and past exposure, whereas feathers are only representative of past dietary exposure.

The objectives of this study are twofold: (1) to determine if migrating birds are useful indicators of Hg exposure on the breeding and non-breeding grounds, and (2) to assess how migratory behavior and performance is correlated to past mercury exposure. To address our first objective, we compared Hg concentrations assessed during migration to Hg concentrations in tissues of the same species gathered on the breeding grounds. For our second objective, we modeled both daily and annual correlates of Hg concentrations in bird tissue using four species during spring and fall to gain a better understanding of how breeding and non-breeding Hg exposure varies among species, how Hg exposure change over time, and how migrants' physiological condition during migration relates to past and current Hg exposure.

## **5.2. Methods**

### **5.2.1. Study Site**

Migration banding data were collected at Bill Baggs Cape Florida State Park on Key Biscayne, FL (25.674°N, 80.161°W) from 2009 to 2012 using a standardized migration monitoring protocol (Ralph et al. 1993). Nets were opened at least 5 days a week at dawn, weather permitting, for a minimum of 6 hours a day in both the spring and fall. Fall netting occurred from mid-August to early November and spring netting was from mid-April to mid-May. Nets were checked once every 15-30 minutes, and birds were extracted and banded with a uniquely numbered USGS aluminum band. For each capture we recorded species, age, sex, time of capture, unflattened wing chord, pectoral score (an estimate of pectoral muscle mass), fat score (an estimate of migratory fat stores), and body mass (*sensu* Ralph et al. 1993). Local wind direction and speed data were gathered from the Miami International Airport (15 km northeast of

the banding station) and averaged on the daily scale. These data were decomposed into the u (East-West) and v (North-South) vector components for ease of analysis.

### **5.2.2. Fall and Spring Migration Sampling Scheme**

We selected nine study species based on their frequency of capture at the banding station, diet at the breeding grounds, and evidence for Hg bioaccumulation in the Biodiversity Research Institute songbird Hg database (see below). We sampled American redstart (*Setophaga ruticilla*), black-throated blue warbler (*S. caeruleascens*), common yellowthroat (*Geothlypis trichas*), and northern waterthrush (*Parkesia noveboracensis*) in both fall and spring, and blackpoll warbler (*S. striata*), black-and-white warbler (*Mniotilta varia*), black-whiskered vireo (*Vireo altiloquus*), ovenbird (*Seiurus aurocapillus*), and prairie warbler (*Setophaga discolor*) were sampled only during spring.

A maximum of four individuals were sampled per species on each day at the monitoring station, to distribute our sampling effort across the entire migration season. During the springs of 2009-2011, blood Hg samples were collected via the brachial vein using a capillary tube. Samples were then capped and stored on ice until the end of the field day, when the sample was frozen until analysis. During the fall of 2011 and 2012, -the fourth, right rectrix was plucked from individuals of the study species and stored in a coin envelope in dry conditions.

Given that spring migration can occur in less time than the turnover rate of blood tissue for some songbirds (Bearhop et al. 2000; Stutchbury et al. 2009), and given the relatively close geographic position of Key Biscayne to our species' wintering grounds (the Caribbean basin), we considered spring blood Hg concentration to be an indicator of wintering-ground Hg exposure. Rectrices, like all feathers, are metabolically inert once grown, so their Hg levels are indicative of circulating blood-Hg during molt (Furness et al. 1986). In all of these species, tail feathers are grown once annually (immediately post-breeding) on or near the breeding grounds (Pyle 1997).

Adventitious molt can occur at any point in the annual cycle, but tail feathers that were clearly regrown outside of the basic molt were not sampled.

### **5.2.3. Breeding Ground Songbird Mercury Database**

To determine the efficacy of using migration-monitoring stations to assess breeding-ground Hg exposure, we compared our samples with those in the BRI database from the same species. The Biodiversity Research Institute (BRI) database includes records for blood and feather Hg concentrations from songbirds captured using active or passive mist-netting techniques in a variety of habitats across North America starting in 2002. To obtain reference values for Hg results from the Florida site, we limited the database to blood and feathers sampled from target species during the breeding season (May to August) at non-point source locations in North America prior to 2012. The resulting data was summarized to estimate population-wide breeding ground Hg exposure from atmospheric deposition. Because of the historical project objectives that led to the creation of this database, mercury sampling the BRI database is still likely to be biased toward habitats where Hg is more likely to be methylated and bioaccumulation are more probable. For our focal species these data still represent the best-known estimates of songbird Hg exposure in North America.

### **5.2.4. Mercury Determination**

Each tissue sample was analyzed for total Hg concentration at the BRI lab in Gorham, Maine. The entirety of the blood sample was consumed in the analysis and the feathers were ground up prior to analysis. Mercury concentration was determined via thermal decomposition coupled with atomic absorption spectroscopy, following EPA method 7473 (e.g., Evers et al. 2005). Prior to analysis, the equipment was calibrated using NIST-certified standard solutions, and accuracy and precision were evaluated within each analytical batch through the inclusion of certified reference materials, continuing calibration verifications, duplicates, blanks, and matrix

spikes. Within each batch of 40 measurements, approximately ten of the samples were for QA/QC purposes.

