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# Behavioral Ecology of Landbird Migrants in a Complex and Changing Flyway System: The Gulf of Maine

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**BEHAVIORAL ECOLOGY OF LANDBIRD MIGRANTS IN A COMPLEX AND  
CHANGING FLYWAY SYSTEM: THE GULF OF MAINE**

By

Adrienne J. Leppold

B.S. California University of Pennsylvania, 2001

A DISSERTATION

Submitted in Partial Fulfillment of the

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## **DISSERTATION ACCEPTANCE STATEMENT**

On behalf of the Graduate Committee for Adrienne J. Leppold I affirm that this manuscript is the final and accepted dissertation. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

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were things worth smiling about;  
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# CHAPTER 1

## INTRODUCTION

Migration allows individuals to exploit seasonal changes in resources. Thus, as higher latitudes experience more disparate seasons, we would expect higher proportions of migrant individuals. In Maine, at 45° latitude in eastern North America, over 70% of all breeding bird species will migrate between northern boreal or temperate breeding areas to southern temperate, sub-tropical, or tropical wintering grounds twice a year (Newton 2008). As a result, large concentrations of birds during migration are common. In and around the Gulf of Maine, over 300 species of birds have been documented during migration. The Gulf of Maine and coastal area is an especially important region for millions of migrants during both spring and fall migration and serves as a nexus for many boreal breeding bird species whose migration routes intersect over the Gulf of Maine (Drury and Keith 1962, Hicklin 1987, Humphrey et al 1995, Leppold and Mulvihill 2011, Richardson 1978 and 1979). The natural orientation of the coastline (southwest to northeast) provides a leading line for migrant birds traveling to and from northern Maine and the eastern Canadian provinces (i.e. Nova Scotia and Newfoundland). Birds are also adapted to follow topographical features like coastlines regardless of the orientation (Åkesson 1993, Bruderer and Liechti 1998). Ecological barriers, such as oceans, may even attract birds (Berthold 1993). When migratory movements converge and funnel along a guiding line, as has been documented along the coast of New England, these mass migrations may develop into migration corridors or flyways (Baird et al. 1958, 1959, Berthold 1993).

Results from Baird's "Operation Recovery" project in the late 1950s provided the first evidence of this funneling effect of migrants, specifically landbirds, along the New England coast (Baird et al. 1958, 1959). In the Gulf of Maine, data collected from radar studies performed near Cape Cod, MA and in the Bay of Fundy in the 1960s and 1970s provided the first evidence that birds were making regular offshore movements over the Gulf during both spring and fall (Drury and Keith 1962, Drury and Nisbet 1964, Nisbet and Drury 1967, and Richardson 1978).

Drury and Keith (1962) documented birds in the fall having a southwestward flow, which follows the leading orientation line of the Gulf of Maine itself. Drury and Nisbet (1964) described fall migration near Cape Cod as a discrete broad front movement characterized by uniformity and consistency with birds arising from a southwesterly orientation. In 1978, Richardson found that while some birds departing from southern Nova Scotia changed course to avoid going offshore, many landbird migrants' departure orientation was to the south-southwest and west over the Gulf of Maine. Recent fall radar studies and orientation tests conducted from the southern tip of Nova Scotia supported Richardson's findings, showing birds heading west to southwest crossing the Gulf of Maine (Fitzgerald and Taylor 2008 and Peckford and Taylor 2008).

In the spring, Nisbet and Drury (1967) documented a northeastward movement trend, again following the leading orientation of the Gulf. Spring radar studies near Cape Cod (from Manomet Bird Observatory) in the early 1980s revealed similar patterns, with many birds orienting to the northeast and flying in a direction that followed the coastline (Williams et al 1981).

These studies collectively demonstrated bird activity in the Gulf of Maine, with individuals moving along the coast and making overwater movements across the Gulf and the Bay of Fundy. Concentrations of birds along coasts, the North Atlantic specifically (McClintock et al. 1978), have been well documented. Some, however, (Murray 1965, 1976) have cited that large numbers of landbirds at sea does not indicate a migration route over the area. These individuals may occur over the water simply as a result of wind drift. Sightings made from ships in the 1950s did not suggest regular movements of landbirds far offshore. Migratory flocks were only recorded on a couple of occasions, and, of the few isolated occasions when individuals were observed, “most did alight on the boats and died shortly thereafter, indicating exhaustion and probable disorientation” (Scholander 1955). The well-documented “coastal effect”, defined by the disproportionate numbers of hatch-year birds occurring along the north Atlantic coast in the fall, also may suggest that the majority of these birds are lost, off course, and doomed to perish (Ralph 1978, 1981).

While the majority of data collected from birds at coastal New England sites is from hatch-year individuals likely having made navigational (wind drift) errors (Baird and Nisbet 1960, Drury and Keith 1962, Leppold 2009, 2010, and 2011, Murray 1966, Morris et al. 1994), we expect the Gulf of Maine to serve as a confluence of wind drift individuals. As a rule, birds should tend to compensate more for wind drift only as they near their destination, which for many of Maine’s fall migrants is thousands of kilometers away (Liechti 2006, Zehnder et al. 2001). Importantly, there is also ample evidence to support that wind drifted birds over the Gulf of Maine are able to reorient and resume their migration in the seasonally appropriate direction (Able 1977, Åkesson 1993,

Alerstam 1978, Baird and Nisbet 1960, Bingman et al. 1982, Drury and Keith 1962, Richardson 1978). Thus, despite being over the Gulf of Maine as a result of wind drift, the coast appears to serve as a critical leading line for reoriented migrants to follow on their southward migration, a similar phenomenon to what Åkesson 1993, Berthold 1993, and Bruderer and Liechti 1998 describe for European migrants.

In addition to wind drift individuals, we know the Blackpoll Warbler (*Setophaga striata*), as well as many shorebird species, actively migrate over the western North Atlantic from New England directly to the South Indies and South America (Deluca et al. 2015, Richardson 1979, Williams and Williams 1978). The departure trajectories from some of the radar studies conducted from the southern tip of Nova Scotia and from Cape Cod, MA also supports this notion of many other individuals making purposeful overwater movements. Observations made from ships at sea in the North Atlantic documented a variety of passerine species far from the coast under conditions that would have required active southeast flight (i.e., conditions counter to those that would explain wind drifted individuals) (McClintock et al. 1978). Thus, migration and/or stopover patterns in the Gulf of Maine could be composed of three categories of individuals, 1) those making “purposeful” (intended) overwater movements (i.e., using route- and map-based navigation, Able 2001), 2) individuals using the shoreline as a leading line for migration (intended or reoriented piloting), or 3) “displaced” individuals present as a result of wind drift (Dingle 1996).

While the information provided by the studies cited above on migration activity around the North Atlantic provides some insight, the magnitude of migration documented by my 2009 pilot season was unexpected and made our lack of understanding the

complexity of migration in the Gulf of Maine apparent. Thus, the goal of my dissertation was to improve our understanding of factors influencing migratory behaviors in the Gulf of Maine, while also providing much needed baseline data for use in future impact assessments before and after development and for assessing population changes and range shifts related to climate change. More specifically, using stable hydrogen isotopes, I infer breeding origins for seven select boreal breeding species to identify populations that the Gulf of Maine flyway is serving as a catchment area for. I also evaluate factors explaining variation in occurrence of birds from differing origins (Chapter 2); I explore differences in physiological condition of migrants captured on island vs. mainland sites to identify priority stopover site placement (Chapter 3); and, lastly, using metabolite data collected from birds at an offshore island site, I test non-exclusive hypotheses to help identify migration strategies (time- vs. energy-minimizing) being employed within the region (Chapter 4).

### **Conservation Implications**

Though evidence is stronger for how migratory survival impacts populations in waterfowl (Owen and Black 1991, Ward et al. 1997), studies over the last decade have shown that events landbirds encounter on migration have the potential to limit populations (Butler 2000, Newton 2006 and 2007, Sillett and Holmes 2002, Wells 2007). Migratory birds depend on suitable and relatively reliable conditions along their migratory routes to meet the challenging physiological demands of migration. If conditions *en route* change and stopover sites or flyways become unsuitable or more challenging, this could result in increasing migratory costs and potential population scale losses. While fully documenting migration mortality is difficult, current estimates for



songbirds suggest more than 80% of annual mortality occurs on migration (Silleet and Holmes 2002). However, the relative importance of different sources of migration mortality is not well understood. Thus, it is imperative to piece together an understanding of regional migratory patterns if we are to minimize future or additional impacts on populations due to anthropogenic changes to the landscape. This is especially critical in areas that concentrate migrants and in areas that are adjacent to or in an ecological barrier (Newton 2008), like the Gulf of Maine. Information provided about migrant individuals *en route* to and from boreal habitats in North America will also be critical for recognizing climate related changes in bird populations and distribution (Leppold and Mulvihill 2011).

My hope is the results presented here will be applicable to 1) government agencies for use in making management decisions regarding migratory birds at a local, site-by-site scale and 2) improving our understanding of complex migratory patterns in the Gulf of Maine and Bay of Fundy region.

## CHAPTER 2

### WHERE DID THEY COME FROM? USING $\delta^2\text{H}$ ISOTOPES TO IDENTIFY MIGRATION PATTERNS IN THE GULF OF MAINE

#### Abstract

The Gulf of Maine is biologically significant, utilized by millions of landbird migrants each year, many of which come from remote areas of the boreal region and whose populations are in decline. Despite this, little is known about the populations of birds using the region during migration. With increased pressure from coastal development projects, a better understanding of regional migration patterns is critical. Here, we used stable hydrogen isotope signatures in feathers ( $\delta^2\text{H}_f$ ) collected from eight select boreal breeding species and a Bayesian assignment framework to depict putative breeding origins of individuals. We provide evidence, not previously documented, of individuals of multiple species utilizing the Gulf of Maine flyway that originated from as far north and west as the Yukon, Northwest Territories, and possibly even Alaska. To better understand migration patterns in the region, we also modeled other factors that might be sources of variation in  $\delta^2\text{H}_f$  using general linear models (GLM). Time of season was only significant for two of the eight species (Yellow-rumped Warbler and Swainson's Thrush), but only individuals coming from farther away were constrained by time, passing through the region later in the season. Age effects were only significant for Yellow-rumped Warblers, with adults having signatures reflective of populations originating much closer to the Gulf of Maine. Wind conditions were meaningful parameters in the top models for three species. For these species, northerly winds coincided with individuals having come from farther away. This result also provided

evidence of the absence of individuals originating near the Gulf of Maine under north winds, suggesting those individuals capitalized on tailwinds and crossed the Gulf in a single flight. While providing some insight into possible migration strategies for birds in the region, the lack of explanatory power for many of our chosen variables demonstrates the stochasticity and inherent management challenges for the Gulf of Maine flyway system.

### **Introduction**

The complexity of a landbird migrant's life cycle presents challenges for management. This is especially true for species that breed in remote areas, such as parts of Canada and Alaska, where Breeding Bird Survey coverage, for example, is limited (Bart et al. 2004, NABCI 2012). As a result, research efforts frequently utilize migration-monitoring data to identify range-wide population trends for landbird migrants. Migration monitoring, specifically counts and mist-netting, has been shown to be useful in estimating population trends (Dunn et al 1997, Hussell and Ralph 1998, Dunn et al. 2006). This is especially valuable at major migration flyways and stopover sites. The utility of these trends, however, is limited without understanding the connectivity of migrant populations at stopover sites. Conservation efforts can be better targeted once we understand the geographic structure (i.e., breeding origin) of the migrant populations used in trend analyses at a respective site (Dunn 2006, Osenkowski et al. 2012, Hobson et al. 2015).

Current estimates of songbird mortality suggest more than 80% of annual mortality occurs during migration (Sillett and Holmes 2002). While the relative importance of different sources of migration mortality is not well understood,

anthropogenic changes to landscapes can present confounding challenges for migrants and be very influential on an individual's migratory success (Newton 2006, Drewitt and Langston 2008). Effects of these changes may be amplified in major bird migration corridors where migrants concentrate (Alerstam and Hendenstrom 1998, Newton 2006, 2008).

Coastal shorelines are widely documented as major bird migration corridors. Ample evidence exists that coastal areas concentrate migrants, and many species make overwater movements (Berthold 1993, Lincoln et al. 1998). Despite the known importance of coastal flyways to migratory birds, little is known about landbird migration patterns within the Gulf of Maine (GOM). Large groups of birds have been documented moving along the coast and making overwater movements across the GOM and Bay of Fundy during both spring and fall migration (Drury and Nisbet 1964, Richardson 1978, Williams et al. 1981, Morris et al. 1994 and 1996, Peckford and Taylor 2008). Much of this research, however, lacks detail about species diversity and prior to Holberton and colleagues (2015), none of it links migrants using the GOM flyway to specific breeding origins. With increasing pressure for energy resource development and changes in coastal land use and planning throughout the GOM (University of Maine and J.W. Sewall Company 2011, Schauffler 2013), a better understanding of regional migration patterns is necessary to make informed management and development decisions.

Our main objective here was to use stable hydrogen isotope signatures in feathers ( $\delta^2\text{H}_f$ ) to infer breeding origins for select migrant species in the Gulf of Maine, eight boreal breeding species (including two sub-species), in particular. We defined boreal breeding species, following Blancher and Wells 2005, as those having 50% or more of

the global breeding population occurring in the boreal regions of North America (see Methods below).  $\delta^2\text{H}_f$  has been successful in demonstrating latitudinal variation in breeding origin for a number of migratory bird species (cf., Hobson and Wassenaar 2008, Van Wilgenburg and Hobson 2011) and most recently was used in characterizing catchment areas (i.e., breeding origins) for select species captured at 22 different Canadian Migration Monitoring Network (CMMN) stations (Hobson et al. 2015).

In addition to mapping origins of migrants captured in the Gulf of Maine, we evaluated three different factors' ability to explain variation in the isotopic signatures. First,

Birds originating from different breeding populations may migrate through a given region at different times of the season. Dunn and colleagues (2006) found northern populations tended to migrate through southern Canada later in the season, such that population trends could be calculated separately for birds from different catchment areas. As a result, conservation efforts could be targeted for populations of greatest concern. We do not know if this pattern persists at migration sites farther south, but based on their findings, we predict the same.

Second,

In addition to testing for seasonal patterns, we investigate whether local scale wind conditions explain any daily variation in isotopic signatures for each of our eight boreal focal species. Daily changes in wind patterns might also differentially influence routes traveled by migratory birds from different populations (Able 1973, Åkesson and Hedenström 2000). Aside from precipitation, wind conditions have been shown to affect migrant's departure decisions the most (Åkesson et al. 2002, Richardson 1978, 1990a,

and references therein). The strength or weakness of tailwinds, headwinds, and crosswinds, in particular, is known to affect migration behavior in birds (Liechti 2006).

Third,

It is possible that isotopic variation could simply be explained by age differences, given the well-known “coastal effect” documents young birds, be more susceptible to wind drift, concentrating along the coast (Ralph 1981). Under this scenario, we expect  $\delta^2\text{H}$  signatures in young individuals to be more heterogeneous and adult signatures to be reflective of origins closer to the Gulf of Maine. This region would be an expected migratory route for adults departing breeding sites in northeastern North America but would mark the periphery of a migratory route for birds originating farther inland.

Examining temporal (both seasonal and daily) and age related variation in isotopic signatures of Gulf of Maine migrants could provide insights into understanding migratory decisions of birds in the region. Our objective for this work was to identify conditions under which populations of special concern might be most at risk to changes in coastal land use practices.

## **Methods**

### **Sample Collection**

We established a banding station on Metinic Island, part of Maine Coastal Islands National Wildlife Refuge in mid-coast Maine (43.8833° N, 69.1250° W), and monitored migration activity from mid-August through mid-October 2009-2011 (see Appendix A). We collected feathers for use in stable isotope analyses from eight (including two subspecies) boreal breeding landbird taxa as part of routine migration banding operations, which included the taking of standard morphological measurements (e.g., body mass,

wing length, etc.) and age and sex, when possible. Individuals were aged as hatch year (HY-young) or after-hatch-year (AHY-adult) using wing molt limits and skull pneumatization patterns (Pyle 1997).

The focal species for this study were Magnolia Warbler (*Setophaga magnolia*-MAWA), Blackpoll Warbler (*S. striata*-BLPW), Yellow-rumped “Myrtle” Warbler subspecies (*S. coronata coronata*-MYWA), Western- and Yellow- Palm Warbler (*S. palmarum palmarum* and *S. p. hypochrysea*.-WPWA/YPWA ), Swainson’s Thrush (*Catharus ustulatus*-SWTH), Hermit Thrush (*C. guttatus*-HETH), and Dark-eyed Junco (*Junco hyemalis*-DEJU). We chose these species to include representatives from different taxonomic families, short- and long-distance migrants, and to also focus our attention on some species suffering known population declines within the boreal region (Sauer et al. 1996, 2014, Crewe et al 2008, Environment Canada 2014).

To be confident sample signatures reflected breeding ground origin, we confirmed in the literature that all species except SWTH complete molt entirely or primarily on the breeding grounds prior to migration (Dunn and Garrett 1997, Pyle 1997). While SWTH can molt during the early parts of fall migration, by their arrival during migration in Maine, all individuals sampled had completed molt, and since all but five SWTH were hatch year birds, for which flight feather molt completes in the nest or shortly thereafter on the breeding grounds (Mack et al. 2000), we feel confident the sample signatures reflect breeding ground origin.

After investigating feathers for sign of loss and replacement, we plucked the right or left third retrix (R3) for all species except Blackpoll Warbler. Because feather loss and molt migration have been shown to influence flight performance, ability to maintain

mass, and are associated with increased mortality risk (Lindstrom et al. 1993, Jenni and Winkler 1994, Holmgren and Hedenström 1995, Swaddle and Witter 1997), we collected upper back (between the scapulars) and nape feathers from BLPW to avoid plucking a flight feather from this known trans-oceanic migrant (Deluca et al., 2015). We made *ad-hoc* decisions when sampling individuals to avoid biases in age or sex class, time of day, or time of season. Feathers were stored in paper envelopes and kept dry until analyzed.

Of note, the same BLPW data used in this study was used by these authors in Holberton et al. 2015 to compare catchment areas of Gulf of Maine BLPWs to BLPWs captured at five other sites outside of Maine.

### **Stable Hydrogen Isotope Extraction**

Whole feathers were cleaned, weighed, and analyzed for  $\delta^2\text{H}$  at the Stable Isotope Laboratory of Environment Canada, in Saskatoon, Canada using standard procedures for isotope ratio mass spectrometry (IRMS), including using calibrated keratin hydrogen isotope reference materials (see Wassenaar and Hobson 2003, Hobson and Wassenaar 2008). All results for non-exchangeable  $^2\text{H}_f$  are expressed with delta notation ( $\delta$ ) in units per mil (‰) and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale.

### **Statistical Analysis**

#### Map assignments of geographic origin

Growing season hydrogen isotope precipitation values (hereafter  $\delta\text{H}_p$ , Bowen et al. 2005) were modeled into a  $\delta^2\text{H}_f$  isoscape using the calibration equation from Clark et al. 2009. We addressed common analytical and spatial assignment sources of error by using likelihood based density models within a Bayesian framework (Royle and Rubenstein



2004, Hobson et al. 2009). Likelihood based assignment models help overcome the limitation presented by the low longitudinal resolution of  $\delta^2\text{H}_p$  across the landscape (Van Wilgenburg and Hobson 2011). We computed assignment models separately for each species.

There is evidence that breeding ground abundance data, like that obtained from the Breeding Bird Atlas (BBS), helps restrict geographic origin probability assignments when incorporated as priors in Bayesian assignment probability maps (Hobson et al. 2007, Hobson et al 2014). Hobson and colleagues (2014) encourage using BBS data, but they also caution using this approach for species where many individuals might breed north of BBS covered region. For the same reason that many of our chosen species are not well monitored through much of their northern breeding range, incorporating breeding bird atlas data for these species would likely result in a southerly bias of mapped origins, especially given our sample sizes. Instead, to improve the resolution of the assignments, we used digital range maps, provided by Ridgeley and colleagues (2011) and Bird Life International and constrained catchment areas to biologically plausible origins. Of note, the range map used in the assignment methods for YPWA and WPWA was for *Setophaga palmarum* and not resolved at the sub-specific level.

For each individual sample (bird), we used a normal probability density function (Van Wilgenburg and Hobson 2011, Hobson et al. 2012, 2014) to assess the likelihood that each cell (i.e. map pixel) of the  $\delta^2\text{H}_f$  isoscape represented a potential origin for the individual. This resulted in a set of spatially explicit probability densities for each individual that were used to determine the odds that a given assignment origin (i.e. map raster cell) was correct (following Hobson et al. 2009). We then recoded any raster cells

that were consistent with the upper 67% of estimated ‘probabilities of origin’ for each sample as ‘1’ and all others as ‘0’. Thus, each sample (i.e., bird) could be assigned to multiple potential origins based on the 2:1 odds ratio. Finally, we summed the results of each individual assignment within a species to depict a probability surface of likely vs. unlikely individual origins (Hobson et al. 2009, Van Wilgenburg and Hobson 2011).

We used functions in the raster (Hijmans and Van Etten 2012), maps (Becker and Wilks 2015), maptools (Bivand and Lewin-Koh 2015), and shapefiles (Stabler 2013) packages of the R statistical computing environment for this analysis (R Core Team 2016).

#### Modeling variation in isotopic signature

Instead of using Julian Day to assess timing of movement through the region, we calculated the median passage date for each species within each year then subtracted the capture date from the median. This resulted in our seasonal timing metric (passage day) being a range of values from -30 to 30; the median passage day was ‘0’, passage day for birds captured prior to that were negative values (i.e., early migrants) and after that were positive values (i.e., late migrants). This accounted for intraspecific differences in the timing of movements among years.

Following visual inspection of the data, there were two noticeable outlier values for Palm Warbler, one each for YPWA and WPWA. We removed these two values *a priori* to analysis because the outliers fell within the range of values expected for each conspecific subspecies. It is possible that an individual was misidentified based on plumage characteristics alone.