### **5.2.5. Statistical Analysis**

To determine how the data collected during migration in this study compare to data collected on the breeding grounds we calculated the proportional difference between the Hg concentration for each species and tissue type sampled on migration and the breeding Hg signal in the BRI database (when data were available). Because Hg data are non-normal, we calculated differences at the 25<sup>th</sup>, 50<sup>th</sup>, and 75<sup>th</sup> quantile of each data set. Thus, our methods compared the two sampling populations at the low, median or high ranges of exposure.

To estimate the effects of individual condition and migratory timing on blood and feather Hg levels in four migrating songbird species in spring and fall (American redstart, black-throated blue warbler, common yellowthroat and northern waterthrush), we used general linear mixed-modeling techniques in Program JMP (SAS Institute, Cary, NC) to estimate the effects of individual condition and migratory timing on log-transformed blood and feather Hg levels. This modeling effort was done with the four migrating songbird species sampled in both spring and fall: American redstart, black-throated blue warbler, common yellowthroat and northern waterthrush. We ran two models (one for spring blood Hg and one for fall feather Hg) to predict Hg levels. Though we chose the same a priori model for both seasons to aid in comparison, explanatory variables could have different interpretations and meaning depending on the season of assessment. Because our sampling tissue was metabolically active in the spring, Hg levels were dependent on both Hg-accumulation on the non-breeding grounds as well as Hg-mobilization related to the condition of the animal at the time of capture. In the fall, the metabolic inactivity of feathers assures that Hg levels only reflect past exposure.

Both models predict the effect of migratory condition on Hg levels included east-west wind speed during the previous evening, north-south wind speed during the previous evening, body mass, wing chord, fat score (treated as continuous), and pectoral score (treated as continuous) as fixed effects. North-south and east-west wind speed vectors were included in the models to determine if conditions that influence landing decisions were correlated with Hg exposure (Chapter 1, Jenni and Schaub 2003). Body mass and wing chord were nested within species. To test if Hg levels are changing at the stopover site, time of capture and an interaction term of mass and time of capture (nested by species) were also added to the models to test if Hg exposure varied at the stopover site and if that variation was related to mass gain during stopover. We did not include age or sex in the models, as not all species could be reliably aged or sexed during migration, and classification was also sometimes dependent on other morphometric measurements in our models (e.g., wing chord and mass).

### **5.3. Results**

We sampled 669 individuals in the fall and 535 individuals in the spring in total. In the fall sample sizes by species ranged from 113 (northern waterthrush) to 262 (American redstart), and in the spring they ranged from 2 (red-eyed vireo) to 106 (northern waterthrush). We included 665 samples in fall and 299 samples in spring for general linear modeling effort. Species showed similar relative patterns of MeHg accumulation in spring and fall ( $r^2 = 0.95$ , though  $n=4$ ). Northern waterthrush had the highest median levels at 1.95 ppm fresh weight (fw) in the fall and 0.13 ppm wet weight (ww) in the spring, and black-throated blue warblers were the lowest at 0.57 ppm fw in the fall and 0.02 ppm ww in the spring (Table 1A and 1B).

Table 5.1. Spring (A) and Fall (B) distribution quantiles of blood and feather (ppm) Hg levels and sample sizes.

A.

Species	Minimum	10%	25%	Median	75%	90%	Maximum	N
American redstart	0.02	0.03	0.05	0.07	0.11	0.14	0.36	71
Blackpoll warbler	0.00	0.01	0.01	0.02	0.03	0.04	0.09	93
Black-throated blue warbler	0.01	0.01	0.01	0.02	0.03	0.06	0.12	86
Black-whiskered vireo	0.01	0.01	0.01	0.02	0.02	0.04	0.04	8
Common yellowthroat	0.01	0.01	0.02	0.03	0.08	0.15	0.37	41
Northern waterthrush	0.01	0.03	0.07	0.13	0.21	0.48	1.55	106
Ovenbird	0.00	0.02	0.03	0.05	0.10	0.14	0.41	101
Prairie warbler	0.00	0.01	0.02	0.02	0.04	0.07	0.09	27
Red-eyed vireo	0.02	0.02	0.02	0.03	0.04	0.04	0.04	2

B.

Species	Minimum	10%	25%	Median	75%	90%	Maximum	N
American redstart	0.12	0.43	0.66	0.99	1.56	2.37	10.88	262
Black-throated blue warbler	0.14	0.27	0.39	0.57	0.86	1.28	3.64	156
Common yellowthroat	0.18	0.33	0.53	0.88	1.57	2.39	6.81	138
Northern waterthrush	0.25	0.73	1.28	1.95	2.88	5.58	19.00	113

### 5.3.1. Comparison to Songbird Mercury Database Values

There were insufficient breeding ground data in the BRI database to make comparisons to stopover Hg for black-whiskered vireo and prairie warbler, but median spring blood Hg values for both species were among the lowest we sampled (Table 1A). With the exception of ovenbirds, spring migration blood Hg levels were considerably lower than those measured on the breeding grounds for the seven species with adequate sampling in the BRI database (Fig. 1). American

redstart and red-eyed vireo spring blood Hg values were more similar to breeding ground database values at lower Hg levels than at higher levels, indicating that there were fewer individuals at higher Hg levels sampled at the Florida site in the spring than might be expected based on chance. Generally speaking, however, there was no consistent trend in the differences between the breeding and spring migratory blood Hg levels among the 25<sup>th</sup>, 50<sup>th</sup>, and 75<sup>th</sup> quartiles. When compared to breeding ground feather Hg levels, fall migrating American redstart and common yellowthroat had much lower feather-Hg concentrations than did birds sampled on the breeding grounds, and northern waterthrush feather Hg was higher than breeding ground levels at all but the highest tested quantiles (Fig. 1).

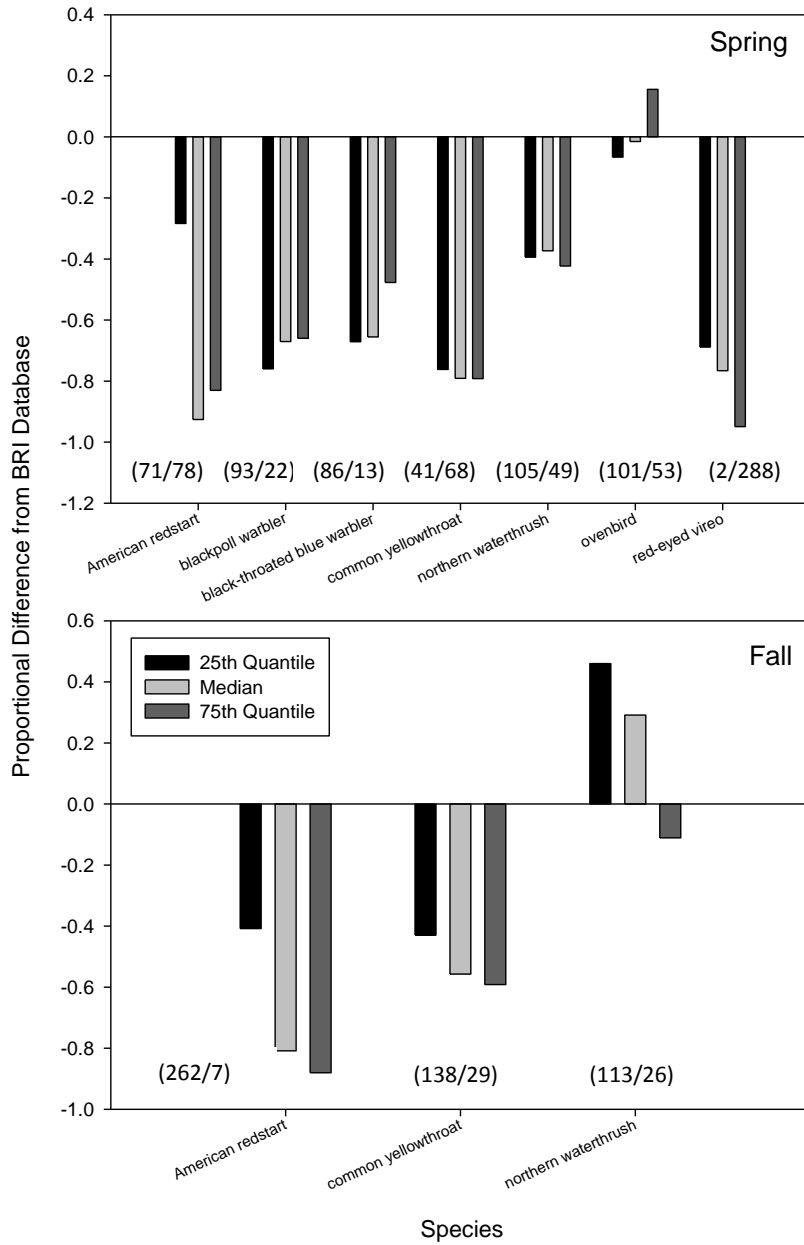


Figure 5.1. Proportion difference between spring blood Hg values (top) and fall feather Hg values (bottom) from Key Biscayne and the BRI songbird database for the same tissues and species on their breeding grounds. Differences were calculated for the 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup> quartiles. Numbers in parentheses indicate sample size for the migratory period/breeding period. We lacked black-throated blue warbler feather data to compare to the migratory data in the fall.



### 5.3.2. Correlates of Blood Hg During Spring Migration

The model describing patterns in spring blood Hg levels had an  $r^2$  of 0.50 and an overall significance of  $F_{22,276}=12.7$  ( $p<0.001$ ). The model terms that were most important to predicting spring blood levels were year ( $F_{2,297}=4.0$ ,  $p=0.02$ ), species ( $F_{3,296}=3.3$ ,  $p=0.02$ ), and time of day ( $F_{1,298}=2.59$ ,  $p=0.11$ ; Table 2). Despite being used in higher level interactions, the base term time of day was moderately negatively correlated with Hg exposure, leading to a decrease in blood Hg levels of about 50% over the course of a standard sampling day (0600-1200) (Fig. 2). Using a post-hoc Tukey HSD test, we found that the mean concentration of samples collected in 2010 (least-squared mean=0.06) were significantly higher than those from 2009 (least-squared mean=0.04;  $p=0.02$ ) and values from both of those years were similar to the mean for 2011 (least-squared mean=0.052). Northern waterthrush (least-squared mean=0.07) was significantly higher than black-throated blue warbler (least-squared mean=0.02,  $p=0.02$ ), with common yellowthroat (least-squared mean=0.07) and American redstart (least-squared mean=0.04) similar to all species. One species, black-throated blue warbler, also showed a significantly negative relationship between Hg levels and mass gain over the course of the sampling day (Table 3).

Table 5.2. Overall variable importance for the spring general linear model.