Prior to analyses with our variables of interest, we used a GLM to evaluate possible confounding factors in explaining variation of  $\delta^2\text{H}_f$ . We included passage day, migration distance (short vs. long), foraging guild (primarily foraging on or within one meter of the ground or not), age, and year because these factors have been documented sources of isotopic variation in other studies (Hobson et al. 2012, Reichlin et al 2010). We based foraging and distance classifications on information available in the Birds of North America species accounts (Poole 2005, Table1).

Following Zuur and colleagues (2009), we used a series of stepwise regression models with backward selection to evaluate each factor and were left with passage day and age. For all subsequent temporal analyses presented here, we removed migration distance, foraging guild, pooled years, and include only passage day and age, along with the wind factors, as our variables of interest.

#### Passage day seasonal effects – Quantile Regression

In looking for possible seasonal patterns, we used passage day as our explanatory variable to assess whether birds from different origins were moving through the region at different times. Because we simplified the ‘seasonal’ analysis to a single explanatory factor, it is possible that relationships among the measured variables were incomplete or lost. Given the heterogeneous variance in the distribution of our data by day, we used quantile regression to test the 10<sup>th</sup> (T= 0.1) and 90<sup>th</sup> quantiles (T=0.9), thereby testing the lower (e.g., birds from far away) and upper (e.g., birds nearer to GOM) limits for each species (Cade and Noon 2003). We used the ‘rq’ function from the quantreg package (Koenker 2015) for the quantile regression analyses with bootstrapping to generate the reported statistics (R Core Team 2016).

### Age and ‘daily’ wind effects – Model Selection

We used a suite of ten candidate models in a general linear model (GLM) framework to evaluate the effect of age and daily changes in wind conditions on  $\delta^2H_f$ . Because WPWA and HETH did not have enough age structure in their samples, we only tested six candidate models for these two species (see Appendix B). Passage day was included in the ‘daily’ models to account for changes in conditions throughout the season that were unmeasured and to also deal with the variation discovered in the quantile regression analyses.

We recognize many other meteorological factors can influence birds’ migratory behavior and ultimately patterns of bird migration. However, we predict wind characteristics, alone, would be the weather variable most closely related to where a bird may have originated. We used local climatological data collected at the Knox County Regional Airport, Rockland, ME (44.060° N, 69.085° W, ~17km north of Metinic Island) and downloaded from the NOAA weather data center web site (<http://www.ncdc.noaa.gov/oa/ncdc.html>). To deal with problems of circularity, following Jammalamadaka and Gupta (2001) and Jammalamadaka and Lund (2006), we converted angular degree directions and wind speed into vector units (u/v), where ‘u’ represented the east-west component and ‘v’ the north-south component. Wind vectors were calculated for conditions at sunrise (SR) the morning of capture and the preceding night at sunset (SS).

We visually assessed residual distribution plots to validate each of the top selected models. No transformations were necessary. Models were selected by second-order Akaike’s Information Criteria (AICc) model weights for small sample sizes following

Bolker 2008 and Zuur et al. 2009. We considered top models to be those within 2 AIC of the most parsimonious model (Burnham and Anderson 2003, Bolker 2008). We used the `bbmle` package in R for calculating all AIC values and weights (Bolker 2014).

For species where there was more than one competing model, we compared parameter estimate strength, sign, and significance. In all cases, values were similar. We refrained from model averaging because we were not interested in making predictions, and the models were not tested within a hypothesis framework. For reader convenience, we present the  $\beta$  coefficients, standard error estimates (SE), and confidence intervals (CI) for parameters in each of the competing models.

## **Results**

We analyzed 413 feather samples. Table 2.1 provides individual species' sample sizes and descriptive statistics, as well as the natural history category assignments. Overall, 16% of our samples indicated bird origins north and west of Manitoba (i.e.,  $\delta^2\text{H}_f < -120^{0/00}$ ), however the majority of these were from only two species, BLPW and DEJU (Figure 2.1). Mean  $\delta^2\text{H}_f$  values for these two species were  $-127.7^{0/00}$  and  $-114.3^{0/00}$ , respectively, indicating points of origin near the 60<sup>th</sup> parallel. Mean  $\delta^2\text{H}_f$  values for all other species fell between  $-90^{0/00}$  and  $-101^{0/00}$ , near the 50<sup>th</sup> parallel.

Table 2.1. Species codes, sample sizes, summary statistics, and natural history classifications - foraging guild assignments (primarily foraging on or within one meter of the ground or not) and migration distance categories (short vs. long) by species. Age (hatch year - HY or after-hatch year - AHY) was only used in analyses for species with at least five individuals in each sub-class. Data were pooled across all years of the study and summary statistics (mean, SD, and 95% CI of the means) for  $\delta H$  are provided.

Species	Sp. Code	n	Age		Mean $\delta H$ ‰ (SD)	95% CI	Foraging Guild	Migr. Distance
Blackpoll Warbler	BLPW	40	16	24	-127.7 (32.2)	±9.99	Not ground	long
Magnolia Warbler	MAWA	55	11	44	-91.9 (14.2)	±3.76	Not ground	long
Myrtle Warbler	MYWA	88	50	38	-91.8 (16.8)	±3.52	Not ground	short
Yellow-Palm Warbler	YPWA	56	12	44	-79.1 (12.9)	±3.37	Ground	short
Western-Palm Warbler	WPWA	29	1	28	-101.0 (11.1)	±4.04	Ground	short
Hermit Thrush	HETH	43	3	40	-92.5 (15.4)	±4.61	Ground	long
Swainson's Thrush	SWTH	31	5	26	-96.9 (22.4)	±7.9	Ground	long
Dark-eyed Junco	DEJU	71	11	60	-114.3 (19.2)	±4.46	Ground	short

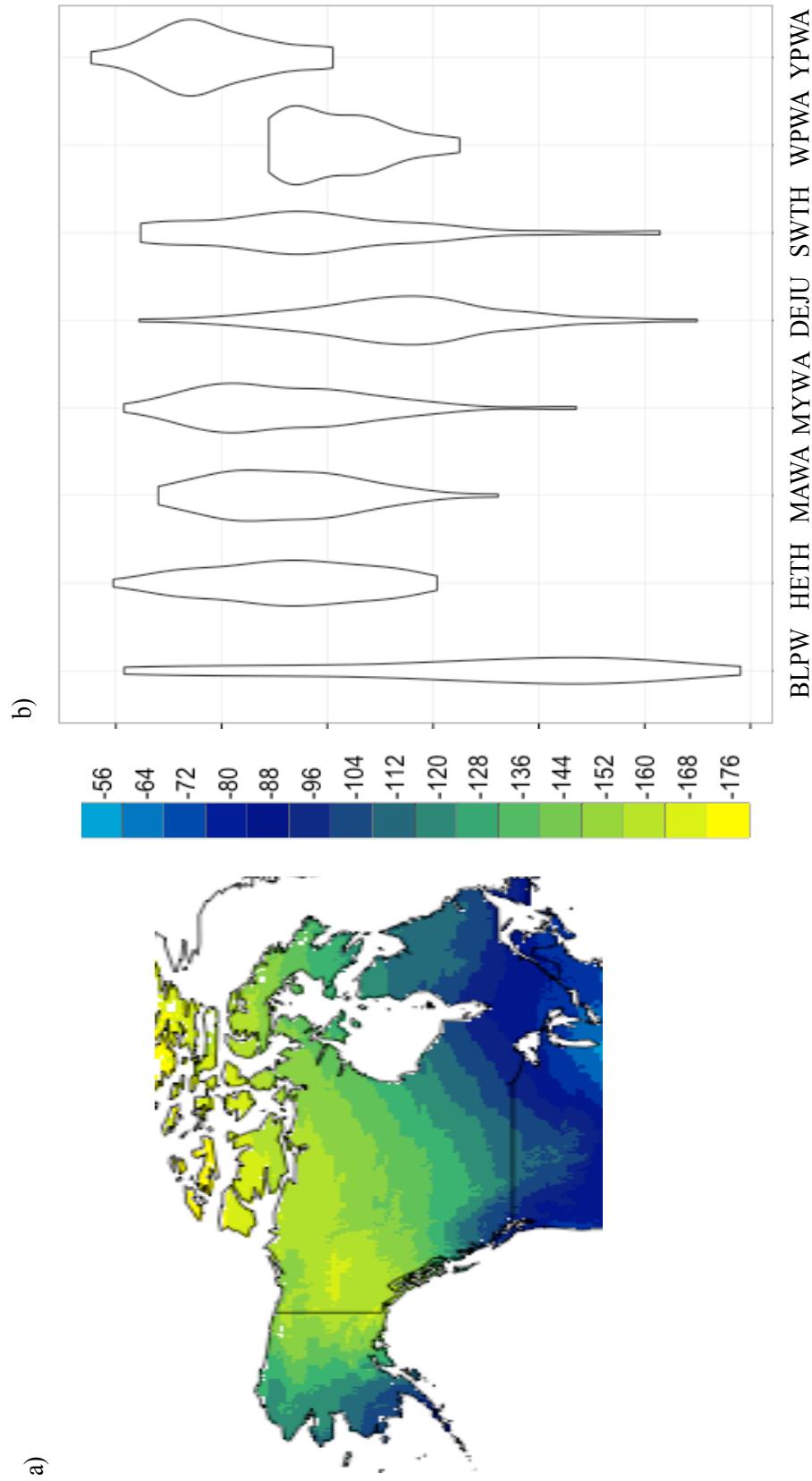


Figure 2.1 Distribution of  $\delta^2\text{H}$  feather isoscapes a) Predicted feather  $\delta^2\text{H}$  isoscapes for North American passerines from the boreal region (see Hobson et al., 2015). b) The relative distribution of  $\delta^2\text{H}_r$  for migrant birds captured on Metinic Island during the Fall 2009-2011 migration seasons.

## Map Assignments

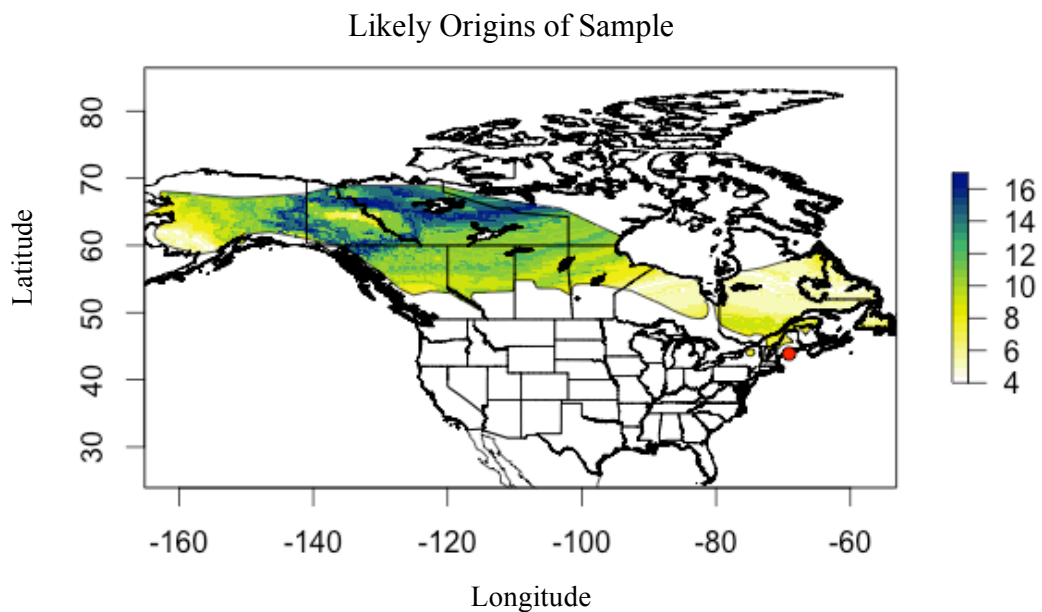
The likelihood based assignment methods using breeding range boundary restrictions were effective in narrowing the possible areas of origin for the eight focal species. We note, while the assignments for three species (MYWA, SWTH, and HETH) suggested the Rocky Mountains between 30° and 50° latitude as a possible site of origin, this is likely only a product of species' ranges extending into this region and the Rocky Mountains being isotopically similar to the true boreal origins of each of these species (Figures 2.2 c, f, g). It is reasonable that individuals from the western mountains of the U.S. would not be using the Gulf of Maine as a migratory flyway. Probable catchment area maps are shown in Figures 2.2 a-h, but we have summarized predominant patterns for the species here.

Overall, the most common catchment area for most of the species was throughout southern Ontario and Québec, east and west of the Hudson Bay. MAWA, MYWA, and YPWA were the only species to show evidence of origins in northern New England, in or near Maine, with few to no individuals originating from the western portion of their breeding ranges (Figures 2.2 b, c, and d). As expected, WPWA had more expansive northerly origins than YPWA (Figures 2.2 d and e).

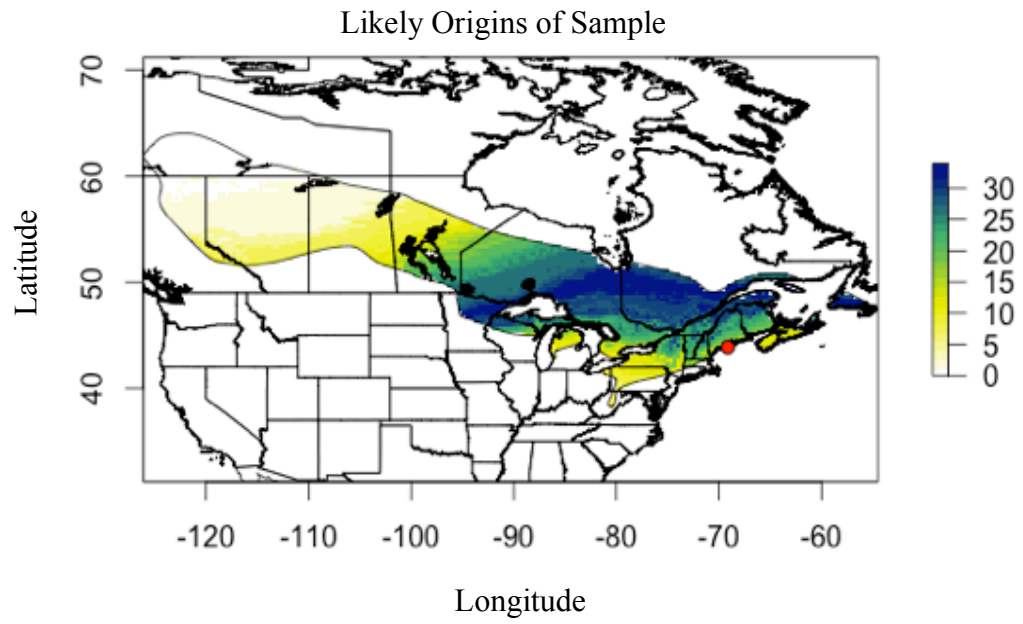


Fig 2.2 a-h. Likelihood-based assigned breeding or natal origins, inferred from analysis of  $\delta^2\text{H}_f$ , for Blackpoll Warbler (BLPW), Magnolia Warbler (MAWA), Yellow-rumped “Myrtle” Warbler (YRWA), Yellow Palm Warbler (YPWA), Western Palm Warbler (WPWA), Hermit Thrush (HETH), Swainson’s Thrush (SWTH), and Dark-eyed Junco (DEJU) captured on fall migration at Metinic Island (red dot). The legend scale depicts the number of birds in each sample that were isotopically consistent with each pixel in the map based upon the likelihood assessment (see Methods for details), thus, providing visual estimates of where birds captured in the Gulf of Maine are most likely from. Note, each map was constrained by the individual species’ breeding range, so maps are magnified to different scales. It is reasonable to assume YRWA, SWTH, and HETH assigned to the Rockies between 30° and 50° latitude were because of the similar precipitation isoscapes between this region and the boreal breeding range of these species and is not reflective of individuals actually originating from those areas.

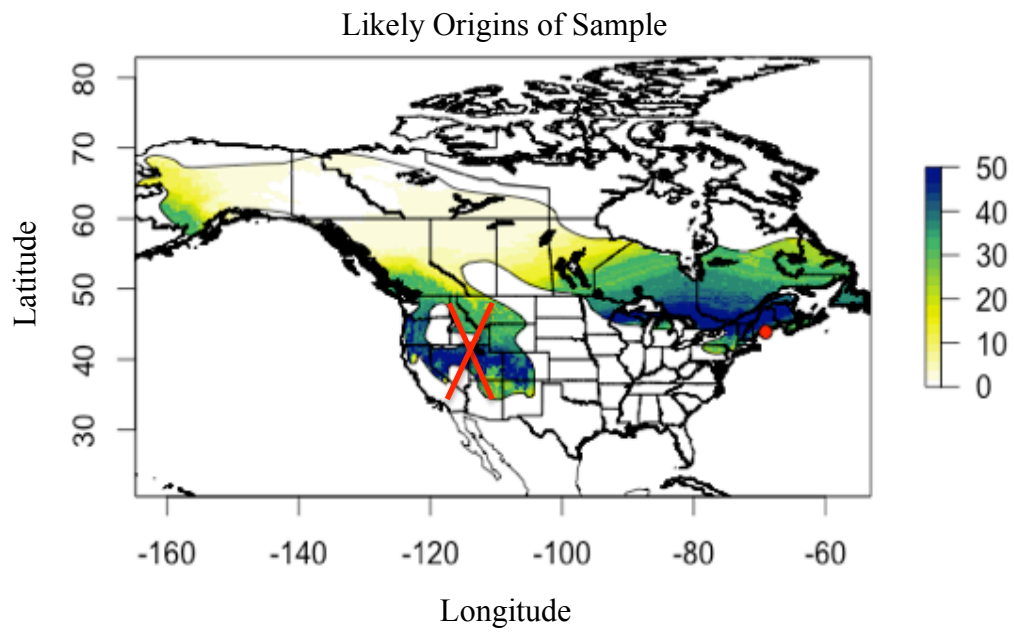
a) BLPW



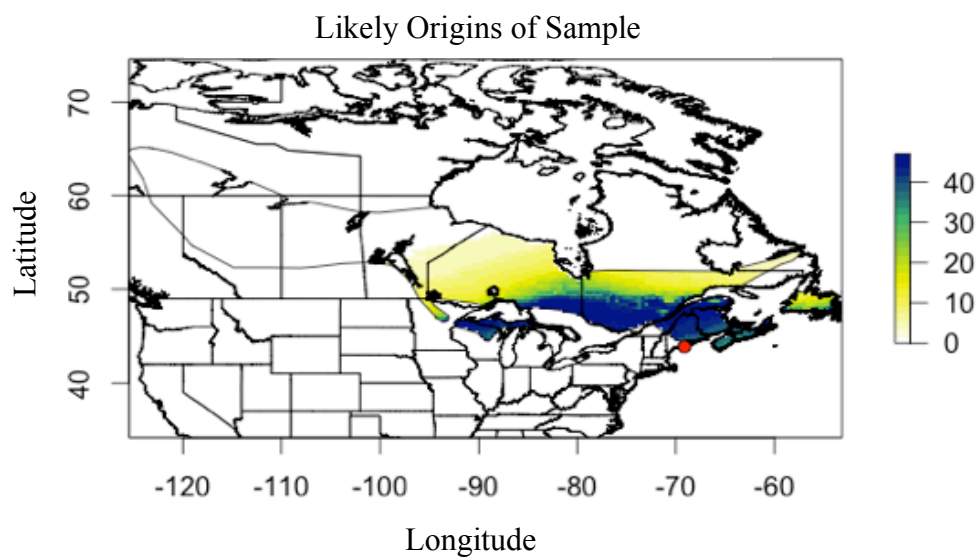
b) MAWA



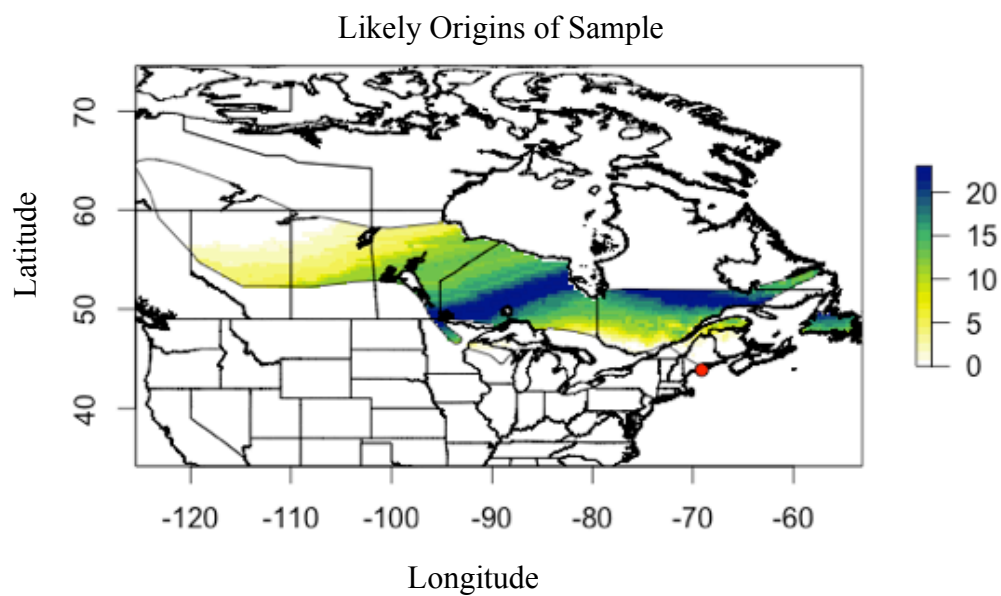
c) MYWA



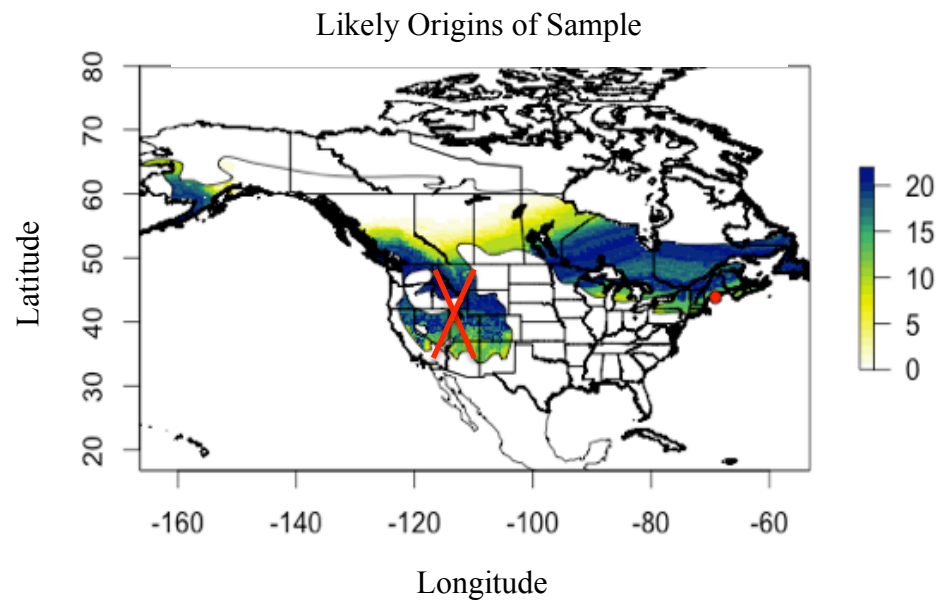
d) YPWA



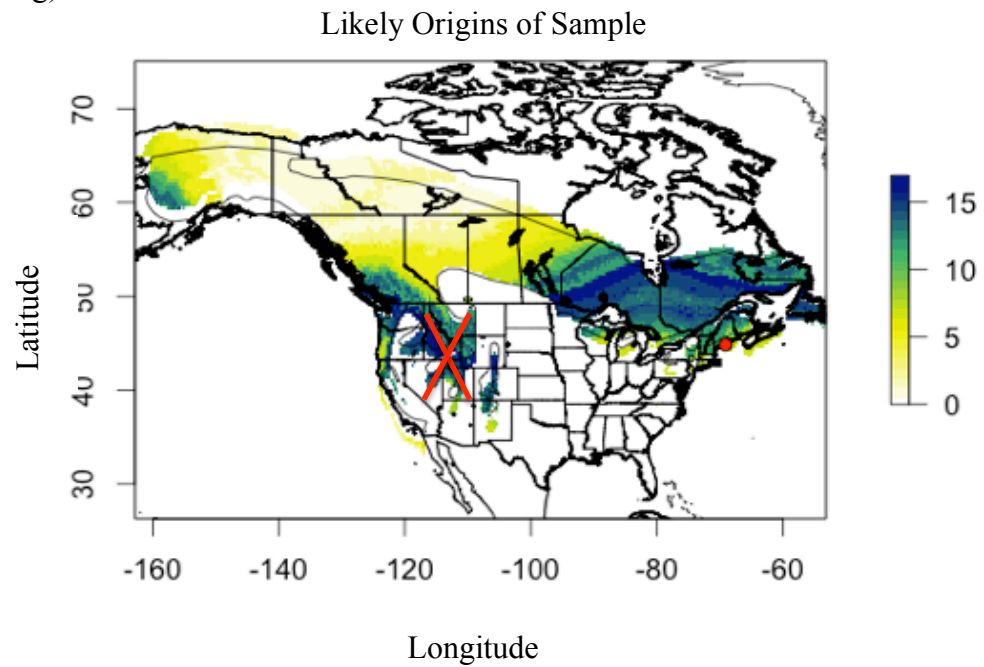
e) WPWA



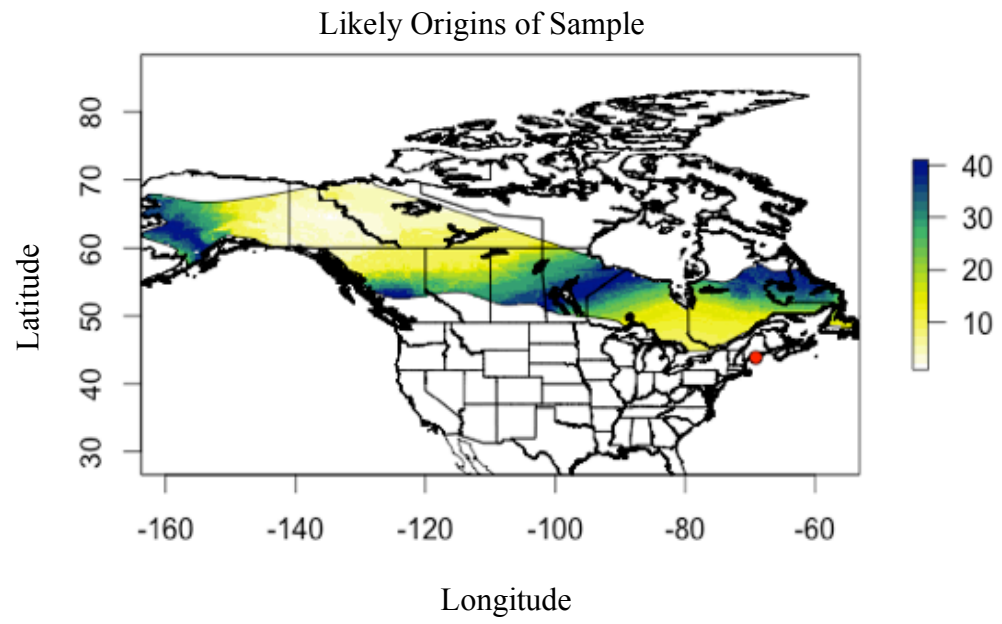
f) HETH



g) SWTH



h) DEJU



Unlike most of the other species, HETH did not have distinct regions or bands of probable origins but spanned almost all of Ontario and central Québec. The Alaska Peninsula also showed a high probability of origin for this species, but this is likely a product of isotopic similarities with the eastern, and more probable, points of origin within the HETH breeding range. The map assignment for SWTH suggested two dense probability bands, one spanning longitudinally from northern Maine across to just north of the great lakes. The second band suggested a strong source origin just north of 50° latitude (Figure 2.2f).

### **Modeling Variation in Isotopic Signature**

#### Passage day seasonal effects – Quantile Regression

After calculating quantile regressions for each species separately to evaluate the relationship between date and  $\delta^2\text{H}_f$ , we found only SWTH ( $t=-1.93$ ,  $p=0.04$ ) and MYWA ( $t=-2.70$ ,  $p<0.01$ ) slopes in the lower 10<sup>th</sup> percentile were different from zero (Figure 2.3). For both of these species, birds from farther away appear to be constrained by date. Results from of the 90<sup>th</sup> percentile showed, for all species, that birds originating nearer to the Gulf of Maine occurred throughout the entire season (Table 2.2). These results, however, were derived from low quantile samples, in the case of some species, fewer than four individuals. In general, quantile regressions require larger sample sizes than ordinary least squares regression. While the results do appear fairly robust, more data points would likely narrow the confidence interval range (Table 2.2).

Table 2.2. Quantile regression results and significance, by species, for the 10<sup>th</sup> and 90<sup>th</sup> quantile analyses of passage day on  $\delta^2\text{H}_f$ . Slope confidence intervals from bootstrapping are in parentheses. \* significant at  $p < 0.05$

Species	10 <sup>th</sup> Quantile			90 <sup>th</sup> Quantile		
	Coefficient	t-value	p-value	Coefficient	t-value	p-value
BLPW	-0.67 (-1.87-1.19)	-0.71	0.48	-0.52 (-1.15-0.17)	-0.62	0.54
MAWA	-0.46 (-0.68-0.46)	-1.36	0.18	0.16 (-0.45-0.19)	0.46	0.65
MYWA	-0.67 (-0.88- -0.30)	-2.70	< 0.01*	0.07 (-0.65-0.17)	0.28	0.78
YPWA	-0.44 (-1.58-0.21)	-0.70	0.49	-0.16 (-0.83-0.31)	-0.33	0.74
WPWA	0.01 (-1.28-0.83)	0.15	0.88	-0.13 (-0.17-0.29)	-0.88	0.39
HETH	-0.09 (-0.15-1.94)	-0.11	0.91	-0.32 (-3.31-1.06)	-0.43	0.67
SWTH	-2.38 (-2.80- -1.24)	-2.91	< 0.01*	-0.18 (-6.45- -0.14)	-0.20	-0.84
DEJU	-0.41 (-0.81-0.87)	-0.58	0.56	-0.49 (-1.69- -0.13)	-0.85	0.39

#### Age and ‘daily’ wind effects – Model Selection

The amount and source of variability explained by top models ( $\Delta\text{AIC}_c < 2.0$ ) differed greatly among species. The null was the single best-fit model for WPWA ( $\text{AIC}_c \omega_i = 0.61$ ) and BLPW ( $\text{AIC}_c \omega_i = 0.56$ ), suggesting none of the chosen parameters explained variation in  $\delta^2\text{H}_f$  for those species (Table 2.3). In fact, for YPWA and HETH, while not the top selected model, the null fell within two  $\Delta\text{AIC}_c$  values of the best fit for these species as well. YPWA had no significant parameters (Table 2.4) and though the north wind component was significant for HETH, we are cautious about interpretation because of model uncertainty. Of the four remaining species, there were significant age effects only for MYWA, with adults having signatures representative of populations originating much closer to the Gulf of Maine, as was predicted (Table 2.4).

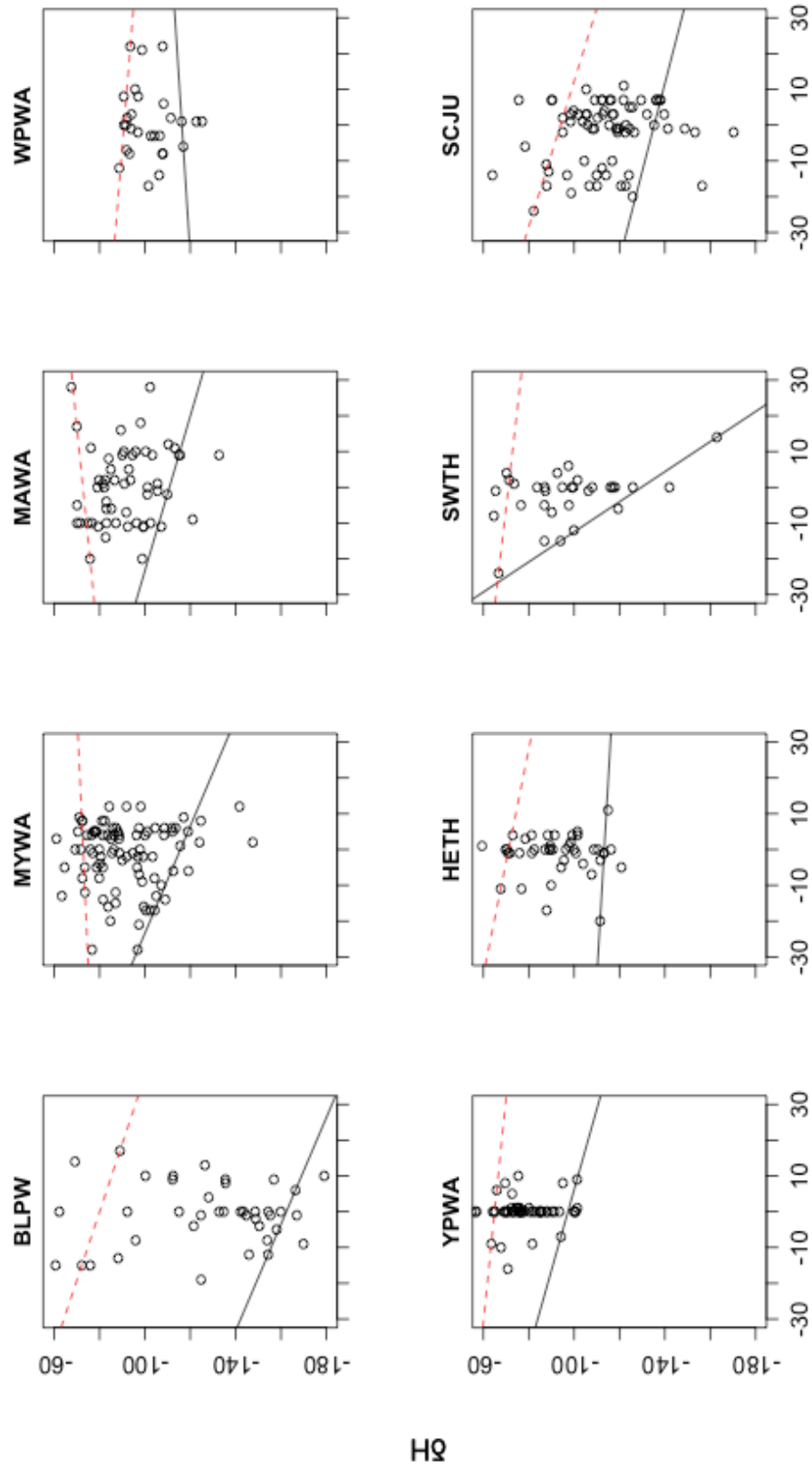


Figure 2.3. Quantile regression plots depicting variation in  $\delta H_f$  by passage day (i.e., before or after the median capture date) for each species. Regression lines for the lower 10<sup>th</sup> quantile and the upper 90<sup>th</sup> quantile are dashed/red.



Table 2.3. Model parameters and AIC values from the best-fit models for each individual species. Only models with  $\Delta AIC < 2$  are presented here. A complete list of candidate models and selection values is provided in Appendices 1.1-1.9.  $K$  = number of estimated parameters,  $AICc$  = Akaike's Information Criterion with second-order bias correction for small sample sizes,  $\Delta AICc$  = difference in  $AICc$  relative to the most parsimonious model, and  $\omega_i$  denotes  $AICc$  weight. WPWA and HETH did not have enough variation in age structure to include candidate models. SS denotes conditions at sunset, SR denotes conditions at sunrise, 'u' is the east/west wind component (where '0' is no wind, a negative value indicates winds from the east, and larger vector values indicate stronger winds), and 'v' is the north/south wind component (where '0' is no wind, a negative value indicates winds from the north, and larger vector values indicate stronger winds).

Species	Model	$K$	$AICc$	$\Delta AICc$	$\omega_i$
BLPW	Null model (Intercept only)	2	394.7	0.0	0.56
MAWA	Passage Day + Age + SR u/v	6	441.1	0.0	0.54
MYWA	Passage Day + Age + SS u/v	6	738.5	0.0	0.39
	Age + SS u/v	5	739.7	1.2	0.21
	Passage Day + Age + SR u/v	6	739.7	1.2	0.21
	Age + SR u/v	5	739.9	1.5	0.19
WPWA	Null model (Intercept only)	2	212.7	0.0	0.61
YPWA	Age + SS u/v	5	428.7	0.0	0.24
	Null model (Intercept only)	2	429.1	0.4	0.20
	SS u/v	4	429.7	0.9	0.15
	Passage Day + Age + SS u/v	6	429.8	1.1	0.14
HETH	SS u/v	4	353.1	0.0	0.32
	SR u/v	4	359.5	0.2	0.29
	Null model (Intercept only)	2	360.6	1.3	0.17
SWTH	Passage Day + SS u/v	5	276.7	0.0	0.64
DEJU	Age + SR u/v	5	618.1	0.0	0.26
	Age + SS u/v	5	618.6	0.5	0.21
	Passage Day + Age + SR u/v	6	619.2	1.1	0.15
	Passage Day + Age + SS u/v	6	619.8	1.7	0.11

Wind conditions at sunset and sunrise appeared in the remaining species' models, but only the northerly component ( $v$ ) was a significant parameter and only for MAWA ( $\beta=1.87\pm0.97$ ), MYWA ( $\beta=0.55\pm0.54$ ), and DEJU ( $\beta=1.23\pm0.96$ ). The timing of the significant wind parameter (sunrise or sunset) varied among the three species, but in all cases stronger northerly winds were correlated with individuals having inferred origins from farther away ( $p < 0.01$ ). Conversely, this indicates a relationship between less favorable, southerly winds and the capture of individuals, of these three species, originating from locales nearer to the Gulf of Maine.

Interestingly, the two 'top' MAWA models (Table 2.3) contained passage day as a significant variable (Table 2.4), the trend only becoming apparent when controlling for age and daily variation in weather conditions. The negative slope result matched our prediction of individuals from farther north and west (i.e., more negative  $\delta^2H_f$  signatures) passing through the region later in the season and also matched our quantile regression findings for MYWA and SWTH. When included in models with age and weather, however, model selection resulted in losing the passage day pattern for MYWA.

Table 2.4. Parameter estimates examining variation in  $\delta H_f$  for each species are presented (separated by commas) for each of the top model(s) as well the standard error (SE). Where a given parameter was absent from the, NA serves as its placeholder. SS refers to conditions at sunset, SR conditions at sunrise, ‘u’ is the east/west wind component (where ‘0’ is no wind, a negative value indicates winds from the east, and larger vector values indicate stronger winds), and ‘v’ is the north/south wind component (where ‘0’ is no wind, a negative value indicates winds from the north, and larger vector values indicate stronger winds). Only estimates from models with  $\Delta AIC < 2$  are presented. Bold typeface denotes a meaningful model parameter.

Species	Parameter	Coefficients	SE
BLPW	Intercept only	Null	
MAWA	<b>Passage Day</b>	<b>-0.40, -0.33</b>	$\pm 0.16$
	Age	-8.5, NA	$\pm 4.33$
	SR – ‘u’	0.21, 0.37	$\pm 0.45$
	<b>SR – ‘v’</b>	<b>1.88, 1.74</b>	$\pm 0.48$
MYWA	Passage Day	-0.36, NA, -0.31, NA	$\pm 0.19$
	<b>Age</b>	<b>-14.37, -12.16, -14.49, -12.75</b>	$\pm 3.52$
	SS – ‘u’	-0.04, -0.03, NA, NA	$\pm 0.46$
	<b>SS – ‘v’</b>	<b>0.55, 0.59, NA, NA</b>	$\pm 0.27$
	SR – ‘u’	NA, NA, 0.26, 0.44	$\pm 0.53$
	SR – ‘v’	NA, NA, 0.49, 0.56	$\pm 0.30$
YPWA	Passage Day	NA, NA, NA, -0.42	$\pm 0.40$
	Age	6.57, NA, NA, 7.03	$\pm 3.66$
	SS – ‘u’	-0.53, NA, -0.59, -0.47	$\pm 0.45$
	SS – ‘v’	-0.36, NA, -0.37, -0.37	$\pm 0.27$
WPWA	Intercept only	Null	
HETH	SS – ‘u’	-0.07, NA	$\pm 0.62$
	<b>SS – ‘v’</b>	<b>1.53, NA</b>	$\pm 0.62$
	SR – ‘u’	NA, 0.27	$\pm 0.70$
	SR – ‘v’	NA, 0.99	$\pm 0.41$
SWTH	<b>Passage Day</b>	<b>-1.41</b>	$\pm 0.59$
	SS – ‘u’	-0.21	$\pm 1.19$
	SS – ‘v’	1.18	$\pm 0.93$
DEJU	Passage Day	NA, NA, -0.32, -0.30	$\pm 0.28$
	Age	-13.54, -11.57, -15.34, -13.76	$\pm 6.46$
	SS – ‘u’	NA, -0.31, NA, -0.32	$\pm 0.55$
	<b>SS – ‘v’</b>	<b>NA, 1.43, NA, 1.23</b>	$\pm 0.48$
	SR – ‘u’	0.08, NA, -0.18, NA	$\pm 0.67$
	<b>SR – ‘v’</b>	<b>1.27, NA, 1.09, NA</b>	$\pm 0.41$

## **Discussion**

This research is the first to document putative breeding origins for a suite of migrant landbird species in the Gulf of Maine. Not unexpectedly, the largest proportion of our samples had more enriched signatures ( $> -120^{0}_{00}$ ), but regions of likelihood varied for each species and were representative of a broad geographic area. Dunn and colleagues (2006) used  $\delta^2\text{H}_f$  values from birds collected at migration monitoring stations across Canada to show a general trend of southeastern movement of western birds and southwestern movement of birds from eastern provinces. Notably, the Atlantic Bird Observatory at the tip of Nova Scotia and at the northern edge of the Gulf of Maine had scarce to no representation of individuals north or west of Lake Winnipeg in Manitoba (i.e.  $\delta^2\text{H}$  less than  $-120^{0}_{00}$ ) and suggested any convergence of individuals from western origins must happen south of Nova Scotia. Based on analysis of samples collected at 22 CMMN sites, Hobson and colleagues (2015) had similar results, particularly with regard to Canadian Maritime banding sites, where sampled birds were also exclusively from eastern Canada. Our study is unique in that it provides evidence, not previously documented, of individuals utilizing the Gulf of Maine flyway that originated from as far north and west as the Yukon, Northwest Territories, and possibly even Alaska.

### **Modeling Variation in Isotopic Signature**

In addition to the map assignments, our attempts at investigating the variance structure in this data were both to identify if individuals dispersed from geographically similar or distinct regions and to identify patterns of occurrence for a previously uncharacterized region.

### Passage day seasonal effects

Understanding variation in passage time is important to interpret population trends, especially in cases where early and late migrants might have different areas of origin. This information would be applicable in assessing change at a large vs. local scale, for example. At our mid-coast Maine site, the quantile regressions only suggested a relationship between origin and passage date for MYWA and SWTH, though inclusion of passage day as a control in our model selection set resulted in a similar pattern for MAWA.

Migration distance as a life history trait did not explain these differences as MYWA is a short distance migrant and SWTH is a long distance migrant, but intraspecific differences in migration distance may matter for these species since individuals originating from the farthest away were the only ones constrained by date. Timing of passage for birds originating closer to Metinic was spread evenly across the entire season for both species. Post-hoc removal of SWTH outliers confirmed the two birds with very depleted signatures drove the quantile regression results for this species.

These results differ from Smith et al. 2003 and Dunn et al. 2006 where data suggested that lower latitude birds passed through their sites earlier than higher latitude birds. One possible explanation for the lack of relationship between date and isotopic signature in our study is that individuals of some of the species could be originating from discrete source populations. If this were the case, we wouldn't expect date to explain variation in  $\delta^2\text{H}_f$ . Based on results of the map assignments (Figure 4), however, this would only be a plausible explanation for MAWA and the two subspecies of Palm Warbler since the other species showed a much broader range of potential origins.

Results for six of our eight species do coincide with results by Hobson and colleagues (2007) and Mazzerole (2005) where no origin-date relationship was found. This evidence suggests that time of year may be both species and region specific and should continue to be investigated in studies of isotopic origin.