Source	Number of parameters	DF	SS	F	p-value
East-West Wind Speed	1	1	0.06	0.09	0.77
North-South Wind Speed	1	1	1.72	2.56	0.11
Year	2	2	5.38	4.01	0.02
Fat Score	1	1	0.51	0.75	0.39
Pectoral Score	1	1	0.05	0.07	0.79
Mass[Species]	4	4	2.49	0.93	0.45
Wing chord[Species]	4	4	2.67	0.99	0.41
Species	3	3	6.59	3.28	0.02
Time	1	1	1.74	2.59	0.11
Mass x Time[Species]	4	4	3.41	1.27	0.28

Table 5.3. Parameter estimates from the general linear model describing the relationships between spring blood-Hg levels and tested covariates.

Term	Estimate	SE	t	p-value
Intercept	-2.27	0.71	-3.20	0.00
U Wind EA	0.01	0.02	0.30	0.77
V Wind EA	-0.05	0.03	-1.60	0.11
Year[2009]	-0.29	0.10	-2.78	0.01
Year[2010]	0.19	0.08	2.24	0.03
Fat Score	-0.06	0.07	-0.87	0.39
Pectoral Score	0.03	0.11	0.26	0.79
Species[AMRE]:(mass-11.1455)	-0.14	0.17	-0.81	0.42
Species[BTBW]:(mass-11.1455)	0.00	0.12	0.02	0.98
Species[COYE]:(mass-11.1455)	0.13	0.14	0.92	0.36
Species[NOWA]:(mass-11.1455)	0.07	0.05	1.37	0.17
Species[AMRE]:(wing_chord-65.6656)	0.02	0.04	0.51	0.61
Species[BTBW]:(wing_chord-65.6656)	0.04	0.03	1.19	0.23
Species[COYE]:(wing_chord-65.6656)	0.05	0.05	0.89	0.37
Species[NOWA]:(wing_chord-65.6656)	0.02	0.02	1.23	0.22
Species[AMRE]	-0.15	0.50	-0.29	0.77
Species[BTBW]	-0.70	0.28	-2.45	0.01
Species[COYE]	0.41	0.51	0.80	0.42
Time of Capture	0.00	0.00	-1.61	0.11
Species[AMRE]:(mass-11.1455)*(time-1023.8)	0.00	0.00	-1.08	0.28
Species[BTBW]:(mass-11.1455)*(time-1023.8)	0.00	0.00	-1.67	0.10
Species[COYE]:(mass-11.1455)*(time-1023.8)	0.00	0.00	-0.74	0.46
Species[NOWA]:(mass-11.1455)*(time-1023.8)	0.00	0.00	0.14	0.89

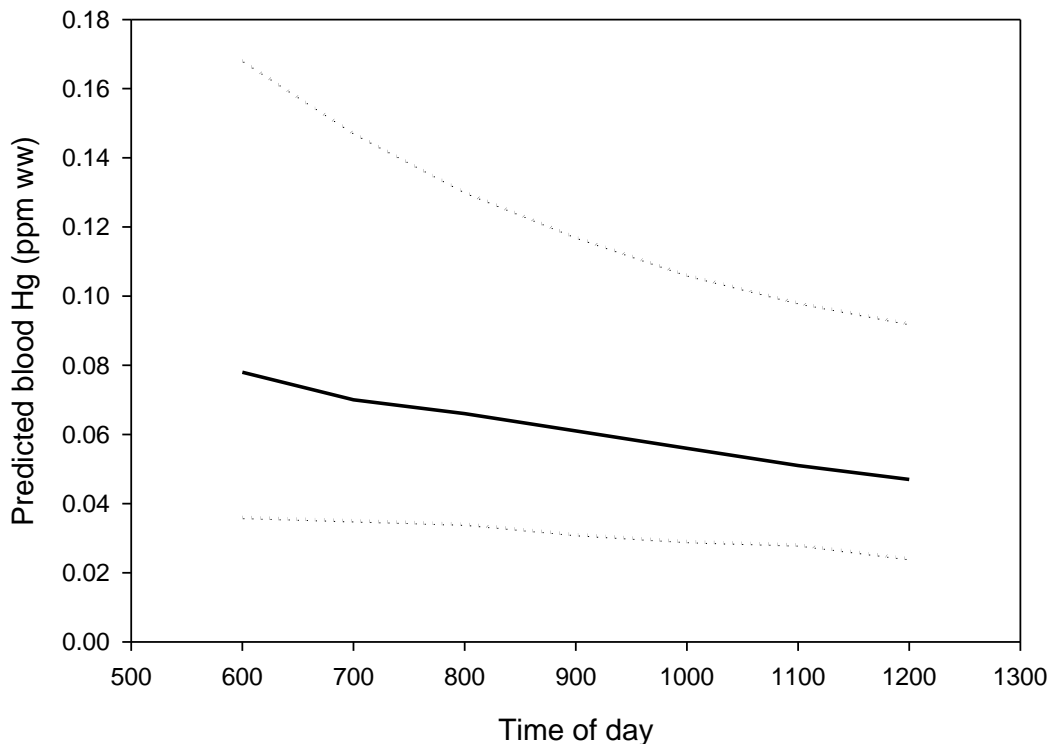


Figure 5.2. Time of day was a moderate predictor of spring blood Hg levels; predicted levels decreased almost 50% over the course of the sampling day. The solid line is the predicted Hg level (in this case for northern waterthrush, though all species showed the same predicted pattern). Dotted lines are the lower and upper 95% confidence intervals.