#### Age effects

While present in the top models for four of the eight species, age was only significant for MYWA and moderately significant for DEJU. Interestingly, our results for MYWA coincide with only two other studies on passerines that showed the same pattern with hatch year birds tending to have lower  $\delta^2\text{H}_f$  values (Langin et al. 2007, Haché et al. 2012). The more depleted HY values in these other two studies were explained by the fact that samples were collected from nestlings. For this study, all samples were of fully-grown HY individuals. In a study with known origin individuals, fully-grown HY birds' signatures were shown to match those of the adults (Langin et al. 2007), so the mechanisms hypothesized in the two cited studies are not applicable here. This lends support for our prediction of HY having more depleted signatures because our study was located at an island site in a region with a well-documented "coastal effect". Ralph 1981 suggests the disproportionately high occurrence of HY birds along the coast suggests this is on the periphery of the species' preferred migratory route. As such, adult MYWAs and DEJUs originating from the far north and west (i.e. with lower isotopic signatures) would preferentially stay inland while HY would be more apt to drift to the coast and end up in our sample.

### ‘Daily’ wind effects

This is the first study, to our knowledge, to investigate relationships among daily changes in wind condition at a migration stopover site and breeding origin, as determined by feather isotopes. Relationships between weather and catchment areas could identify conditions when individuals from populations of conservation concern occur in the region and could help explain migratory strategies being employed. Adding wind as a factor in any migration study adds considerable complexity, especially when also in the context of an ecological barrier. Optimal migration strategies depend on multiple conditions as birds weigh costs of departing on migration, settling at rest sites, or continuing flight, and wind selectivity can be especially influential in these decisions (Alerstam and Hedenström 1998, McCabe 2015). Without exact resolution of our isotopic assignments, we could only evaluate wind conditions at our capture site. Relationships between SS conditions and origin, however, might suggest similar conditions at an individual’s point of departure. Relationships between SR condition and origin would be more indicative of influences dictating decisions to land.

Only three of the eight species (MAWA, MYWA, and DEJU) showed any significant relationships between origin and wind condition. The lack of significant relationships could be attributed to variation in wind selectivity. Because wind selectivity greatly depends on fuel loads and deposition rates (Alerstam 1979), it will vary among species and among individuals within a species. There is great variation in the reliability, duration, strength, and timing of wind conditions such that similar conditions could lead to different responses in different birds depending on energy loads (Weber et al., 1998, Liechti and Bruderer 1998). While for some long distance migrants,

tailwind support is invaluable, especially when faced with barriers (Liechti 2006), Weber and colleagues (1998) suggest that because of time constraints and regular adherence to time minimization strategies, long distance migrants, like SWTH and BLPW, demonstrate less selectivity in waiting for favorable conditions. For these species, we would not expect to see any relationships between wind and origin

For the three species showing wind/origin relationships, all indicated that birds coming from farther away (i.e., more negative  $\delta^2H_f$ ) were correlated with more northerly wind conditions the preceding night or morning of capture at our capture site. MYWA and DEJU showed relationships with conditions at sunset the preceding night. DEJU also showed significant effects with SR conditions, along with MAWA. Without knowing exactly where individuals departed from, one explanation we hypothesize is that conditions at Metinic reflected regional wind conditions and birds from farther away were likely occurring in the Gulf of Maine as a result of wind drift. Birds should tend to compensate more for wind drift only as they near their destination, which for many of Maine's fall migrants is thousands of kilometers away (Liechti 2006 Zehnder et al., 2001). As such, it makes sense these individuals would have landed at dawn to reorient and follow the coastline in the seasonably appropriate direction (Able 1977, Drury and Keith 1962, Horton 2016, Richardson 1978). This interpretation is consistent with conclusions drawn from isotopic orientation experiments on MYWA in Nova Scotia (Fitzgerald and Taylor 2008), which suggested a similar pattern with individuals from northwestern origins orienting in headings that corrected for probable displacement. Though not significant, the direction of the relationship with the east-west component ('u') suggested that birds from farther away occurred following nights with north-



northwesterly winds. Interestingly, MYWA and DEJU were also the two species that showed age effects, with immatures being from significantly farther away than adults. The displacement of HY birds is much more expected than adults.

An alternative, but not mutually exclusive, hypothesis explaining these results is that we were also not catching birds originating near the Gulf of Maine under more favorable wind conditions because flight range and air speed given a tailwind component, for any given fat load, is easily doubled (Liechti and Bruderer 1998). The increase in range with tailwinds could likely be enabling those individuals from central Québec, Newfoundland, New Brunswick, and Nova Scotia to just fly over the Gulf of Maine, only landing on islands in the Gulf under headwind conditions that decrease flight range (Erni et al. 2002, Richardson 1978 and 1990). These results are consistent with radar work conducted in Nova Scotia where southwest, overwater migrant departures were denser with N, NE, and E winds (Richardson 1972). Recent work involving radio tracked individuals along the Maine coast has provided evidence of individuals making trans-oceanic flights across the Gulf of Maine but also site-“hopping” along the coast and offshore as they move south (Smetzer unpublished data).

One important assumption here is that we have interpreted more enriched signatures to identify individuals originating from the N or NE and more negative signatures to identify individuals originating from the NW. The longitudinal resolution of isotopic assignments, however, does not definitively distinguish these different populations. So, it is possible, for example, that some of the individuals with more negative isotope signatures originated within the same latitudinal isoscape, just farther east. If this were the case, our hypotheses of birds either being displaced or supported by

tailwind assistance would not be valid. We feel the consistencies among our hypotheses and results of other regional migration studies (Drury and Keith 1962, Fitzgerald and Taylor 2008, Richardson 1972 and 1978), however, help substantiate this assumption. If our assumption is valid, relationships between isotopic assignment of tracked individuals and weather conditions (Smetzer unpublished data) should provide support for these conclusions.

## **Conclusion**

Migration is a complex phenomenon that comes with inherent challenges. Additional anthropogenic changes to the landscape can present unexpected challenges and have dire consequences. For boreal breeding species, where the quality of region wide monitoring is lacking (NABCI 2012), management decisions are often made without conclusive scientific information being available. This is the first multi-species analysis identifying ranges of putative breeding origins for migrant individuals in the Gulf of Maine and provides necessary baseline information critical for understanding changes in populations and bird distribution throughout the region. Collectively, this work shows that stopover habitat loss and coastal development in the Gulf of Maine could affect populations from a broad distribution of the boreal region, and specifically, some populations of greatest conservation need for species like the BLPW and SWTH (Rodewald et al. 2015).

While this study could surely benefit from larger sample sizes (Hobson et al 2014) and substantial ground truthing of North American isoscapes would improve the application of isotopic methods at a continental scale, it provides much needed information about fall migrants in the Gulf of Maine. It adds to the growing body of

knowledge of migration routes for boreal landbird migrants and complements other recent isotopic assignment studies (Hobson et al. 2015, Holberton et al. 2015). It demonstrates the Gulf of Maine is a major nexus for migrants from sensitive boreal regions across North America, and as such, is a region of high conservation concern.

Finally, it highlights the importance of continued efforts throughout the region to monitor and track migratory bird populations. Overall, our exploratory analyses resulted in few of our chosen parameters explaining variation in  $\delta^2\text{H}_f$ . Perhaps, our model selection approach and chosen parameters did not capture the variables affecting movements of birds from different origins, or our results simply highlight the stochasticity, and consequential management challenges, in the Gulf of Maine migration system. More research will be needed to disentangle some of the mechanistic explanations related to breeding origins of migrants in the Gulf of Maine.

**CHAPTER 3**  
**FIRE ESCAPES, CONVENIENCE STORES, AND FULL SERVICE**  
**HOTELS: COMPARING CONDITION OF MIGRANT**  
**COMMUNITIES TO IDENTIFY STOPOVER**  
**SITE CONSERVATION PRIORITIES**

**Abstract**

Migration is an energetically challenging phase of many birds' annual cycle. Suitable stopover habitat is, therefore, important to the success of migrant individuals. This is especially true along major migration corridors and geographic features, like coastlines, where migrants concentrate along ecological barriers to movement. Predictors of relative quality of stopover sites to migrant species are therefore important for prioritizing conservation actions in these regions. In this study, we use variation in fat content and size-corrected body mass of fall migrants in the Gulf of Maine to understand migration patterns and the relative importance of individual stopover sites. We investigated differences in these condition metrics as a function of species-specific migration distance, foraging guild, age, and stopover site geography (offshore vs. on the mainland). Geography and age were important factors explaining differences in both condition indices. Immature individuals of all species carried less fat on average and had lower size-corrected mass than adults. The strongest relationship, however, was geographic location, where individuals on islands possessed significantly lower masses than individuals on the mainland. We also showed that birds at all sites and of all ages significantly increased in mass, on average, over the capture day, providing evidence that both island and mainland sites can serve as functional stopover habitat. Our finding that

birds offshore are in poorer body condition on arrival to stopover than those on the mainland is also suggestive that over water movements may be more energetically taxing than flights over land or along the coast. As a result, the loss of island stopover site availability or alteration of habitat quality may be more likely to result in individual fitness or population-level consequences.

### **Introduction**

For migrant landbirds, the annual movement between breeding and wintering areas can be the most dangerous part of the annual life cycle (Newton 2004, 2006, Berthold et al. 2003), and some estimates show over 80% of annual songbird mortality happens on migration (Sillett and Holmes 2002). It is difficult, however, to make decisions regarding land management or conservation without knowing the relative importance of particular areas for migratory species. For most landbirds, migration is comprised of alternating periods of flight and periods of refueling (stopover), with the majority of a bird's time spent on stopover (in some cases more than 70%: Åkesson et al. 2012, Callo et al. 2013, McKinnon et al. 2013). Thus, conservation priorities and management plans that successfully protect high quality stopover locations likely have the greatest potential impact for migrants.

Prioritizing and conserving stopover habitat along the Atlantic Coast is of particular importance because these habitats are experiencing some of the most rapid increases in development across the continent (Mehlman, et al. 2005, Schauffler 2013). Further, the open ocean acts as a barrier to movement, naturally concentrating migrants. This effect is even more exaggerated when the orientation of the coast follows the leading line of migration, like in the Gulf of Maine.

Due to the temporal and spatial variability of stopover site use by migrants, it is difficult to identify relative site importance without also knowing the most important function of a particular site to migrants. Mehlman and colleagues (2005) identified a continuum of site functions from those simply offering resting opportunities to those with resting and significant refueling opportunities (e.g., “fire escape” sites to “full-service hotel” sites). They used geographic position and habitat resources to inform where a stopover site fell along this continuum. They suggest this information could be used to classify and identify areas of conservation priority, especially along ecological barriers where different functions may be important to migratory success at different points along the migratory corridor.

The energetic condition of individual migrants can heavily influence behavioral decisions birds make on migration. Further, overall condition, energy stores, and a bird’s ability to refuel (i.e., accumulate fat reserves) is affected by weather events, competition and predation risk on stopover, overall migratory strategy, position along the migratory route, and time of season. Thus, individual condition integrates many constraints on migratory success and can indicate both recent energetic challenges experienced by the bird (i.e., condition on arrival) and the ability of a particular site to ameliorate the costs of those challenges (i.e., changes in condition during stopover). Understanding condition’s influence on the above factors can help classify site importance for resting and refueling, respectively.

Geographic variation in the energetic condition of migrants on stopover can therefore indicate relative variation in the function and importance of sites for migrants. For example, in coastal areas such as the Gulf of Maine, island vs. mainland sites may

vary in their function (resting vs. refueling) and quality (refueling rate). Some studies suggest that over-water migrants are likely dominated by “off-course” individuals that arrive at stop-over sites in poor physical condition and carrying low fat reserves (Delingat et al. 2008, Murray 1965, Newton 2008, Scholander 1955). If this is the pattern in the Gulf of Maine, individuals captured at island sites should have lower fat stores and lower size-corrected body masses.

Variation in condition as a function of age can also show the relative importance and function of stopover sites for different proportions of the migratory community. For instance, the well-documented “coastal effect” of the Atlantic coast of North America, where migrant populations are dominated by disproportionate numbers of hatch-year (i.e., immature) birds in the fall, suggests that young birds are more likely to make navigational errors (Ralph 1971, 1978, 1981) and may have different energetic costs, stopover needs, and subsequent consequences than “on-course” individuals. Regardless of location, young birds can also tend to have lower body mass on stopover than adults (Jones et al. 2002, Morris et al. 1996, Woodrey and Moore 1997), and if hatch year birds are less efficient foragers (Jones et al. 2002, Morris et al. 1996, Wunderle 1991), we would expect an age effect on the rate of refueling.

Importantly, condition might also vary with other species characteristics, like migratory strategy and foraging guild, which might obscure relative differences in site function and quality if not controlled for. Differences in migratory strategy between short- and long-distance migrants influence fat deposition rates and departure fuel loads such that long distance migrants should be carrying more fat on average across all stopover sites (Alerstam and Lindström 1990, Weber et al. 1998, Carlisle et al. 2004).

Further, diet composition can influence mean overall energetic condition (Parrish 2000, Suomala et al. 2010, Smith et al. 2007, 2013). For example, Smith and colleagues (2007) found that while frugivorous migrants may be able to meet daily energy demands, they may not meet protein requirements, which could ultimately affect their ability to gain mass and influence length of stopover. Controlling for both of these species characteristics is thus important before assessing relative site importance for stopover.

In this study, we explored the degree to which regional geography, age, migration distance, and foraging guild explain observed variation in three different measures of a migrant's energetic state: fat content, size-corrected body mass, and mean daily mass change over time. While related, condition index and fuel loads can be applied differently to understanding broader migration strategies within the region, and diel patterns in mass gain is useful for assessing stopover site quality (Adams 2014, Bonter et al. 2007, Dunn 2002, Winker et al. 1992). We use the information summarized here to characterize four stopover sites in the Gulf of Maine and inform the prioritization of sites for conservation and management. Given the increase in development along the northern Atlantic coastline, it is important to identify a network of suitable migration stopover sites to be considered in regional conservation planning efforts.

## **Methods**

### **Field Sites and Data Collection**

Data used in this study were collected during the autumn as part of a regionally standardized mist-netting effort at four previously unstudied migration monitoring stations in the Gulf of Maine: Seawall, in Acadia National Park (ANP), Petit Manan Point, part of Maine Coastal Islands National Wildlife Refuge (MCINWR), Metinic



Island (MCINWR), and Great Duck Island (The Nature Conservancy, Maine Department of Inland Fisheries and Wildlife, and College of the Atlantic; Figure 3.1). Petit Manan Point and Seawall were defined as mainland sites. Despite Seawall technically being located on Mount Desert Island (MDI), MDI is very large (250km<sup>2</sup>) and is only 800 m from the mainland at its nearest point. We only included dates in the analysis that overlapped at all sites (29 August - 11 October, 2010 and 24 August - 12 October, 2011). While habitats vary among sites (e.g., the ratios of coniferous to mixed forest or grassland/shrubland), the broad plant communities are similar and the relative proportion of habitat available for stopover is comparable within the two island and two mainland sites (McCabe and Olsen 2015b).

When conditions permitted, we opened mist-nets at each site 30 minutes before sunrise and closed six hours after opening. We banded all individuals with unique serially numbered bands issued by the U.S. Geological Survey and collected standardized banding information. All individuals were identified to species. We also determined age (local, hatch year-HY, or after hatch year-AHY), sex when possible, recorded wing length (to the nearest 0.5mm), body mass (to the nearest 0.1g), amount of subcutaneous fat (rank score from 0-5), and tarsus and bill morphometrics (to the nearest 0.1mm) when time permitted (Appendix A). We aged locally hatched young when the majority of body plumage was still juvenile down feathers and when wing and tail feathers were still largely in sheath, suggesting they were incapable of sustained flight.

Banders at each of these sites calibrated measurements and measuring practices before the onset of each season to ensure standardized practices. We used multiple measures of energetic state (fat score, size-corrected body mass, and daily mean mass

change) because morphometric estimates of condition commonly used in the ornithological literature vary widely, and there is no support for a single best method (Labocha and Hayes 2012).

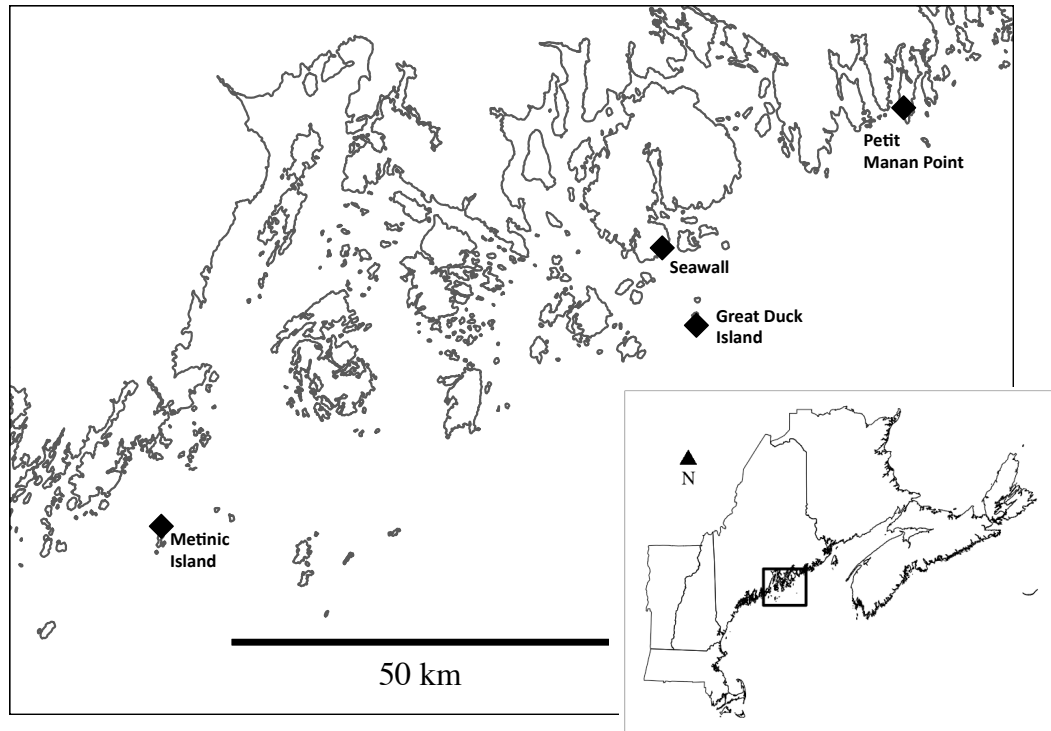


Figure 3.1. The location of the four migration monitoring sites in mid-coast and Downeast Maine.

We restricted the analyses to new captures and only those migratory species for which we had  $\geq 5$  captured individuals within a season. To minimize the inclusion of local breeding individuals, we removed all locally hatched young. We also confirmed breeding species (e.g., Common Yellowthroat, *Geothlypis trichas*; Gray Catbird, *Dumetella carolinensis*; Savannah Sparrow, *Passerculus sandwichensis*; Song Sparrow, *Melospiza melodia*) for each site based on observations reported in Fisichelli et al. (2014) and Leppold (2010, 2011) and removed all individuals captured within the first quartile of sampling for breeding species in all but two cases. For Myrtle Warbler (*Setophaga coronata c.*) and Hermit Thrush (*Catharus guttatus*), based on a pattern of single digit

daily totals being followed by absences of both species on multiple days to an increase in daily captures of twenty or more individuals, we decided using this rule excluded obvious migrants. Instead, we adjusted the cutoff date by five and six days, respectively, based on the peak distribution of abundance and likelihood of captures representing migrant individuals.

## **Statistical Analysis**

### Model Selection

We constructed a set of eight, linear-mixed-effects models (including a null) to explore variation in energetic condition and fat content of migrant communities by geographic location (island vs. mainland) and species characteristics. We used the same candidate models in two separate analyses with fat (hereafter “fat models”) and size-corrected body mass (hereafter “condition index [CI] models”) as our dependent variables. Every model used in these analyses, including the null, included a fixed effect for passage day, to control for seasonal temporal patterns in condition, capture time (minutes after sunrise) to control for daily temporal effects, year to control for inter-annual variation, and a random effect for species to control for interspecific differences beyond those we tested explicitly. We calculated passage day by determining the median Julian Day of capture for each species within each year. We then subtracted the capture date from the median. This resulted in a range of passage days from -39 to 39, where median passage day is zero, passage day for birds captured prior to the median date are negative values (i.e., early migrants), and passage day for those captured after the median date are positive values (i.e., late migrants).

We categorized each site as either mainland (Petit Manan Point and Seawall) or island (Metinic and Great Duck Island) and included this variable in all candidate models except the null. We also considered age (young or adult), foraging guild (insectivore, granivore, frugivore, or generalist), and migration distance in models. Foraging guilds were based on categorizations in Erickson et al. (2011), Suomala et al. (2010), and Parrish (1997). We calculated migration distance as the distance left in each species' migratory journey based on the difference between the latitudinal midpoint of our study sites and the latitudinal midpoint of each species' non-breeding range (based on Erickson et al. 2011, Rodewald 2015). We also considered two-way interactions between geographic location and each of the three community characteristic variables in our set of candidate models. This allowed possible differences in bird condition between the mainland and island sites to vary by age, foraging guild, and migration distance.

We evaluated the possibility of a non-linear relationship between condition and time of season, but the quadratic term was not significant ( $p=0.82$ ), so it was removed from the final set of candidate models (Table 3.1). We conducted all analyses in the R statistical computing environment (R core team 2016).

### Fat

We used the cumulative link model (function "clm" in the 'ordinal' package for logistic regression analyses; Christensen 2015) to compute ordered logistic regressions with fat as the response variable. Because graphics produced from these analyses are not easily interpretable, we also tested the same models using a linear mixed effects model approach. To satisfy linear model assumptions, we converted fat into a continuous variable and used a  $\log_{10} + 0.25$  transformation. Both analyses resulted in the same top-

selected model with comparable parameter estimate strength, significance, and direction of relationship; tabular results of the fat models are from the logistic regression, graphics of fat results are from the linear models.

Table 3.1. Set of candidate models used in fat and CI analyses. All models (including the null) included fixed effects for passage day, capture time, and year, and a random effect for species.

### **Candidate Models**

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Null

Island

Island + Age

Island + Migration Distance

Island + Foraging Guild

Island + Age + (Island x Age)

Island + Migration Distance + (Island x Migration Distance)

Island + Foraging Guild + (Island x Foraging Guild)

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### Condition Index

We regressed body mass on  $\log_{10}$  transformed wing length and tarsus measurements for each species separately and used the residual values from those analyses as our size-corrected body mass (CI) (function “lmer” with maximum likelihood in the ‘lme4’ package; Bates et al., 2015). We scaled the residuals (i.e., converted to z-scores) to allow for direct comparison among species by subtracting the mean residual from each residual value and dividing by the standard deviation. We also scaled passage day and capture time in all models.

We used Akaikei's Information Criterion (AIC) scores to rank candidate models for both fat and CI response variables. We determined the top selected model(s) to be those with a  $\Delta\text{AIC} < 2.0$  (Burnham and Anderson 2002). We present the difference in AIC relative to the top model ( $\Delta\text{AIC}$ ), number of model parameters ( $k$ ), and model weights ( $w$ ) for all candidate models. We present parameter estimates  $\pm$  SE only for variables in top selected models. We refrained from using model-averaged parameter estimates in making multi-modal inferences since our intent with model selection here was purely exploratory and not predictive (Cade 2015). Thus, we considered parameters as important for describing variation in condition when, 1) the strength of parameter estimates in the top selected models were consistent, and 2) when the 95% Confidence Intervals did not overlap zero. We also used Type III sum of squares statistics to evaluate post-hoc significance for any variables uniquely occurring in a 'best fit' model.

We calculated a conditional  $R^2$  value for our linear mixed effects models using the "sem.model.fits" function in the 'lme4' package (Nakagawa and Schielzeth 2013).

### Mass Change Over Time

We constructed two general linear models to test for the effects of location or age on differences in daily fueling rate of migrants ("lm" function in the base R package; R core team 2015). Each fully specified model tested size corrected body mass (CI) against time of capture. We included island or mainland location and age, in separate models, as interaction terms with capture time to allow fueling rate to vary by these two main effects. We considered age or island location to have an important effect on the rate of mass change if the interaction term was significant ( $p < 0.05$ ).

As with all of the previous models, we controlled for passage day and year in testing differences in fueling rates. We controlled for age (no interaction with time) in the model testing the interaction between time and location, and we controlled for site location (no interaction with time) in the model evaluating whether adults were gaining mass differently than young. To infer that the average change in mass of a migrant community over a day represented the average mass gain of individuals at each site, we assumed all captures were of birds that arrived on site the day of capture and that capture time was independent of mass upon arrival.

## **Results**

Our final analysis included just over 5,000 banding records of 50 different species from all four sites combined (Appendix C).

### **Model Selection (Fat and Condition Index)**

Our cumulative-link mixed model selection with fat as our response had one clear top model. Controlling for passage day, capture time, species, and year, the top ranked model contained both geographic location and age factors but not the interactive effects of them (Table 3.2). Fat content was lower for both immature birds and individuals captured on islands (Table 3.3; Figure 3.2, conditional  $R^2 = 0.17$ ). Significance of our control variables validated their inclusion in the models (Table 3.3).

Table 3.2. AIC model selection results for the cumulative link ordinal regression models (clm) using fat as the response variable, the difference in AIC relative to the top model ( $\Delta AIC$ ), number of model parameters ( $k$ ), and model weights ( $w$ ). All models (including the null) include passage day, capture time, species, and year as control variables.

Model	$\Delta AIC$	$k$	$w$
Location + Age	0	12	0.55
Location + Age + (Location x Age)	2.0	13	0.21
Location + Migration Distance + (Location x Mig. Distance)	2.2	13	0.19
Location	5.7	11	0.03
Location + Migration Distance	7.7	12	0.01
Null	10.1	10	0.004
Location + Foraging Guild	10.1	14	0.004
Location + Foraging + (Location x Foraging Guild)	12.6	17	0.002

Table 3.3. Comparison of parameter estimates ( $\pm$  SE) and 95% confidence intervals for the top selected cumulative link ordinal regression model using fat as the response variable. Estimates for the categorical variables are calculated against the reference listed.

Variable	Parameter Estimate	95% Confidence Interval	
		Lower	Upper
Mainland	Reference		
Island*	-0.13 ( $\pm$ 0.03)	-0.24	-0.02
Age*	-0.24 ( $\pm$ 0.08)	-0.40	-0.07
Passage Day*	0.45 ( $\pm$ 0.03)	0.40	0.51
Capture Time*	0.30 ( $\pm$ 0.03)	0.25	0.36
Year 2010	Reference		
Year 2011*	-0.29 ( $\pm$ 0.05)	-0.39	-0.18

Significant parameters are indicated with \*



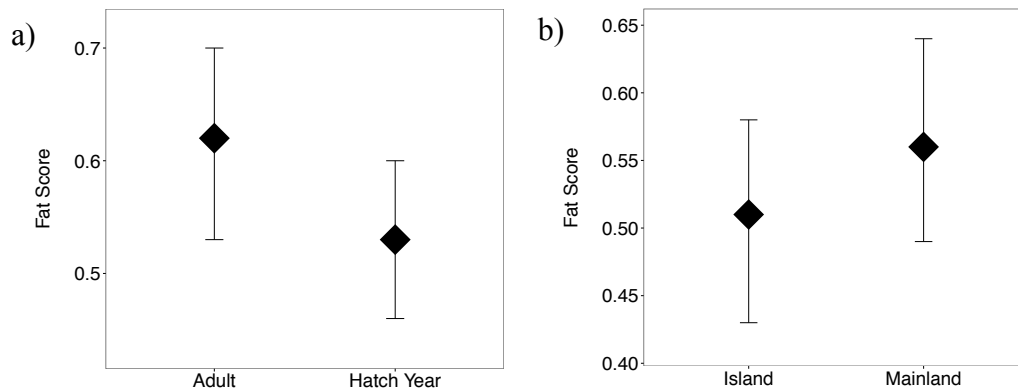


Figure 3.2. Mean fat content ( $\pm$  95% CI) of birds by a) age and b) geographic location. The Y-axis is the back-transformed fat score results from the linear mixed effects model.

We found two top models (within  $\Delta$  2AIC of each other) in the candidate set with condition index as our dependent variable (Table 3.4). Both included age and location, similar to the fat results, but one also included the age x location interaction term (Table 3.5). A Type III SS error test, however, showed the interaction term was not significant ( $p=0.11$ ). Thus, regardless of location, adults were in better condition than hatch year birds, and regardless of age, birds captured at mainland sites were in better condition than those captured at island sites (Figure 3.3). Significance of our control variables, again, validated their inclusion in our candidate models (Table 3.5).

Table 3.4. AIC model selection results for linear mixed effects models using CI as the response variable.  $\Delta AIC$  is the difference in AIC relative to the top, ( $k$ ) is the number of individual model parameters, and ( $w$ ) is the model weight. All models (including the null) included passage day, capture time, species, and year as control variables.

Model	$\Delta AIC$	$k$	$w$
Location + Age + (Location x Age)	0	9	0.55
Location + Age	0.7	8	0.39
Location	6.2	7	0.02
Location + Migration Distance	6.3	8	0.02
Location + Migration Distance + (Location x Mig. Distance)	7.7	9	0.01
Location + Foraging Guild + (Location x Foraging Guild)	9.7	13	0.004
Location + Foraging Guild	12	10	0.001
Null	118.2	6	<0.001

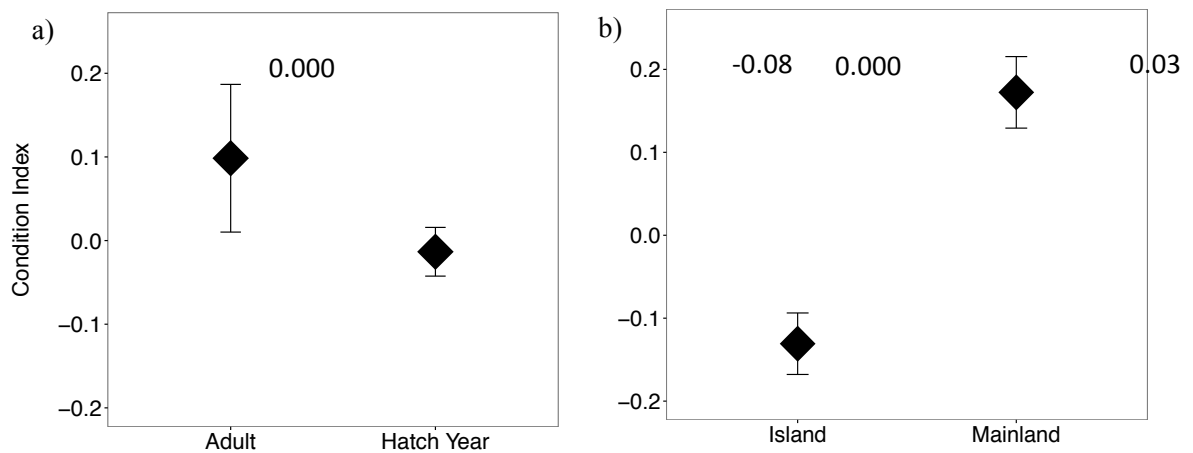


Figure 3.3. Age (a) and location (b) differences in condition index controlling for passage day, capture time, species, and year.

### Mass Change Over Time

Mean daily mass change over time did not vary by age ( $t=-0.62$ ,  $p=0.53$ ; Adjusted  $R^2=0.04$ ). On average, adults (AHY) captured later in the day were 2.1g (0.32g/hour) heavier and immatures (HY) captured later in the day were 1.14g (0.17g/hour) heavier than individuals captured early in the morning.

The additive effect of geographic location (i.e., island vs. mainland) was a significant predictor of mass change ( $t = -4.99$ ,  $p = <0.001$ ; Adjusted  $R^2=0.04$ ). Early morning masses were slightly higher for birds captured on the mainland, but mass was similar at island and mainland sites (Figure 3.4).

Table 3.5. Conditional  $R^2$  values, parameter estimates ( $\pm$  SE), and 95% confidence intervals for the top two linear mixed effects models using CI as the response variable. Estimates for categorical variables were calculated against the reference listed.

<b>Model Variable</b>	Conditional $R^2$	Parameter Estimate	95% Confidence Interval	
			Lower	Upper
<b>Location + Age + Loc. x Age</b>	0.041			
(Intercept)*		0.29 ( $\pm$ 0.06)	0.18	0.40
Mainland		Reference		
Island*		-0.43 ( $\pm$ 0.09)	-0.60	-0.27
Age – Adult		Reference		
Age – Hatch Year*		-0.17 ( $\pm$ 0.06)	-0.29	-0.05
Age x Location		0.14 ( $\pm$ 0.09)	-0.03	0.32
Passage Day*		0.09 ( $\pm$ 0.01)	0.06	0.12
Capture Time*		0.13 ( $\pm$ 0.01)	0.10	0.16
Year 2010		Reference		
Year 2011*		0.07 ( $\pm$ 0.03)	0.01	0.12
<b>Location + Age</b>	0.041			
(Intercept)*		0.24 ( $\pm$ 0.05)	0.14	0.33
Mainland		Reference		
Island*		-0.30 ( $\pm$ 0.03)	-0.36	-0.25
Age – Adult		Reference		
Age – Hatch Year*		-0.11 ( $\pm$ 0.04)	-0.20	-0.02
Passage Day*		0.09 ( $\pm$ 0.01)	0.06	0.12
Capture Time*		0.13 ( $\pm$ 0.01)	0.10	0.16
Year 2010		Reference		
Year 2011*		0.07 ( $\pm$ 0.03)	0.01	0.12

Significant parameters are indicated with \*

## **Discussion**

Both geographic location of stopover sites (island vs. mainland) and age (hatch year vs. adult) explained significant variation in fat content and size-corrected body mass (CI), with immatures and individuals captured at island sites carrying less fat and mass than adults and individuals captured on the mainland. These differences were consistent with previous studies assessing age-related condition differences of migrants during stopover (Jones et al. 2002, Morris et al. 1996); however, the difference in condition index between birds captured on islands vs. the mainland appeared to be stronger than the relationships with fat. We hypothesize that this is because CI is a measure of both fat mass and lean tissue mass (e.g., organs and lean muscle). Thus, in addition to having less fat, immatures and birds on islands had more compromised lean tissue mass as well.

Seewagen and Guglielmo (2011) found that lean mass accounted for 48-53% of individual differences in size corrected body mass (i.e., condition index) for migrant passerines sampled in New York City (USA) parks. Some evidence suggests that a difference in lean mass may be explained by migration distance, with short distance migrants preferentially burning more lean mass than fat (Bauchinger and Biebach 1998, Jenni-Eirmann and Jenni 1991, Jenni and Jenni-Eirmann 1992). This explanation is not supported by our data, however, because migration distance as a community characteristic did not appear in any of the best-fit CI models.

We didn't necessarily expect the "coastal effect" and predominance of young birds along the coast to explain differences in condition of birds between island and mainland sites because we expected a similar proportion of young to adults at both island and mainland locations, given our mainland sites' proximity to the coast. Island sites did

have a slightly higher percentage of young sampled, however, with Great Duck and Metinic island captures being comprised of 92.5% HY individuals and Petit Manan Point and Seawall only having 85% and 88%, respectively.

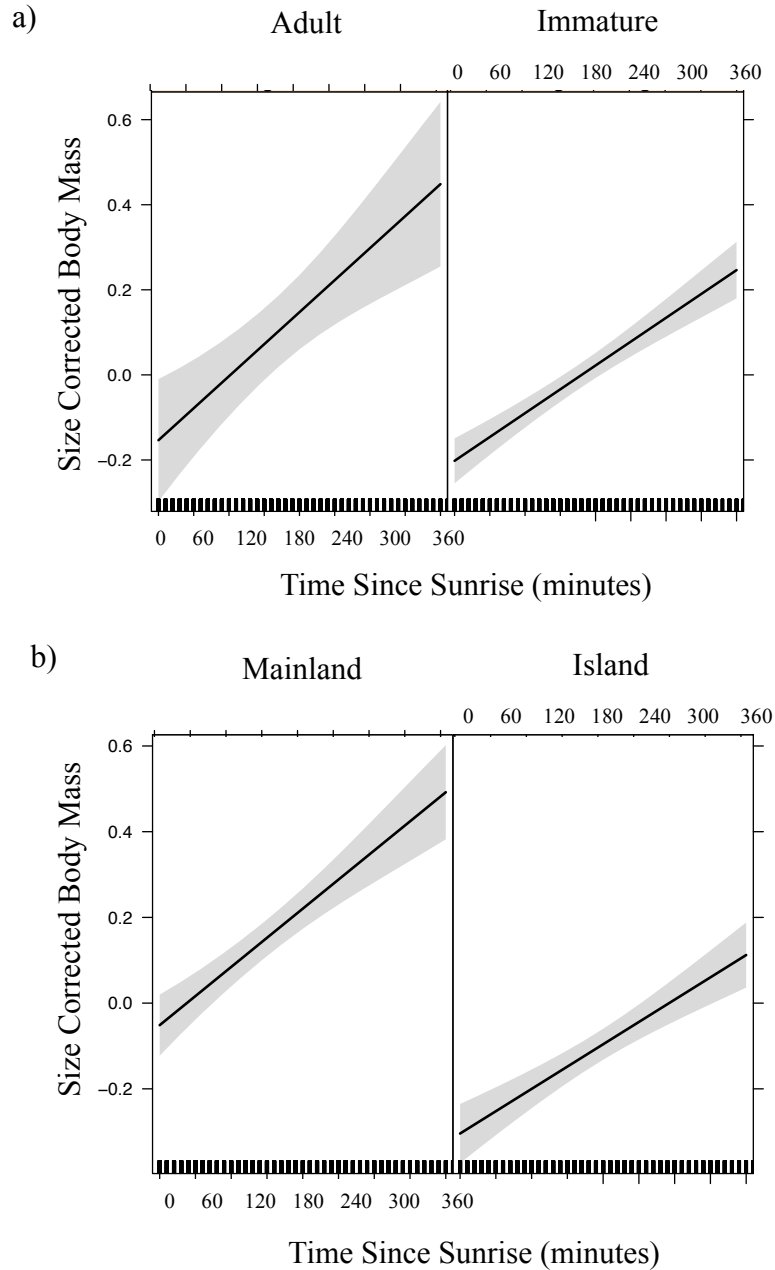


Figure 3.4. Comparisons of change in size corrected body masses over time (minutes since sunrise) for birds as a function of age (a) and location (b). Gray shaded area depicts the 95% confidence intervals.

This difference in age composition by site does not explain the difference in condition between island and mainland individuals, however, because the location x age interaction term in the model was not significant (Table 3.5).

There are a number of reasons why we might expect young birds to be in poorer condition than adults, whether from being less efficient foragers or choosing less nutritious foods, having higher thermoregulatory costs because of poorer quality feathers, or being more prone to navigational errors and having less efficient flight mechanics that result in higher consumption of energy reserves prior to arrival at a stopover site. Recent work, has shown that immatures are much less choosy about the wind conditions they depart in (Mitchell et al., 2015). Further, Mitchell and colleagues (2015) found that despite being less selective about flight conditions, immatures had similar flight durations and airspeeds as adults. Increased energetic expenditure was likely the cost in compensating for flying under less efficient conditions than the more selective adults.

One possible alternative to this interpretation could be that the higher condition index for birds caught on the mainland is simply a product of capturing birds that had been on stopover for longer and had more opportunity to feed and recover energy stores. Because of the size and distribution of habitat on the islands, we are more certain that birds rarely stayed on site for more than a day. Island recapture rates were very low (3 and 4%), and daily visual surveys (protocol in Appendix D) of habitat surrounding the banding area resulted in very few re-sightings of banded birds (<10) over the course of the season

Mainland recapture rates (3 and 8%) did not suggest birds remained on site there either, but a study conducted at Petit Manan Point (one of our two mainland sites) following tagged Blackpoll Warblers and Red-eyed Vireos in 2013 and 2014 found some individuals remained in the area near the banding site for ten to fifteen days (Smetzer, unpublished data). Because tagged individuals on the ground could be tracked up to 2 km away, it is likely smaller scale stopover movements could occur within a few kilometers but be outside of the immediate banding area where they might be recaptured. Given the data from tracked individuals, we cannot rule out the possibility that the observed difference in condition between mainland and island birds can be explained by length on stopover. Regardless of the uncertainty in the role that age differences or length on stopover might have in explaining the site location effect, our data supports the notion that there is an energetic cost to birds being farther offshore.

While the presence of a particular species or a certain number of individuals at a stopover site might suggest important habitat for migrants, this may not always be the case (Winker et al. 1992). Usage of stopover sites may vary widely depending on status of migration, distance left to travel, individual molt condition, or weather, so some studies have used these diel patterns of mass gain to infer stopover site quality and classify good quality stopover sites within a functional category (Adams 2014, Bonter et al. 2007, Dunn 2001, 2002b, Winker et al. 1992). As mentioned in the methods, we assumed all captures were of birds that arrived on site the day of capture. As Dunn (2002) noted, heavier early morning masses at some sites relative to others and relative to throughout the day could be indicative of stopover length and suggest birds being present for multiple days. We had the opposite trend with early morning mass values being much

lower and increasing throughout the day at mainland and island sites (Figure 3.4). Thus, we felt confident in this assumption.

While birds captured early in the morning on islands averaged slightly lighter, there was no difference in birds' ability to gain mass at mainland or island sites. This suggests, while birds on islands may start at lower a lower mass, they are able to gain mass equally as well as at mainland sites. There was also no difference in the ability of adults and young to gain mass on stopover, suggesting that hatch-year birds were just as efficient at foraging as adults. These results are consistent with those found by Morris and colleagues (1996), though their analysis used recapture data to assess mass gain, and, unlike here, they did find that young birds started out leaner than adults. Since foraging guild was not an important variable in any of our top selected models, differences in diet did not predict condition, possibly suggesting that food availability was not a limiting factor for frugivores or omnivores at any of the sites.

Using the framework suggested by Mehlman and colleagues in 2005 to classify stopover sites, these results provide evidence that the island sites, in particular, likely function as "convenience stores". It is typical of convenience store sites to usually be small and isolated, having more density-dependent limits for food and shelter, which result in migrants staying for shorter periods of time. "Convenience store sites" are critical for helping birds meet short-term rest and refueling demands and support shorter distance flights to "full-service hotel" sites. Our results showed that birds were able to refuel at all sites, but we found no evidence that they stayed for longer than a day at our island sites. Of note, we also documented greater predation pressure at offshore sites than the coastal/mainland sites (Leppold, McCabe, and Grunzel unpublished data).



Full service hotel sites are categorized as higher quality habitat that meets all an individual's resource needs with little risk of competition or resource depletion. At a minimum, our mainland sites could be classified as "convenience stores", but because we have evidence that birds may have remained on or near the banding site for multiple days, our mainland sites likely offer "full-service hotel" resources.

In identifying site usage and spatial structure of stopover sites, the need for "full service" sites is apparent, but "convenience stores" are of special conservation priority. Habitat fragmentation in eastern North America and throughout the Mid-Atlantic region has caused loss of contiguous tracts of land offering "full service hotel" resources, making "convenience stores" even more necessary for filling in gaps in migratory routes (Buhler and Moore 2011, Mehlman et al., 2005). With the conservation of suitable "convenience store" sites, birds may be able to successfully migrate by making shorter distance flights with more frequent stops. With a large enough network of "convenience store" sites, collectively, habitat throughout the Gulf of Maine might even be able to function in place of a single "full service" site.

Suitable stopover habitat, where resting and refueling needs can be met (measured in this study by condition at arrival and mass gain over the course of a day), is critical for migrant survival and long-term sustainability of migratory bird populations. As many others have stated, sites where migrants concentrate, especially along an ecological barrier, are a clear priority (Buler and Moore 2011, Smith et al. 2007, McCabe and Olsen 2015, Mehlmann et al. 2005, Petit 2000). Our data showed individuals on islands were carrying less fat and were in poorer condition upon arrival than those on the mainland. Regardless of site location, however, bird communities were able to gain mass and

improve in condition throughout the day, evidence of the critical support these onshore and offshore habitat “islands” provide landbird migrants. McCabe and Olsen (2015b) found that landscape composition at small spatial scales (radius 4km) best predicted stopover site use in a study of fall migrants at eleven different monitoring sites in the Gulf of Maine, including the four used here. At smaller spatial scales, obtaining land, protecting sites from development, and managing specific habitat characteristics may be much more feasible while still maximizing benefits to migrants.