### 5.3.3. Correlates of Rectrix Mercury During Fall Migration

The fall feather Hg model had an  $r^2$  of 0.25 and an overall significance of  $F_{21,643}=10.48$  ( $p<0.0001$ ). The factors that were most important for describing feather-Hg levels were species ( $F_{3,662}=6.87$ ,  $p<0.01$ ), fat score ( $F_{1,664}=5.2$ ,  $p=0.02$ ), wing-chord nested within species ( $F_{4,661}=2.2$ ,  $p=0.07$ ), and the interaction of mass and time nested within species ( $F_{4,661}=2.1$ ,  $p=0.07$ ; Table 4). A post-hoc Tukey HSD test indicated that common yellowthroat (least-squared mean=1.37) and American redstart (least-squared mean=1.08) were each significantly higher than black-throated blue warblers (least-squared mean=0.62,  $p=0.02$  and  $p<0.01$ , respectively) with northern

waterthrush similar to the means to all species (least-squared mean=1.07). Fat score was negatively associated with feather Hg levels (Table 5, Fig. 3). All species showed positive parameter estimates between body mass and feather Hg, suggesting a consistent relationship between body mass and Hg among species, although the relationship was significant or approaching significance in only black-throated blue warblers ( $p=0.04$ ) and northern waterthrushes ( $p=0.08$ ). Black-throated blue warblers with larger wing chords had lower Hg levels ( $p=0.02$ ), whereas common yellowthroats with larger wing chords had higher Hg levels ( $p=0.09$ ). Common yellowthroats did show a negative relationship between the interaction of mass and time with feather Hg ( $p=0.03$ ), however; yellowthroats with higher mass later in the day tended to have lower feather Hg levels (Fig. 4).

Table 5.4. Overall variable importance for the fall general linear model.

Source	Number of parameters	DF	SS	F	p-value
U Wind EA	1	1	0.29	0.58	0.45
V Wind EA	1	1	0.21	0.42	0.52
Year	1	1	0.12	0.25	0.62
Fat Score	1	1	2.54	5.20	0.02
Pectoral Score	1	1	0.96	1.97	0.16
Mass[Species]	4	4	3.20	1.64	0.16
Wing Chord[Species]	4	4	4.34	2.22	0.07
Species	3	3	10.06	6.87	0.00
Time of Capture	1	1	0.00	0.00	1.00
Mass x Time[Species]	4	4	4.18	2.14	0.07

Table 5.5. Parameter estimates from the general linear model describing the relationships between fall feather Hg levels and included covariates.

Term	Estimate	SE	t	p-value
Intercept	-0.34	0.44	-0.77	0.44
U Wind EA	-0.01	0.02	-0.76	0.45
V Wind EA	0.01	0.02	0.65	0.52
Year[2011]	0.02	0.04	0.50	0.62
Fat Score	-0.07	0.03	-2.28	0.02
Pectoral Score	0.11	0.08	1.40	0.16
Species[AMRE]:(mass-10.5731)	0.04	0.06	0.64	0.52
Species[BTBW]:(mass-10.5731)	0.14	0.07	2.04	0.04
Species[COYE]:(mass-10.5731)	0.02	0.06	0.38	0.71
Species[NOWA]:(mass-10.5731)	0.06	0.04	1.78	0.08
Species[AMRE]:(wing_chord-62.3594)	-0.01	0.02	-0.27	0.79
Species[BTBW]:(wing_chord-62.3594)	-0.06	0.03	-2.35	0.02
Species[COYE]:(wing_chord-62.3594)	0.05	0.03	1.70	0.09
Species[NOWA]:(wing_chord-62.3594)	0.01	0.03	0.48	0.63
Species[AMRE]	0.08	0.16	0.51	0.61
Species[BTBW]	-0.48	0.13	-3.70	0.00
Species[COYE]	0.32	0.21	1.50	0.13
Time of Capture	0.00	0.00	0.00	1.00
Species[AMRE]:(mass-10.5731)*(time-922.519)	0.00	0.00	0.14	0.89
Species[BTBW]:(mass-10.5731)*(time-922.519)	0.00	0.00	1.41	0.16
Species[COYE]:(mass-10.5731)*(time-922.519)	0.00	0.00	-2.23	0.03
Species[NOWA]:(mass-10.5731)*(time-922.519)	0.00	0.00	-0.7	0.4828