While crossing the Gulf of Maine in a seasonably appropriate direction is within the range of a normal nocturnal migrant’s flight behavior (Newton 2008), our results show that some individuals moving over areas of open water in the Gulf could be physiologically stressed, carrying fewer energy reserves than those moving over land. If some individuals in the Gulf of Maine are closer to an energetic threshold (i.e., to the point of catabolizing lean muscle tissue), displacement and barrier effects from new developments in and around the Gulf (e.g., offshore wind turbines, changes in island habitat quality or availability) could have individual fitness and population level consequences. Making estimates for the maximum distance a bird in poor condition can achieve would be helpful for further identifying stopover site spacing needs and assuring that suitable stopover habitat is available in the Gulf of Maine.

**CHAPTER 4**  
**OVER OPEN WATER: VARIATION IN PHYSIOLOGICAL CONDITION**  
**OF ISLAND BIRDS IS INDICATIVE OF MIGRATION**  
**STRATEGIES IN THE GULF OF MAINE**

**Abstract**

Migration poses extreme physiological challenges, especially for small migratory passerines navigating ecological barriers. Those challenges greatly increase when development results in changes to the landscape, necessitating a better understanding of regional migration strategies to make environmentally sustainable development decisions. In flight, overall energy reserves and location of a suitable stopover site ultimately influence a bird's decision to land. Conversely, departure decisions most strongly depend on an individual's ability to reach a minimum fuel load. Since a birds' migratory decisions may be driven by its individual physiological condition, understanding energetic trajectory is essential to further explaining observed behavioral patterns. Here, we used fat scores and blood plasma triglyceride levels (TRIG), indicating fat building, from eight species of small passerines captured on an island in the Gulf of Maine to assess site quality by exploring differences in energetic trajectory over time of day. We also evaluated the extent to which breeding origin, age, progress of season, foraging guild, and migration distance left to travel explained variation in TRIG, fat content at time of capture, and fat building. In addition to showing significantly higher fat scores and TRIG values over the course of the day, our research supported predictions related to our foraging guild and time of season hypotheses. Though they didn't show a difference in the amount of fat they were carrying at time of capture,

frugivores had significantly higher TRIG than omnivores. Though early season TRIG values and fat scores varied among species, each showed the same significant difference between early and late season individuals, thus suggesting that migrants in the Gulf of Maine operate along a continuum of optimal strategy behaviors depending on the time of the season. Here, we provide critical baseline information on the physiological condition of fall migrants at an offshore site in the Gulf of Maine that will be useful in informing habitat management practices for landbird migrants facing changing landscapes.

### **Introduction**

Migrant birds face numerous challenges on migration, many of which have serious consequences that can result in decreased survivorship (Newton 2006, 2007, Sillett and Holmes 2002). Many of these challenges involve environmental factors such as finding quality stopover sites with adequate food supply, dealing with competition, predation, dramatic weather events, and sometimes crossing landscape barriers such as oceans. Anthropogenic changes in the landscape may further amplify the challenges already facing migrants.

Over the last couple decades, optimality models organized around time, energy, and predation risk minimization have been used to explain strategies that migrants may use to overcome some of the aforementioned challenges (Alerstam 2011). Making predictions about migrant's ability to adapt to changing a landscape and climate is critical in mitigating potential risks. The challenge, then, for biologists, is to identify migration strategies employed in a region, understand mechanisms constraining those strategies, and understand to what extent strategies can shape the evolution of different mechanisms.

Despite an existing body of evidence that many landbird migrants are time minimization strategists (as reviewed in Hedenström 2008), the optimum strategy will vary depending on the locale or stage of migration. So, species or individuals likely employ a mixed set of strategies throughout their entire migratory journey (Bayly 2007 in Alerstam 2011). Thus, it is important to understand migration strategies at specific regional scales.

The Gulf of Maine is an area of particular interest, especially during fall migration, because it is a major nexus for millions of birds originating from a wide expanse of the boreal region (Drury and Keith 1962, Hicklin 1987, Holberton et al. 2015, Leppold and Mulvihill 2011, Richardson 1978 and 1979). Migratory stopover sites along ecological barriers are especially important, particularly when that barrier follows the leading line of migration and concentrates migrants like in the Gulf of Maine (Berthold 2001). Areas along the Atlantic Coast are among sites with the least amount of assessment for conservation planning purposes and some of the most rapid increases in coastal development (Mehlman, et al. 2005, NOAA 1998). The Gulf of Maine is also one of only three regions in the United States being explored for off- and near-shore wind energy development (University of Maine and Sewall Company 2011).

While weather events, competitors and predators on stopover, distance to goal, and time of season will influence individual migratory decisions and subsequent use of a particular stopover site, in an optimal migration framework, when to land or depart is most strongly limited by energy stores and a bird's ability to refuel (i.e., accumulate fat reserves); (Covino et al., 2015, Smith and McWilliams 2014, Covino and Holberton 2011, Jenni and Schaub 2003). For example, some night migrating passerines, provided

adequate resources, may exhibit more rapid fuel deposition rates, higher departure fuel loads, and make fewer longer flights while others minimize energy consumed on migration by making decisions to carry smaller fuel loads, and reduce a single night's flight range. Thus, understanding individual migration strategies and behavioral decisions is dependent upon also understanding a bird's physiological state during migration.

The main energy source for migratory flights is fatty acids stored in the form of triglycerides (TRIG). As such, circulating levels of TRIG in blood plasma are indicative of fat deposition, and changes in TRIG levels represent changes in overall energy reserves (Jenni-Eirmann and Jenni 1994). Despite being a point-in-time measure, TRIG levels serve as a proxy for the short-term rate of change in fuel stores (hereafter rate of fattening). Changes in TRIG over time have also been shown to reflect body mass changes (Jenni-Eirmann and Jenni 1994), fattening ability, and stopover site quality (Guglielmo et al. 2005).

A number of factors have been shown to influence overall body condition in migrants. For example, if young birds are less efficient foragers or flyers than adults (Ralph 1981, Wunderle 1991, Morris et al. 1996), they should not have as much fat at the time of capture and/or will not show as high rates of fattening as the adults. If endogenous time programs are influential in the Gulf of Maine and the progress of season accelerates fuel deposition (Dänhardt and Lindström 2001, Lindström et al. 1994, Schaub and Jenni 2000), then birds captured later in the season would be on a higher energetic trajectory (i.e., higher TRIG values) than birds captured early in the season. This would provide support for a time minimization optimal strategy late in the season. If diet is

important in determining condition, more frugivorous species should show higher rates of fattening (i.e., higher TRIG values) than omnivores, as high quality fruits are more fat and energy dense and previous studies have documented highly frugivorous species to be in better body condition and have higher fat deposition rates than omnivores (Bairlein and Gwinner 1994, Jenni-Eirmann and Jenni 2003, Smith et al. 2007). Lastly, migration distance, both distance traveled and distance remaining, may influence optimal strategies for birds in the Gulf of Maine. Given evidence that long-distance migrants use fuel differently than short distance migrants (Jenni-Eirmann and Jenni 1991, Jenni and Jenni-Eirmann 1998), long-distance migrants might be carrying larger fat loads and have higher TRIG values than short-distance migrants, also suggesting time minimization (Hedenström and Ålerstam 1997).

Here, we used blood plasma metabolite profiles, hereafter triglycerides (TRIG), as an index of refueling performance. Because it is hard to understand rates of fattening in the context of migration strategies without knowing what the bird's fat load is at time of capture, we also include fat score as a second response variable. Our first objective was to test how triglyceride values changed within each day to assess the quality of our sample location as a refueling site for migrants. Under our second objective, we tested five different, non-exclusive hypotheses based on the above factors to explain observed variation in plasma metabolite levels and fat content at a single stopover site: the 1) "experience matters" hypothesis, 2) "matter of time" hypothesis, 3) "you are what you eat" hypothesis, 4) "time for a break?" hypothesis (migration distance from origin) and 5) "are we there yet?" hypothesis (migration distance to goal).

## Methods

### **Field Site and Data Collection**

We established a banding station on Metinic Island, part of Maine Coastal Islands National Wildlife Refuge in mid-coast Maine (Figure 4.1). The entire island is 330 acres with the refuge owning just under half on the northern end. The banding station occupied approximately two acres on the northeast side of the forest, which bisects the island. There, the bayberry (*Myrica pensylvanica*) shrub-land transitions into a black spruce (*Picea mariana*) dominated forest with a few mixed hardwoods. Fruit producing plants, namely, bristly dewberry (*Rubus hispidus*), northern bayberry (*Myrica pennsylvanica*), chokeberry (*Aronia melanocarpa*), ilex (*Ilex sp.*), and mountain ash (*Sorbus americana*) are abundant around the banding area. The island is just over eight kilometers from the nearest point of mainland.

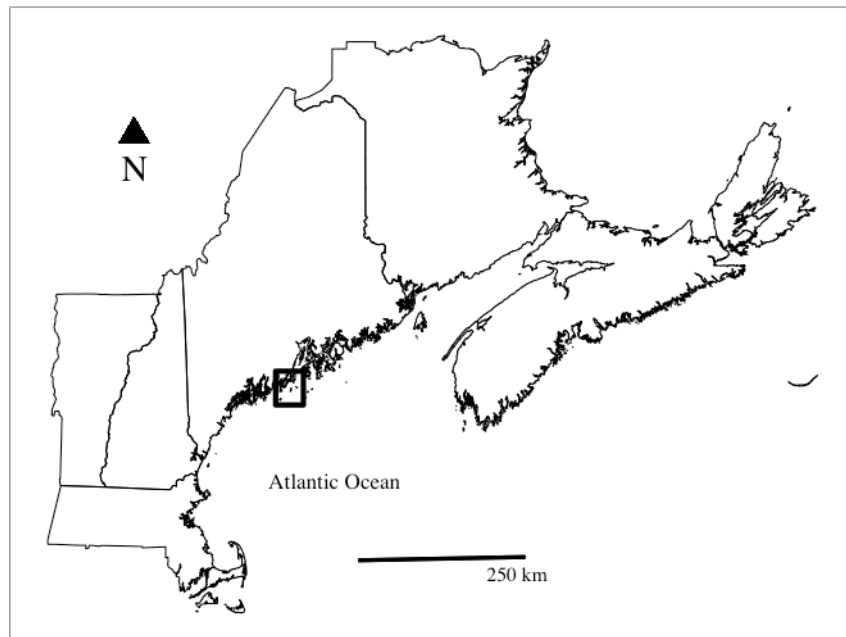


Figure 4.1. Map depicting location of Metinic Island in mid-coast Maine.



We monitored migration activity from mid-August through mid-October 2009-2011. We collected blood samples for use in metabolite assays from eight (including two subspecies) select boreal breeding landbird taxa as part of routine migration banding operations (Appendix A). We defined boreal breeding species, following Blancher and Wells 2005, as those having 50% or more of the global breeding population occurring in the boreal regions of North America. The focal species for this study were Magnolia Warbler (*Setophaga magnolia*-MAWA), Blackpoll Warbler (*Setophaga striata*-BLPW), Yellow-rumped Warbler (*Setophaga coronata*-YRWA), Western- and Yellow- Palm Warbler (*Setophaga palmarum palmarum* and *S. p. hypochrysea*.-WPWA/YPWA ), Swainson's Thrush (*Catharus ustulatus*-SWTH), Hermit Thrush (*Catharus guttatus*-HETH), and Dark-eyed Junco (*Junco hyemalis*-DEJU). We chose these species to include representatives from different taxonomic families, short- and long-distance migrants, and to also focus our attention on some species suffering known population declines within the boreal region (Crewe et al 2008, Environment Canada 2014, Sauer et al. 1996, 2014).

As part of routine data collection, fat scores included in this analysis were assigned on a scale from 0-5 based on the amount of visible subcutaneous fat in the furcular hollow and abdominal cavity, where '0' was no visible fat deposits and '5' was fat completely covering the breast and abdomen (no to very little skin visible); (see also Appendix A for detailed protocol). Using skull pneumatization patterns and presence or absence of molt limits, we aged all individuals as either adult - After Hatch Year (AHY) or young - Hatch Year (HY).

## **Blood Sampling**

For all captured birds of these species, we chose individuals to sample irrespective of age, sex, or time of season, but for bird welfare reasons, we did not bleed individuals that were exhibiting visible signs of stress or in a weakened state. Importantly, this did not exclude all individuals in fat category '0' because birds with no visible fat were not necessarily in "poor" or "weak" condition. Because handling time can influence blood chemistry (Guglielmo et al., 2001, Jenni-Eiermann and Jenni 1991), we only bled individuals that could be sampled within ten minutes of approaching them in the net. In the majority of instances, birds were bled within five minutes of initial handling.

We obtained our blood samples by puncturing the brachial vein with a 27-gauge needle and used an 80  $\mu$ L heparinized capillary tube(s) to collect, depending on species size, a maximum of 150 $\mu$ L per individual. We centrifuged all blood samples at 6,000 rpm for 10 minutes and recorded the ratio of plasma to packed red blood cells. We extracted the plasma using a 50- $\mu$ L Hamilton syringe. Plasma TRIG (Tmmol/L) were measured with enzymatic endpoint metabolite assays (Sigma-Aldrich, St. Louis, MO) and modified for a Packard Spectracount reader using 96-well plates and 5  $\mu$ L plasma volume.

Glycerol (GLYC), a blood metabolite indicative of mass loss or fat mobilization and necessary for determining plasma levels of TRIG, has sometimes been used as another measure of energetic trajectory, (Jenni-Eirmann et al., 2002, Jenni-Eirmann and Jenni 1994). Because plasma GLYC levels have been shown to be high at both low and high levels of TRIG (Cerasale and Guglielmo 2006, Guglielmo et al., 2005), however, we

first investigated the relationship between GLYC and TRIG in our data. The relationship between GLYC and TRIG was U-shaped (i.e., not linear), so we did not include it in this analysis. When glycerol serves a dual role in both lipolysis and fat deposition, it should not be included in metabolite profile analyses (Guglielmo et al., 2005).

### **Feather Sampling**

We collected feathers from all bled birds and analyzed them for stable hydrogen isotope signatures ( $\delta^2\text{H}_f$ ) to provide an index of distance already traveled (i.e., distance from breeding origin). We confirmed in the literature that all species except SWTH complete molt entirely or primarily on the breeding grounds prior to migration (Dunn and Garrett 1997, Pyle 1997). While SWTH can molt during the early parts of fall migration, by their arrival on migration in Maine, all individuals sampled had completed molt, and since all but five SWTH were hatch year birds, for which flight feather molt completes in the nest or shortly thereafter on the breeding grounds (Mack et al. 2000), we feel confident the sample signatures reflect breeding ground origin.

After investigating feathers for sign of loss and replacement, we plucked the right or left third retrix (R3) for all species except BLPW. Because feather loss and molt migration have been shown to influence flight performance, ability to maintain mass, and are associated with increased mortality risk (Holmgren and Hedenström 1995, Jenni and Winkler 1994, Lindstrom et al. 1993, Swaddle and Witter 1997), we collected upper back (between the scapulars) and nape feathers from BLPW to avoid plucking a flight feather from this known trans-oceanic migrant (DeLuca et al., 2015). Feathers were stored in paper envelopes and kept dry until analyzed.

## **Stable Hydrogen Isotope Extraction**

Feathers were cleaned, weighed, and analyzed for  $\delta^2\text{H}_f$  at the Stable Isotope Laboratory of Environment Canada, Saskatoon, Canada using standard procedures for isotope ratio mass spectrometry (IRMS), including using calibrated keratin hydrogen isotope reference materials (see Wassenaar and Hobson 2003, Hobson and Wassenaar 2008). All results for non-exchangeable hydrogen in feathers,  $^2\text{H}_f$ , are expressed with delta notation ( $\delta$ ) in units per mil (‰) and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale.

## **Statistical Analysis**

### Objective 1

To assess the quality of our stopover location as a refueling site for migrants, we used linear regression models with Gaussian error distribution to regress fat score and the  $\log_{10}$  transformed TRIG values against capture time, holding year and species constant.

### Objective 2

We used different explanatory variables to test each of the five hypotheses. In addition to testing age (experience matters hypothesis) effects on both TRIG values and fat content, we explored possible explanatory power of foraging guild (you are what you eat hypothesis), passage day (matter of time hypothesis), migration distance already traveled (time for a break? hypothesis), and migration distance to goal (are we there yet? hypothesis). We based foraging guild classifications on data in Erickson et al. 2011, Suomala et al. 2010, and Parrish 1997. If more than half of the individuals sampled in these studies consumed fruit or insects, and of those individuals, if 70% or more of their diet was comprised of fruit or insects, species were classified into the more specific

frugivore (or insectivore) categories. None of the species met the above (70% or more of the diet) criteria for classification as predominantly insectivore, thus all others were designated as omnivores (Table 1). To control for differences in the timing of migration for each species, we used passage day to evaluate any relationship between physiological condition and time of season. We calculated passage day by determining the median Julian Day for each species within each year. We then subtracted the capture date from the median. This resulted in passage day being a range of values from -39 to 39; median passage day was '0', passage day for birds captured prior to the median are negative values (i.e., early migrants), and passage day for those captured after the median are positive values (i.e., late migrants).

We determined migration distance left to travel by measuring the distance from Metinic to the latitudinal midpoint of each species' non-breeding range (based on Erickson et al. 2011, Rodewald 2016), and to provide an index of distance already traveled (i.e., distance from breeding origin), we used stable hydrogen isotope signatures from feathers ( $\delta^2\text{H}_f$ ) grown on the breeding grounds prior to migration. Typically, more negative signatures, relative to the Gulf of Maine, reflect individuals having traveled farther.

We computed separate univariate ANCOVA models to test each of the aforementioned exploratory hypotheses (n=5). We used this suite of models to evaluate relationships with triglyceride and fat response variables separately, so the total number of models tested equaled 10. We transformed triglyceride values ( $\log_{10} + 1$ ) to satisfy model assumptions. We included capture time, year, and species as control variables in all models except the one testing the “are we there yet” migration distance hypothesis

because migration distance as a continuous variable was already species specific. Year was important to control for possible inter-annual variation (Tsvey et al. 2007), and measures of physiological condition have also been cited to vary depending on time of capture because birds caught later in the day could have had more opportunity to feed (Jenni-Eirmann and Jenni 1997, Jenni and Jenni-Eirmann 1996).

Except where noted otherwise, all analyses were computed using the ‘lm’ function in the R Statistical Computing Environment (R Core Team 2016). For each model, we evaluated residual plots to assess fit of model assumptions. When testing fat, under both objectives, we used the cumulative link model (clm) to compute ordered logistic regressions with fat as the ordered response variable because it better fit the model assumptions (Christensen 2015). Graphics produced from clm analyses are not easily interpretable, however, so we also tested the same models using a linear mixed effects model approach. To satisfy linear model assumptions, we converted fat into a continuous variable and used a  $\log_{10} + 0.25$  transformation. Because both analyses resulted in comparable parameter estimates, significance, and direction of relationship, graphic (qualitative) results are based on the linear model and the quantitative output values presented are from the ordered logistic regression.

#### Post-hoc Analyses

We conducted two post hoc analyses to identify possible mechanisms explaining the results of our ‘you are what you eat’ and ‘matter of time’ hypotheses. First, given the difference in energetic trajectory between omnivores and frugivores, we questioned whether ultimate causation could be better explained by birds in a particular foraging guild being unable to fatten (e.g., differential resource availability or predation pressure)

or not fattening because they didn't need to (i.e., by choice or strategy). Since condition improved over time of day for each of our eight taxa, we reran the foraging hypothesis model with an interaction term to test whether a change in TRIG values and fat score throughout the day varied by foraging guild. Because TRIG change over time of day did not vary by foraging guild, but fat did, we subsequently explored the same relationship using mass (in grams; log10 transformed) as our response variable. Given the difference in fat content between foraging guilds, we predicted mass would show a similar relationship.

Second, to better understand our 'matter of time' hypothesis, we conducted a similar post hoc analysis as above except the interaction term was with passage day and and capture time, allowing the relationship between TRIG and time of day to vary with time of season, for each species separately.

## **Results**

We used a total of 273 samples in testing our first objective (the refueling potential at our stopover site) and each of the hypotheses we tested to explain observed variation in migrant's condition except migration distance from origin hypothesis. Because we were only able to analyze feather isotopes for a subset of the bled birds, our sample for the distance from origin hypothesis was smaller (n=118). TRIG values were variable among the eight species sampled in this analysis, and thrushes were carrying the least amount of fat upon capture (Table 4.1).

## Objective 1

Under our first objective, we examined variation in metabolites and fat scores over the course of a day to indicate stopover site quality. Birds captured later in the day had more than double the concentration of blood plasma triglycerides as individuals captured early (2.76 mmol/L vs. 1.27 mmol/L), suggesting an active fattening state for birds on Metinic (Figure 4.2,  $F_{1,1} = 87.58$ ,  $p < 0.001$ , adjusted  $R^2 = 0.30$ ). For birds captured later in the day, fat scores also indicated significantly higher levels of fat (0.96 vs. 1.66,  $z = 3.194$ ,  $p = 0.001$ , adjusted  $R^2$  from GLM=0.07).

Table 4.1. Summary statistics ( $\bar{x} \pm se$ ) for TRIG values and fat scores by species.