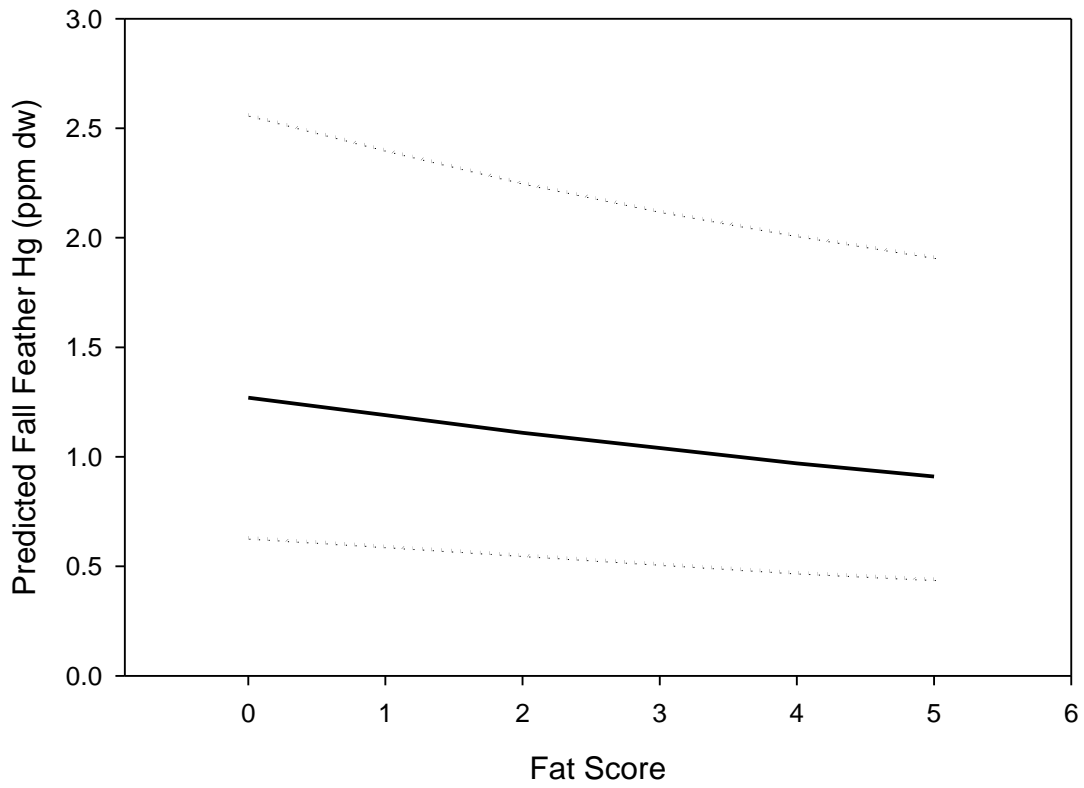


Figure 5.3. Fall fat score was a strong predictor of Hg feather levels during post-breeding molt for all species. The solid line is the predicted Hg level (in this case for northern waterthrush, though all species showed the same predicted pattern). Dotted lines are the lower and upper 95% confidence intervals.

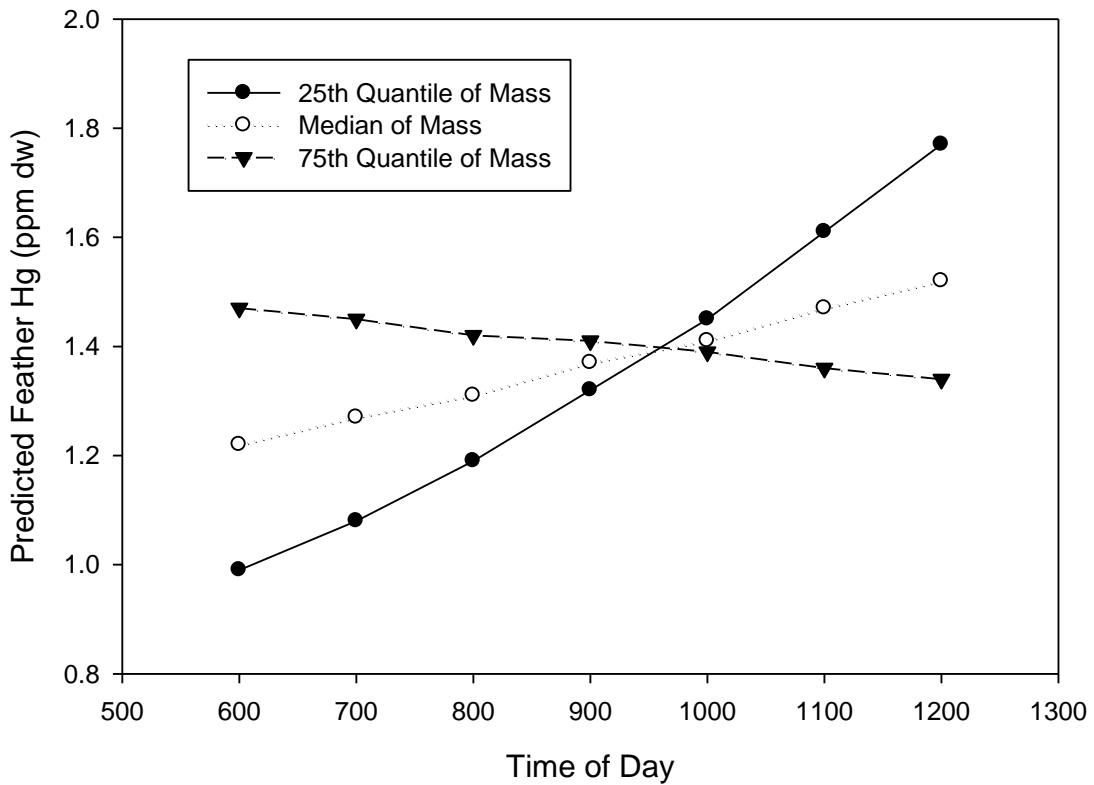


Figure 5.4. The relationship between time of capture and feather Hg levels for common yellowthroats of the 25<sup>th</sup> quantile of mass, median mass and 75<sup>th</sup> quantile of mass. Error of predicted values is not shown to increase the clarity of graph (the relationship is statistically significant).