Species	Total n	Isotope n	TRIG (mmol/L)	Fat Score (0-5)	Foraging Guild Assignment
BLPW	94	20	$1.24 \pm 0.07$	$1.13 \pm 0.14$	Omnivore
MAWA	27	25	$1.43 \pm 0.23$	$1.15 \pm 0.20$	Omnivore
YRWA	86	9	$1.41 \pm 0.07$	$1.04 \pm 0.12$	Frugivore
WPWA	10	10	$2.22 \pm 0.42$	$1.40 \pm 0.26$	Omnivore
YPWA	17	17	$1.92 \pm 0.20$	$1.24 \pm 0.22$	Omnivore
SWTH	19	18	$2.20 \pm 0.35$	$0.75 \pm 0.16$	Frugivore
HETH	14	13	$2.27 \pm 0.28$	$0.18 \pm 0.84$	Frugivore
DEJU	6	6	$1.68 \pm 0.34$	$1.25 \pm 0.36$	Omnivore



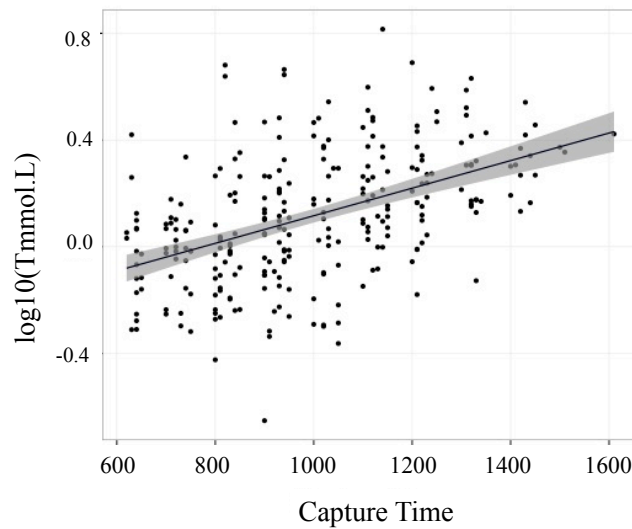


Figure 4.2. Relationship between TRIG values and capture time. Note: the y-axis is the log10 transformed TRIG values.

## Objective 2

In all five ANCOVA models testing the individual hypotheses, each control variable (capture time, year, and species) was significant at  $p < 0.05$ , showing inter-annual and inter-specific variation, along with confirming the variation over time of day. In each model, the control variables captured the majority of the observed variation, which we expected. This helped validate our models.

### Experience Matters (Age) Hypothesis

Neither TRIG values or fat score differed between adults and hatch year (i.e., young) birds (TRIG  $F_{1,1} = 1.115$ ,  $p = 0.29$ ; fat score  $z = -0.85$ ,  $p = 0.39$ , adjusted  $R^2$  from GLM=0.30; Figure 4.3).

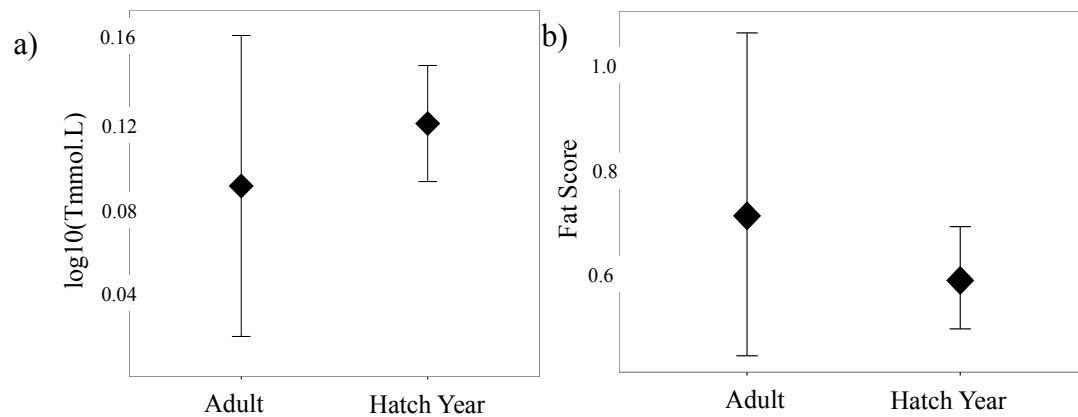


Figure 4.3. Relationship between a) age and TRIG values. Note: the y-axis is the log10 transformed TRIG values, and b) age and Fat Score.

#### Matter of Time (Passage Day) Hypothesis

Birds captured later in the season had significantly higher TRIG values than those captured earlier (Figure 4.4;  $F_{1,1} = 12.13$ ,  $p < 0.001$ , adjusted  $R^2 = 0.29$ ), increasing from 1.17 mmol/L to 1.45 mmol/L. Birds later in the season also carried significantly more fat than birds earlier in the season ( $z = 5.51$ ,  $p < 0.001$ , adjusted  $R^2$  from GLM=0.06). The variable intercept, constant slope species plots (Figures 4.4 and 4.5) highlight intra-specific variation in TRIG over the course of the season, not inter-specific.

#### You Are What You Eat (Foraging Guild) Hypothesis

Frugivores had significantly higher TRIG values than omnivores ( $F_{1,1} = 7.54$ ,  $p < 0.001$ , adjusted  $R^2 = 0.30$ ), 1.82 mmol/L vs. 0.98 mmol/L, respectively (Figure 4.6a) but showed no difference in the amount of fat they were carrying at time of capture ( $z = 0.26$ ,  $p = 0.79$ , adjusted  $R^2$  from GLM=0.05; Figure 4.6b).

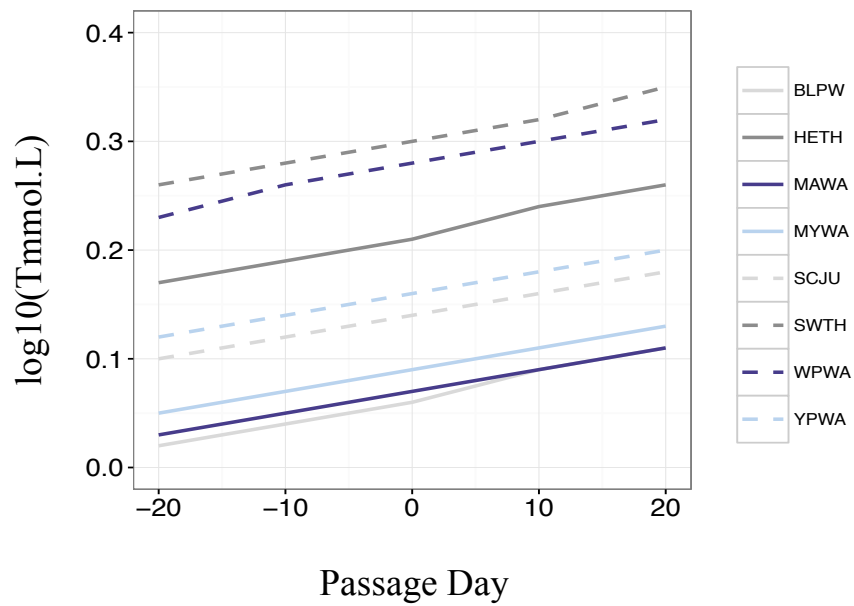


Figure 4.4. Relationship between TRIG values and passage day (time of season) by species. Note: the y-axis is the log10 transformed TRIG values.

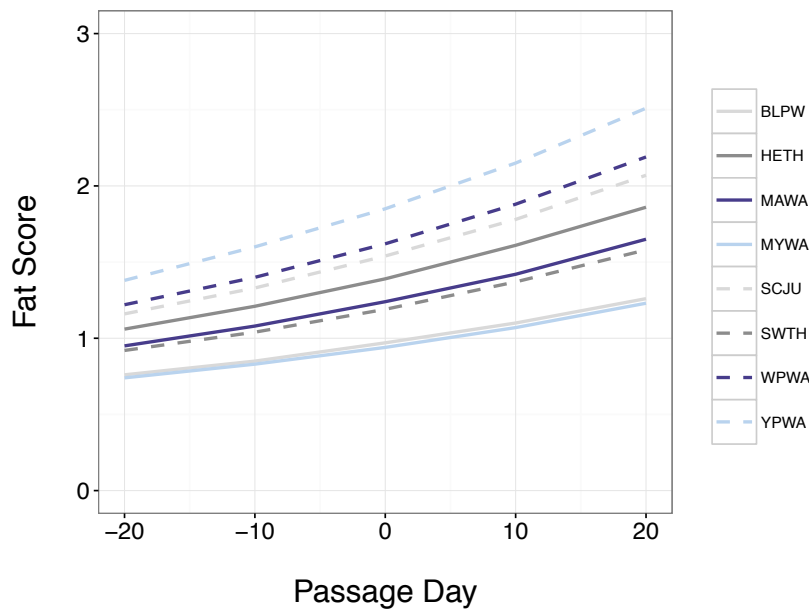


Figure 4.5. Relationship between Fat Score and passage day (time of season) by species.

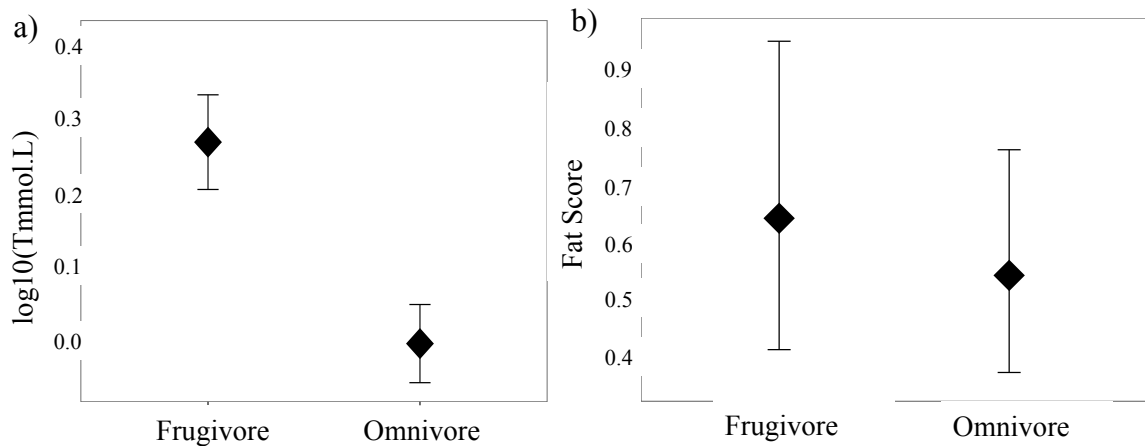


Figure 4.6. Relationship between a) foraging guild and TRIG (Tmmol/L) values. Note: the y-axis is the log10 transformed TRIG values, and b) foraging guild and Fat Score.

#### Time for a Break? (Distance from Origin) Hypothesis and Are We There Yet?

##### (Distance to Goal) Hypothesis

Neither measure of migration distance explained any of the observed variation in TRIG values (distance from origin  $F_{1,1} = 0.67$ ,  $p = 0.41$ , adjusted  $R^2 = 0.32$ ; distance to goal  $F_{1,1} = 5.79$ ,  $p = 0.02$ , adjusted  $R^2 = 0.23$ ; Figure 4.7) or fat scores (distance from origin  $z = -0.57$ ,  $p = 0.57$ ; distance to goal  $z = 0.49$ ,  $p = 0.62$ ).

##### Post-hoc

After including a foraging guild x time of day interaction term in the ‘you are what you eat model’, we found rates of TRIG increase throughout the day did not vary by foraging guild (interaction term;  $F_{1,1} = 1.795$ ,  $p = 0.18$ ; Figure 4.8). When testing fat as our response variable, however, omnivores showed no change in subcutaneous fat content over the course of a day, while frugivores did ( $z = -2.87$ ,  $p = 0.004$ ).

Interestingly, when we included mass as the response variable in an attempt to better understand the difference between the TRIG and fat response, we found mass increased

equally for both guilds (i.e., interaction term - not significant;  $t = -1.1$ ,  $p = 0.27$ ). Thus, omnivores, on average, started each day in leaner condition than frugivores but did not differ in the rate of increase for either TRIG or mass throughout the day.

Our test of whether change in condition over time of day varied with the season was not significant ( $F_{1,1} = 0.321$ ,  $p = 0.57$ ), i.e., there was no difference in rate of TRIG increase or fat gain between early and late season individuals.

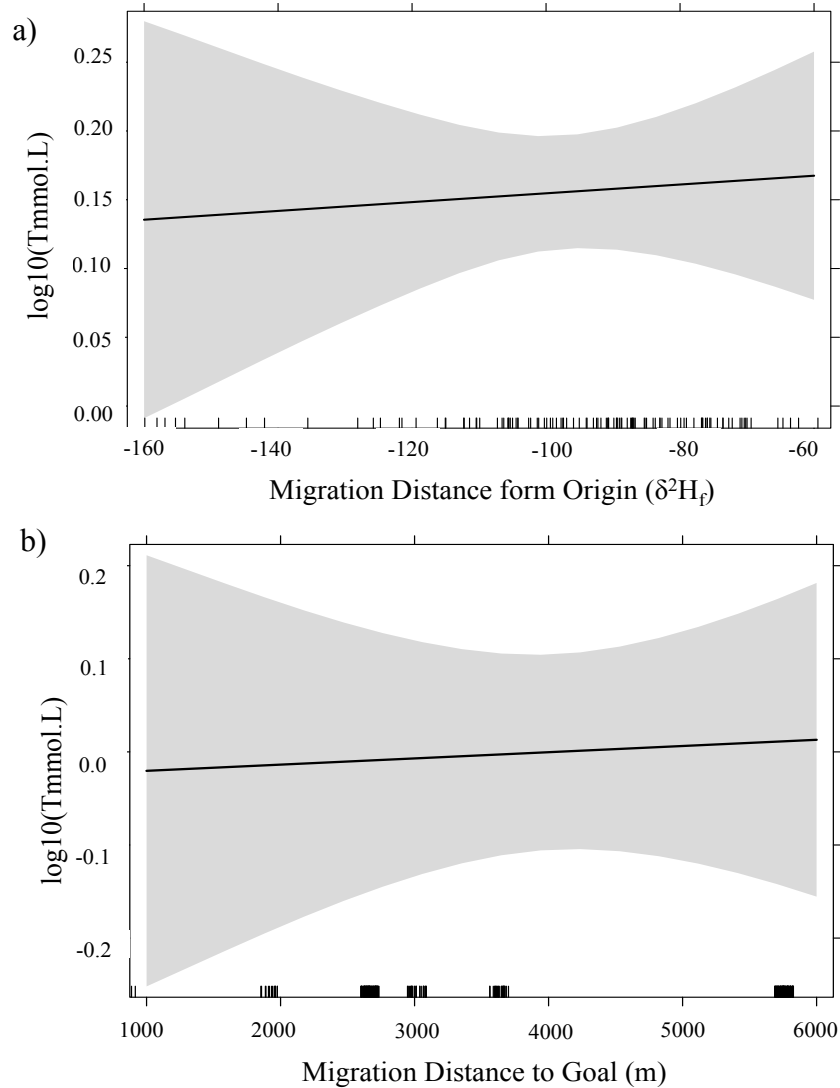


Figure 4.7. Relationship between TRIG values and a) migration distance from origin, and b) migration distance from goal. Note: the y-axis is the  $\log_{10}$  transformed TRIG values.

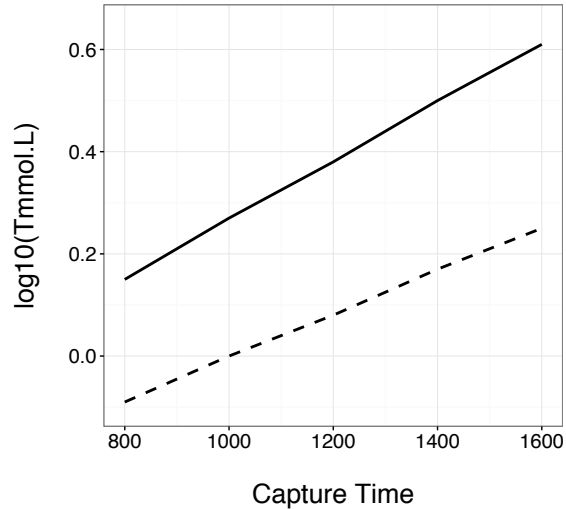


Figure 4.8. Results of post-hoc analysis interacting foraging guild and capture time with TRIG. The solid black line is the frugivores, and the dashed is the omnivores.

## **Discussion**

Under our first objective, we showed birds captured later in the day had higher TRIG values and fat scores, supporting the hypothesis that birds are actively fattening on Metinic Island. Our data largely represent birds that were only on Metinic Island the day of capture. In each of the sampling years, only 3-4% of birds were captured on multiple days, and daily surveys (Appendix D) to locate banded birds remaining in the area resulted in very few re-sights. Thus, it appears that, on average, habitat quality on Metinic is sufficient to support daily improvement in condition.

Under our second objective, two of the five tested hypotheses (“matter of time” and “you are what you eat”) explained some of the observed variation in both fat score and TRIG levels. Young birds did not have lower amounts of fat upon capture than adults, and consistent with some other studies (Benson and Winker 2005, Carlisle et al., 2005, Seewagen et al., 2013), age did not predict the rate at which a bird gained fat or increased mass.

Our findings indicated that frugivores were on a significantly higher energetic trajectory than omnivores. Though foraging guilds did not differ in the amount of visible subcutaneous fat upon capture, frugivores had significantly higher TRIG values. We expect fat deposition to be higher where high quality foods are abundant because they are energy dense (Bolser et al., 2013, Skrip et al. 2015, Smith et al., 2007, 2013, Smith and McWilliams 2010). Many of the most abundant fruit species on Metinic (e.g., bristly dewberry and northern bayberry) have been shown to be energy dense in nutritional analyses and appear, especially in combination, to meet birds' fat and protein requirements (Smith et al., 2007). This result demonstrated the advantage of frugivory for rapid lipid deposition and why many autumn migrants readily switch to a more frugivorous diet (Bairlein 1996, 1998, 2002, Newton 2008, Parrish 1997).

While lower on average (Table 4.1), frugivores did not have significantly less fat upon capture than omnivores. Given both foraging guilds showed similar rates of increase in TRIG throughout the day (Figure 4.8, post hoc analysis results), we inferred that the ability of birds to fatten on Metinic was not constrained by foraging. These results suggest that resources or other environmental pressures are not limiting omnivore's ability to fatten, though they begin the day with lower TRIG on average (Figure 4.8). Using a similar post-hoc interaction term between time of day and foraging guild to model variation in subcutaneous fat content, the change over the course of the day was significantly different for omnivores (no change) vs. frugivores (increase). It is possible that omnivore individuals are simply carrying a lighter, optimal fuel load and just maintaining, not gaining, mass. Our final post-hoc investigation, however, contradicts that explanation because mass increased equally for both guilds. This, again,

suggests similar opportunities for birds in both guilds to improve condition, but omnivores do not, however, appear to be gaining visible subcutaneous fat while frugivores are.

It has been suggested that, especially after a long, endurance flight, migrants recover lean (i.e., muscle and organ tissue) mass before accumulating fuel in the form of fat (McWilliams et al., 2004). It is possible that omnivores are recovering lean mass more so than frugivores. This would not explain the pattern described by TRIG, however. In a controlled diet study, Smith and McWilliams (2009) showed no correlation between lean mass acquisition and plasma metabolite levels. TRIG showed a stronger relationship in describing increases in fat mass. It is possible that this conflicting result for omnivores is due to differences in subcutaneous versus deeper fat deposition. Or, fat score may be too coarse a measure with an inherent assignment bias confounded by foraging guild.

A more likely alternative to explain an increase in TRIG without a corresponding increase in fat content for omnivores could be specific macronutrients in the diet. Smith and McWilliams (2009) and Gannes (2001) showed that short-term changes in blood metabolite concentrations, specifically TRIG, were more strongly influenced by specific macronutrients than actual fat mass. Smith and McWilliams (2009) emphasized the importance of considering diet composition when using blood plasma metabolites to explain fuel use or deposition. Perhaps, increasing TRIG values could be indicative of lipid consumption while simultaneous high dietary protein consumption could inhibit actual fat deposition to some degree. Controlled diet experiments on different omnivorous species and incorporating metabolites specific to identifying changes in



protein composition (e.g., uric acid) will help disentangle the mechanisms explaining this difference.

Our results also provided support for the “matter of time” hypothesis, with individuals of each species carrying more fat and increasing energetically (e.g., fattening) as the season progressed. Our post hoc result suggested that the difference in condition from the beginning to the end of the season was not resource driven. Thus, it could be suggestive of early season migrants in the Gulf of Maine operating under a more energy-minimization strategy. Time minimization strategies are typically characterized by higher fuel deposition rates and departure fuel loads (Alerstam 2011, Hedenstrom 2008), which we saw in birds captured late in the season on Metinic. Each of the species included in this study showed intraspecific variation in migration strategy across the season (Figures 4 and 5). These results provide evidence that as the migration season progresses for any given species, it becomes “just a matter of time” before individuals shift along the continuum to a more time-minimization-like strategy. Results from our “matter of time” hypothesis highlight the flexibility of the optimal migration theory and strategies in being applied within and between species, populations, and even individuals. Importantly, our results also highlight the need to control for differences in species’ relative passage dates before making inter-specific comparisons.

Given the results of our “matter of time” hypothesis, we were surprised neither the “time for a break?” (distance from origin) or “are we there yet” (distance to goal) hypotheses explained any of the variation in fat score or energetic trajectory. In an optimal migration framework, we would typically expect longer distance migrants, especially ones traveling from extreme northern latitudes to the tropics, as is the case

with some of the species in this study, to be following a more time-minimizing strategy. The results of this study, however, suggest that variation in physiological condition is explained more by intra-specific variation in strategies than between species variance. Intra-specific variation was not explained by differences in passage timing for birds arriving from different breeding origins (Leppold 2016, Chapter 2).

We can extend the meaningfulness of our findings beyond our hypothesis-testing framework by comparing TRIG values to those published for the same species in studies that identified or measured food availability and quality of stopover directly. While our species averages were somewhat lower than known high quality sites, most of the values were comparable or, in the least, higher than documented low quality sites (Table 4.2). Given the abundance of fruit on Metinic, *Myrica* (bayberry) in particular, which MYWA eat in abundance on fall migration, we were surprised the TRIG value was not any higher. Predictability of resources at future sites has been linked to energy minimization behaviors (Schaub and Jenni 2000, 2001), and bayberry is a fairly reliable resource along the coast of New England. Thus, MYWAs could simply be demonstrating a more plastic response to environmental (e.g., exogenous) factors that influence their migratory decisions and fuel departure load. MYWA was also the only species with individuals consistently captured over multiple days.