#### 5.4. Discussion.

##### 5.4.1. Mercury Exposure Risk to Migrating Songbirds

Unadjusted Hg levels indicated that northern waterthrush and American redstarts experienced the highest levels of Hg exposure during both the breeding season (fall feathers) and during late wintering and spring migration (spring blood), while black-throated blue warblers, blackpoll warblers, black-whiskered vireos and prairie warblers experienced the lowest median levels.

All spring blood Hg levels were below the concentrations at which reproductive success is reduced by 10% at the breeding grounds (0.70 ppm ww blood Hg; Jackson et al. 2011a), with the exception of for five northern waterthrush (5% of the total waterthrush sample size). Mercury effects are best described at the breeding grounds and represents period where contaminants can affect population growth rates. While organismal risk from a given blood Hg level on migration might not be directly comparable to that measured during the breeding or wintering periods (see discussion below), blood Hg concentrations are likely a reasonable estimate of relative risk among species.

Many fall samples possessed feather Hg concentrations above the 10% reproductive impairment level of 3.2 ppm Hg fw in feathers (Jackson et al. 2011b), including 20 waterthrush (18% of the total sample), eight yellowthroats (6% of the total sample), three redstarts (1% of the total sample), and one black-throated blue warbler (less than 1% of the total sample). This comparison suggests that songbirds migrating through Florida may face more ecologically concerning Hg exposure on the breeding grounds than during the wintering period, though challenges in using blood Hg during migration could be a confounding factor in this analysis (see below).

#### **5.4.2. Comparison to Database Mercury Levels**

Ovenbirds (in spring) and northern waterthrushes (in fall) were the only species to display similar Hg levels over migration in comparison with their documented breeding ground exposure. Migrating ovenbirds matched the relatively low values found in breeding populations, while extreme values detected in fall waterthrushes, as much as 19 Hg ppm fw in feathers, match some of the highest found in the >9000 sample BRI songbird database. However, mercury levels measured during migration in the remaining species were generally uniformly lower than those in the BRI database. This was true for feather Hg as well as blood, though feather Hg



concentrations are established at or near the breeding grounds, and thus should be directly comparable to values in the database. Three types of sampling bias could explain these differences: (1) species means in the BRI songbird database are biased high by the preferential sampling of areas where Hg is likely to accumulate, (2) the birds sampled at Key Biscayne are not representative of the population sampled in the BRI database because of strong migratory connectivity (Norris and Marra 2007), and/or (3) mercury exposure decreases capture probability at the migration banding station by increasing ataxia (Spalding et al. 2000b). Though these explanations are not mutually exclusive, we believe that habitat-related biases in sampling on the breeding grounds may play a role in the observed discrepancies for some species. Despite these differences from the database values, we view the migration data to be fairly consistently negatively biased in this study and thus still useful for Hg monitoring generally once this bias is accounted for.

#### **5.4.3. Correlates of Mercury Exposure During Spring**

During spring migration we found few correlates of blood Hg levels in our model. Sample year and species were significant factors, indicating that our sampling scheme was sufficient to detect annual and interspecies variation in Hg exposure. Time of day was a marginally significant negative correlate of blood-Hg levels, such that blood levels dropped as birds rested and refueled for their next migratory flight. Locally ingested food sources could be low in Hg and dilute Hg in the blood stream. Notably, we found no evidence that of birds with lower fat or protein stores had higher Hg levels than birds in higher condition. We suspect that the rapid physiological changes that birds undergo during migration could be masking the effects of tissue catabolism on blood Hg levels. However, it is also possible that the birds sampled at the Florida station are simply not catabolizing tissues with large Hg stores during spring migration—at least at this relatively early stage in migration.

#### **5.4.4. Correlates of Mercury Exposure During Fall**

Unlike spring, several individual-level variables were correlated with feather Hg, including fat, wing chord (for black-throated blue warblers and common yellowthroats) mass (for black-throated blue warblers and northern waterthrushes), and changes in mass over time (in common yellowthroats). Fat stores were negatively correlated with feather Hg across all species, suggesting that birds with higher Hg exposure during the post-breeding period arrive at the stopover site in worse physiological condition. This pattern could be produced through Hg's action as an endocrine disruptor (altering the actions of metabolic hormones that control fat storage, like corticosterone: Adams et al. 2009, Frederick and Jayasena 2011) and through Hg's action as a neurotoxin, altering migratory efficiency (Carlson et al. 2014) or decision-making. For the three species where mass was positively associated with Hg exposure, heavier or larger birds might be feeding from a different prey base, within a different habitat, or in a different geographic region. There is support for this sort of relationship being produced by competitive dominance or territoriality (e.g., American redstarts with higher mass occupy wetter habitats with higher Hg exposure; Studds and Marra 2005).

The significant interactions with wing chord and feather Hg in black-throated blue warblers and common yellowthroats suggest that breeding ground origin may be a driver of exposure risk, as wing chord length is often positively correlated with migratory distance (Yong and Moore 1994, Piero 2003, Voelker 2008), though also can be confounded with age and sometimes sex (Mulvihill and Chandler 1990). If this pattern is related to age then it suggests that younger black-throated blue warblers (smaller wing chord length) and older common yellowthroats (larger wing chord length) are exposed to higher mercury levels. As young birds have physiological mechanisms that reduce Hg body burden, this seems unlikely (Evers et al. 2005). We propose that migratory distance is a more probable explanation. Mercury is unequally distributed across these birds ranges with a hotspot in the northeastern United States for example

(Evers et al. 2003) and if wing length is correlated with different breeding population subgeographies we could be documenting a latitudinal gradient in exposure in these species.

Common yellowthroats in our study showed a negative correlation between body mass gain and past Hg exposure. A previous study of northern waterthrush during fall migration attempting to quantify the correlation between Hg exposure and migratory mass gain did not find any correlation between the two variables (Seewagen 2013). Our study similarly found no correlation for this species, but we did find a relationship for yellowthroats. There is nothing to suggest this effect is widespread among all species and all situations, but these data indicate that such an effect is possible even at relatively low exposure levels and that the pattern varies by species. The mechanism for such a process is unclear given the many physiological pathways (neurological and endocrine) that could lead to such an effect (Scheuhammer et al. 2007, Adams et al. 2009, Frederick and Jayasena 2011).

#### **5.4.5. Synthesis Between Seasons**

The only factor that was consistently similar among the models for each was species. In both seasons, black-throated blue warbler Hg showed lower exposure levels than the other species. This suggests that the species-specific factors influencing Hg accumulation appear to be relatively consistent across the breeding and non-breeding seasons. Weather conditions were consistently unimportant in both seasons, suggesting that Hg exposure was not influencing the landing decisions of birds in our study.

Mercury exposure during the breeding season successfully predicted both fat and mass for some species during fall migration, but appeared to be unrelated to condition measurements during spring migration. We posit three general hypotheses for this discord. First, we cannot reject that our seasonal differences are due entirely to our different tissue endpoints for Hg quantification. Because blood is a metabolically active tissue, we were unable to test for the

effect of non-breeding exposure on spring migratory condition directly, but instead we tested for the composite effect of the end of the non-breeding season and the beginning of spring migration. Because it is reasonable to suppose that Hg exposure affects migratory performance directly, which in turn influences blood Hg levels, it will be difficult to interpret what blood Hg concentrations mean on migration without a more detailed understanding of the dynamics of this relationship. Add to this the increased variance in our blood signal relative to our feather signal, as described above, and our power to detect physiological effects during the spring migration was likely lower than it was during the fall.

Second, the magnitude of exposure documented in this study appears higher on the breeding grounds than the non-breeding grounds for most species and this could produce more harmful effects during fall migration. Using the blood to tail feather conversion in Jackson et al. (2011b) and the effect thresholds in Jackson et al. (2011a), we documented that the proportion of the northern waterthrush population over the lowest exposure limit was 3.6 times higher in the fall than the spring (see above for more detail). These are ecologically significant differences in exposure that could create more deleterious effects in the fall.

Third, songbirds migrate differently in fall and spring and these behavioral differences may change the relationship between Hg exposure and individual condition. Fall migration, tends to occur over a more protracted period, while spring is a hurried trip to the breeding grounds (Stutchbury et al. 2009). These differences in speed of migration influence how quickly birds have to refuel during stopover and change migratory behavior. During spring, birds are also investing in reproductive systems for the upcoming nesting season, which is an energetic expense that fall migrants do not incur that also significantly alters the birds physiology (Bauchinger et al. 2009, Tonra et al. 2013). With predicted higher energetic costs in the spring, we would expect the impacts of Hg exposure to therefore be higher in the spring relative to the fall, but our results suggest the opposite. Perhaps the relatively early timing of our sampling during spring migration

means that most birds are not developing their reproductive organs and are yet to incur these energetic costs. Overall, we think it is likely that effects are more difficult to detect during spring because of the potentially complex relationship between migratory physiology and blood mercury birds, our results lend credence to the idea that exposure levels were not high enough to achieve harmful effects in spring.

#### **5.4.6. Conclusions**

This study is the first to find correlations between migratory performance and Hg exposure in a wild population, and our results suggest that Hg exposure could be affecting migratory species in a more complicated manner than previously considered. We show clear relationships between Hg in the tissues of migratory birds and their physiological condition at daily, annual, and interannual time scales. Migration is period with high mortality where populations can be limited; that Hg can affect migratory performance suggests a new pathway by which Hg can affect animal populations. While blood and feathers have different strengths and weaknesses as Hg monitoring tissues, we think that migrating songbirds should be further explored as sensitive and cost-effective indicators of broad-scale species-level Hg exposure. The within day levels we show here and the suspected interactions between migratory behaviors with blood Hg make blood sampling less useful as an indicator of absolute Hg risk during the previous stationary period than feather sampling, though blood Hg concentrations ranked the relative risk among species similarly to feathers. Mercury is global contaminant but unevenly distributed across the landscape; some habitats have high sensitivity to the compound while others do not. Using a variety of songbird species that preferentially use different habitats during their sedentary times of year, Hg monitoring at migratory monitoring stations could be used to identify what habitats tend to accumulate high amounts of Hg.

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## **BIOGRAPHY OF THE AUTHOR**

Evan was born and raised in eastern Washington State. In the high desert, Evan learned at an early age the importance of understanding the environment in which we live when grasshoppers devoured his beloved strawberry plants. His desire to conduct science has taken him from particle physics and material sciences at a nuclear facility to understand the effect of environmental contaminants on wildlife to modeling populations of migratory birds. After the completion of his degree at the University of Maine, he will continue to work at the Biodiversity Research Institute as an ecological modeler where he tries to understand how wildlife interact with their environments and how changes to that environment influence their populations. Evan now lives in Gorham, ME with his wife Kate. He is a candidate for the degree of Doctor of Philosophy in Ecology and Environmental Sciences at the University of Maine in December 2014.