Table 4.2. Mean TRIG values for five of the eight focal species in this study compared to those from three other studies. Guglielmo et al., data were collected from two different Long Point Bird Observatory sites in Ontario in 2002, Seewagen et al., data were collected in 2007-08 at five different sites in or near New York City, and Smith and McWilliams data were collected from birds on Block Island, RI, in 2005. Metinic Island TRIG values in bold.

Species	Average TRIG $\pm$ SE (n)	Citation	Species	Average TRIG $\pm$ SE (n)	Citation
SWTH	<b>2.15 <math>\pm</math> 0.34 (19)</b>	This Study	HETH	<b>2.27 <math>\pm</math> 0.23 (14)</b>	This Study
	2.52 $\pm$ 0.62 (110)	Seewagen et al., 2011		2.53 $\pm$ 0.29 (16)	Seewagen et al., 2011
	2.01 $\pm$ 0.13 (35)			3.16 $\pm$ 0.53 (8)*	
	2.03 $\pm$ 0.24 (8)*			2.12 $\pm$ 0.48 (5)	
	2.61 $\pm$ 0.65 (7)*			1.64 $\pm$ 0.17 (5)*	
	1.24 $\pm$ 0.18 (6) <sup>-</sup>			2.17 $\pm$ 0.34 (8) <sup>-</sup>	
	2.14 $\pm$ 0.22 (13)*	Guglielmo et al., 2005		3.35 $\pm$ 0.27 (46)*	Guglielmo et al., 2005
	2.46 $\pm$ 0.22 (15) <sup>-</sup>			2.45 $\pm$ 0.18 (28) <sup>-</sup>	
MYWA	<b>1.41 <math>\pm</math> 0.07 (86)</b>	This Study		2.44 $\pm$ 0.12 (43)*	Smith and McWilliams 2010
	0.85 $\pm$ 0.13 (12)	Seewagen et al., 2011	MAWA	<b>1.35 <math>\pm</math> 0.26 (27)</b>	This Study
	1.53 $\pm$ 0.11 (31)*			1.72 $\pm$ 0.24 (30)*	Guglielmo et al., 2005
	0.42 (1)			1.01 $\pm$ 0.06 (10) <sup>-</sup>	
	1.75 $\pm$ 0.12 (36)*		SCJU	<b>1.68 <math>\pm</math> 0.34 (6)</b>	This Study
	1.75 $\pm$ 0.17 (12) <sup>-</sup>			1.80 $\pm$ 0.17 (16)*	Smith and McWilliams 2010
	1.75 $\pm$ 0.11 (34)*	Smith and McWilliams 2010			

\* denotes a “good” quality site as defined by the respective authors. Typically based on measures of food abundance and quality (fruit and arthropod)  
<sup>-</sup> denotes a “poor” quality site relative to others in the study

## **Conclusion and Conservation Implications**

Here, we provided critical baseline information on the physiological condition of fall migrants at an offshore site in the Gulf of Maine. Given the degree of within species variation in concentration of TRIG and fat deposition, our data suggests time minimization may not be optimal for all individuals. This conclusion is synonymous with that of recently published research conducted in the Gulf of Maine (Covino et al., 2015, McCabe 2015). Identifying migration strategies is important in understanding landscape level processes and constraints, without which it would be impossible to run predictive models to test birds' ability to change optimally in the face of climate induced shifts, habitat loss, etc. In addition, because birds near an ecological barrier are potentially already at an energetic threshold (i.e., in a state of reduced muscle mass or detrimentally catabolizing protein for fuel), displacement and barrier effects from coastal developments, such as offshore wind farms, could dramatically increase the potential energy expenditure of an individual and have serious fitness consequences.

Our results highlight the importance of conserving maritime shrubland habitats, especially for frugivores. Migratory success is dependent upon birds finding stopover sites of high enough quality that they can complete their migration. Fruits are abundant on Metinic, and fruit availability at stopover sites with shrubland habitat in the Gulf of Maine has been positively correlated with migrant abundance (McCabe and Olsen 2015a). If birds are not adapted to making long overwater flights in the GOM, meeting a minimum fuel load to deal with a potential water barrier crossing may require using coastal stopover sites as a detour (McCabe and Olsen 2015b). In which case, migrants

will benefit most from coastal stopover sites with an abundance of insects and native plant species that produce energy-dense fruits (Smith et al., 2007, 2013).

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## **APPENDIX A: NORTHEAST REGIONAL MIGRATION MONITORING**

### **NETWORK BANDING PROTOCOL**

#### **The Bander's Code of Ethics**

Banders are primarily responsible for the safety and welfare of the birds they study so that stress and risks of injury or death are minimized. Some basic rules:

- handle each bird carefully, gently, quietly, with respect, and in minimum time
- capture and process only as many birds as you can safely handle
- close traps or nets when predators are in the area
- do not band in inclement weather
- frequently assess the condition of traps and nets and repair them quickly
- properly train and supervise students
- check nets as frequently as conditions dictate
- check traps as often as recommended for each trap type
- properly close all traps and nets at the end of banding
- do not leave traps or nets set and untended
- use the correct band size and banding pliers for each bird
- treat any bird injuries humanely

Continually assess your own work to ensure that it is beyond reproach.

- reassess methods if an injury or mortality occurs
- ask for and accept constructive criticism from other banders

Offer honest and constructive assessment of the work of others to help maintain the highest standards possible.

- publish innovations in banding, capture, and handling techniques

- educate prospective banders and trainers
- report any mishandling of birds to the bander
- if no improvement occurs, file a report with the Banding Office

Ensure that your data are accurate and complete.

Obtain prior permission to band on private property and on public lands where authorization is required.

### **Operations**

#### **Dates - Migration only**

Banding takes place every day, weather permitting. Actual dates will vary by site location and personnel available. The following dates are offered as a guideline.

Spring Season - 7 April - 7 June

Fall Season - 20 August – 1 November (when feasible)

#### **Mist Net Types and Maintenance**

The number and type of mist net varies among sites. Sites may have some combination of full-length (12-meter) 30-36mm black nylon or polyester mesh nets and half-length (6-meter) 30-36mm mesh nets. 30-36mm mesh nets are the recommended size for migration songbird banding (Heimerdinger and Leberman 1996).

Mist nets should be repaired regularly or replaced as needed. Holes can negatively impact capture rates and can make extractions more difficult, increasing chance for stress or injury to the birds.

#### **Weather Conditions**

For migration banding stations, in general, nets should NOT be operated under the following conditions:

- Temperatures in direct sun above 70-75°F, as birds easily become overheated or hyperthermic.

- Temperatures below 45°F, as birds caught along the coast in migratory condition can be exhausted and easily become hypothermic, especially when being held at an outdoor banding site.

- Steady rain heavier than a light mist/drizzle.

- Sustained strong winds or intermittent gusty winds that repeatedly billow or blow nets into nearby brush.

The above are just provided as guidelines and, certainly, multiple factors will influence final decisions regarding weather. For example, it will depend on where the birds are being processed (e.g. tent or temperature controlled building), the amount of help available, the condition of the birds, and potential effects from confounding elements (e.g. cold AND rainy).

### **Opening Procedures**

As long as weather permits (see weather conditions, section III above), crews should strive to have nets opened a half-hour before local sunrise to catch birds at first light. Adjustments should be made accordingly as each season progresses. Open only as many nets as is possible to *safely* monitor.

In the morning, because of dewy grass and wet areas, the bottom trammels of the nets should be about a foot off the ground to prevent large birds caught in the bottom shelf from sagging into wet grass or streams of water. The latter, of course, is to be avoided at all times, not just in the morning. Typically, nets can be lowered as the day progresses and the grass dries. At sites where birds in nets may be subject to ground



predators and other small mammals, nets should be set no closer than about six inches from the ground. A good gauge is to throw an empty bird bag in the bottom shelf. Under dry conditions, a properly set net (with empty bird bag) should be just barely grazing the ground.

The top trammel loops, generally, should be opened to a height of about 2.5 meters (using a stick if necessary). The vertical shelf strings should never be stretched taut. Visually inspect every net at opening, *and throughout the day*, to ensure there is adequate pocketing along each net shelf, trammel lines are evenly spaced, and that netting is not snagged on loop ends or doubled over itself. As a general rule, anything that makes a net more visible to our eye makes it more visible to the birds.

### **Net Checks**

Ideally, two or more people should check nets each round, starting in opposite directions and always meeting somewhere in the middle (this insures that if one person has a lot of birds or a difficult extraction, help from another extractor is always on the way). Each person must continue to walk along the circuit, checking all nets, until meeting up with the other net checker. After all nets are cleared, checkers return directly to the station to assist, where needed, in the banding and processing of birds.

Net runs are to be done every 30 minutes, or more frequently (every 20 minutes) depending on the weather conditions (i.e. wind, rain, heat, cold) or if predators have been observed in the banding area (raptors, juvenile gulls, bear, deer - YES, deer!, etc.). If need be, birds not yet banded and processed from a previous round should be left in the tent while another round is completed. Birds in nets always have priority over birds safely resting in bags. Birds should not be held for more than about one hour beyond the

round in which they were gathered. With few exceptions, birds are processed in the order in which they were caught.

Net checkers should report changes in weather conditions (see above) throughout the day to the bander in charge so decisions can be made about doing more frequent net checks or closing nets if necessary.

Net checkers MUST walk the full extent of every net and check each net carefully, paying special attention to the bottom shelf. Even with nets set rather high off the ground, it is easy to pass by a bird lying still and hidden in the grass. To avoid this, net checkers should lift the bottom trammel of every net as they walk past.

Net checkers should always carry two-way radios and communicate with each other, as well as the bander-in charge.

### **Net Extractions**

When approaching a net to extract birds, net checkers should always look down the length of the net or line of nets to see if one bird appears to require more immediate attention (e.g. a tongued bird or a bird caught by one leg or one wing). Always work to extract these birds first, even if it means passing up “good” or easier birds.

Banders should be familiar with and strive to use the “body grasp” method of extraction, which when done properly, results in the rare (< 5% of entanglements) need to actively disentangle feet and toes. When the net is freed from around their wings and head, most birds actually will “let go” of netting that may, at first glance, appear to be badly tangled around their feet and toes! This has proven to be the quickest, most efficient, and safest method of extraction, as is also pointed out in Ralph (2005).

In extracting birds, you should be extremely careful to not unnecessarily damage or disarrange the bird's plumage, (i.e. take care to not bend flight feather shafts to the breaking point and be especially careful of growing pin feathers on molting birds which can cause excessive bleeding if broken). In general, strive to extract every bird with little or no feather loss. This is simply a good practice for protecting the welfare of each bird.

A trained net checker should not spend more than about a minute extracting any bird. *Excessive handling, especially during net extraction, and especially when progress is not being made for freeing the bird quickly, leads to physiological stress that can weaken birds.* This is particularly critical when working with birds that are actively migrating and not “resting”, as they are even more vulnerable to the stresses of over-handling. As stated at the outset, the well being of every bird is the top priority at all times. With nets being checked at appropriately frequent intervals, extractions, ordinarily, should take no more than about 15-30 seconds each. Too much time spent handling birds both during extraction and during processing (i.e., when banders are trying to determine the species, age, and sex of birds in hand) are the primary sources of physiological stress for birds caught for banding purposes.

Of course, occasional birds will be much more entangled in the nets, requiring far more than the minimum amount of time to extract, so if a net checker is having trouble extracting a bird, he or she should **never** hesitate to ask for help. Two- way radios should be carried by each bander/extractor so someone is always within a radio call away. The walkie-talkies should be used right away to contact another bander for help. Unless real progress at an extraction is being made, it is better for the net checker to simply wait with the bird (keeping the net slack, if necessary, but not handling the bird further) until

another person arrives. Or, better yet, leave the bird in the net, if this can be done safely (i.e. no risk of strangling) and continue on to other birds/nets, while another person works on the badly tangled bird.

*Continued handling of a badly caught bird when no real progress is being made with the extraction is stressful for that bird—again, it is **always** better to allow for a more experienced bander, or in the least someone with fresh eyes, to take over.* As a last resort (and something that should not be necessary more than once in several hundred or more extractions), it always is permissible to carefully cut or snap one or a few strands of net in order to free a bird that appears to be stressing rapidly. When done correctly, cutting the net *should never* result in netting remaining on the bird, however, should this happen, make sure to remove all pieces of net from the bird before release!

Individuals who are having persistent difficulty in extracting birds from nets should request guidance from the bander-in-charge in order to improve their extraction skills.

Especially on busy days, banded birds that are same day recaptures should be released at the nets and not brought back for repeated processing. This is especially true for still dependent locally hatched young birds (i.e., birds in full juvenal plumage and/or in active heavy first prebasic molt) and nesting adults (i.e. individuals with an active brood patch). For these individuals, band numbers may be written down or remembered at the net and written on the recapture sheet with “released at net” in the comments.

Radios can also be used to check numbers with someone at the station to determine recapture status. Data from recaptured migrant individuals is most valuable because fat and mass amounts can change even over a 24-hour period. However, as

mentioned above, try to avoid bringing back same day recaptures as these constant interruptions can have serious physiological consequences. Same day migrant recaptures should never be processed if less than 4-6 hours have passed from the time of the original captured.

Unless a licensed and permitted hummingbird bander is on site, all hummingbirds should be released at the net and recorded on the unbanded sheet with the time and the net they were released from.

NOTE: All birds should be evaluated upon extraction. Because of their migratory state and sometimes harsh environmental conditions along the coast, birds may be weak and in need of immediate attention. These individuals should either be released unbanded at the net or should be given priority status for processing.

### **Bags and Clips**

Lightweight cloth bags are used to carry birds from the nets to the station for processing. Heavier weight bags should only be used for larger, stronger birds such as jays and woodpeckers. Small lunch size paper bags can be used as back up. If using paper bags, banders should make sure that the paper bags are opened (inflated) all the way for ample airflow and then clipped closed with net clothespin.

Do not put birds in bags with loose strings along the seams. Bags should be sewn with a surge stitch, flipped inside out, or trimmed regularly to prevent injuries. Loose strings can easily become entangled around birds' head and legs.

Each bag should be clipped with a numbered clothespin from its respective net. Bags should also be hung on colored carabineers to be carried back to the banding tent.

The different color carabineers indicate the size of the bird and identify any individuals that need priority processing.

While in the banding tent or building, care should be taken to protect birds in bags from the elements. Do not hang bags in direct sunlight or allow them to get blown in the wind.

Bags should be shaken out and counted at the end of every day to ensure none are missing and all are “freshened” for the following day. Bags should be washed thoroughly as needed. Bags that carried a bird with foot pox, scaly leg, or conjunctivitis need to be washed thoroughly before using with any other bird. These conditions are all very contagious between birds

Some non-aggressive birds may be temporarily double-bagged (more than one bird/bag of the same species), for example, most warblers, goldfinches, and kinglets – but do not mix different species. In these cases, double-bagged birds **MUST** be separated upon returning to the banding tent. Otherwise, because of their migratory state, they may injure one another. Many birds **are** aggressive and should **NEVER** be double-bagged (even temporarily), for example, chickadees, titmice, vireos, strong-billed finches.

### **At the Banding Station**

Banding priority should be given to small birds (because of their higher per gram metabolic demand compared to larger species), individuals identified as in stress or weak at the net, recaptures, recently fledged young, and in the spring, females with brood patches. The last two should always be returned, as soon as possible, to the nets where they were extracted.

Ideally, there are at least two people involved in the banding process: a Bander and a Recorder. To maintain safety for the birds and ensure accurate data collection, no more than one person should be processing a bird at any one time. If there is ample help, a qualified third person may help expedite the process by physically banding the birds, re-bagging them, and lining them up in order to be processed. On busy days, others can assist by helping sort bags of birds waiting to be processed by species.

Each individual round should be marked in some manner so the Bander can gauge his/her rate of processing to the rate of captures. For example, a blank clothespin can be hung on the line in between the last bird from the previous round and the first bird from the most recent round. Importantly, banders should strive to have birds processed within an hour of capture. During busy days (>50 birds/hour), birds may be held no more than **two** hours from the time of capture. If this is not possible, nets should be closed and some birds may need to be released unbanded. Make sure to record species and net number on the unbanded sheet for that day

### The Bander

Only one bird is processed at any given time.

After removing a bird for banding, the Bander is responsible for insuring that the bag is empty and a double-bagged bird was not missed.

First, the Bander should call out the band size (so the recorder can pull up the appropriate data sheet); identify the species to the recorder, and then double check the band number with the recorder (it is best to double check band numbers every time, but it is critical to do this at least every few birds).

If using species' four letter codes, clarify these with the Recorder.

The Bander is responsible for selecting and attaching the proper band size to each bird, being careful to insure a good fit (e.g., correct “spiraled” or overlapping bands; file any sharp edges).

The Bander should try to band birds in order of priority, as stated above, generally working from small insectivores (0 and 0A size bands) up. Whenever possible, the bander should also sort the birds by species and band all individuals of like species in sequential order so data collection, recording, and subsequent computer data entry are more efficient.

Upon processing, the Bander is responsible for identifying the species, efficiently and accurately ageing/sexing all birds, and taking all necessary measurements, which are dictated to the Recorder. The entire processing procedure should take no more than a minute, except in cases when additional data or notes are being taken.

In order to keep up with the volume of birds on busier days and to speed up processing, Banders may skip certain measurements. The culmen and exposed culmen, followed by tarsus are to be thrown out first. Efforts should be made to, at a minimum, collect wing, fat, and body mass from each individual. If this is not possible, Banders need to compensate by closing nets and reducing capture rate. Banding data is of little value if collected in quantity without quality! Again, Banders should strive to have birds processed within an hour of capture and should not hold any bird longer than two hours.

\*(see below) Banders should not take tarsus or bill measurements on weak winged species that are prone to wing strain (e.g. Eastern Phoebe, Purple Finch, American Goldfinch, *Empidonax* Flycatchers (esp. HY), Cuckoos), as this increases the



handling time and chance for injury. Measuring the tarsus, in particular, also puts the bird in a position where the wings are not completely restrained and are prone to injury.

### The Recorder

The Recorder arguably may have the most important job of all! Scribing data without error for up to hundreds of birds in a day, often in the face of distractions of many kinds (e.g., visitors, conversation, etc.), can be a real challenge. Recording is not a spectator sport. Unless the data are recorded correctly as taken by the Bander, their scientific value is compromised. To some extent, it is the Bander's responsibility to also keep an eye on data being scribed by the Recorder. A good Recorder is worth his/her weight in warblers!

Each band size should have its own data sheet from 0A, 0, 1, 1B, and 1A+. Recaptures are recorded separately as are unbanded birds.

The recorder must check band numbers with the Bander frequently (every bird is not too often!).

The common names for each species, as well as the four-letter code, are recorded. It is important to write out the entire species name to avoid mistakes resulting from confusing four letter codes.

When more than one individual of the same species are processed in series, ditto marks can be used in the species field on the data sheet instead of rewriting the full common name again. (ultimately, this helps the Bander process more efficiently and makes data entry easier).

The entire nine-digit band number should be written down at the beginning and end of every band string, at the top of every data sheet, at the start of a new day, and

every time band series switch on a single data sheet (i.e., in the case of band sizes 1A and larger which get recorded on a single data sheet). Otherwise, the last two numbers of the sequence is sufficient.

The recorder is responsible for the completeness of each record and should ask the Bander for any data he/she has forgotten to announce.

It is the Recorder's responsibility to write down the weight of each bird by watching the readout from the digital scale (unlike the other data, the Bander will not call out the weight). On busy days, it is helpful for the Recorder to also release birds after being weighed.

Time is recorded in ten-minute intervals. As with species, the Recorder should use ditto marks instead of writing out the time for each record within a same ten-minute block.

#### Miscellaneous

Outside conversation should be taken away from the banding tent as this is distracting and can interfere with the accurate recording of data. All persons in the tent should keep the noise level low, both for the sake of data accuracy and for the bird's welfare. Some birds can be very sensitive to loud noise, especially raptors. This will cause undue stress to the birds and can make handling more difficult.

Care should also be taken when moving things around on the banding table or setting equipment down after use (e.g. wing rule, pliers, etc.). These noises can be very startling to birds during processing. Placing a rubber mat or some other sound absorbent material on the banding table is recommended.

After processing, birds are to be promptly released. Usually this is from the weigh cups. Photos of birds may **ONLY** be taken if time permits and if the bird is in **GOOD** condition (i.e. bright eyed, smoothed feathers, not showing signs of handling stress). Importantly, this rule also applies for the unexpected or unusual/rare bird. If photo documentation is necessary, pictures should be taken while the bird is being processed so it does not have to be held for extra time following banding. A bird's welfare should **NEVER** be compromised to take a picture.

**Banding Data (example datasheet file available upon request)**

- a. Date - month and day written once for the first record each day
- b. Band number – prefix and suffix of the band
- c. Species – full common name should be written out. The only acceptable abbreviations are “N.” for Northern, “Am.” for American, and “E.” for Eastern.
- d. 4-letter Alpha Code - use capital letters and if unsure, confirm in Pyle. Do Not make up codes.
- e. Age – The most precise and accurate (95% reliable) banding age codes (i.e. HY, AHY, SY, ASY, TY, ATY) should be assigned based on degree of skull pneumatization, wing molt limits, and/or plumage or soft part coloration.
- f. How Aged - Codes listed on datasheet. If the bander arrives at a definitive age using skull pneumatization, the “skulled” code should always be written down in this category. Otherwise, record the predominant method used to age the bird.

- g. Sex – M or F based on physical evidence or reliable (95% confidence) plumage and/or wing length criteria, U (undetermined) should be used for cases of overlap and for monomorphic species.
- h. How Sexed - This is especially important to fill in, in the fall, because many species' can no longer be sexed by plumage (Mulvihill et al 2004). In spring, if a bird is sexed by physical evidence, "C" or "B" should always be recorded over any other code.
- i. Wing length – length of the longest primary measured from the wrist on the unflattened folded right wing, to the nearest half millimeter. Factors affecting the length of the primaries, which would ultimately underestimate the wing length, (e.g. wear, active molt of the feathers, or bent tips of feathers), should be taken into consideration and, when appropriate, the wing should not be measured. Instead, record wing "worn," "bent," or "molt" in the comments field.
- j. Fat score – rated on a scale of 0-5, determined by amount of subcutaneous fat in furculum and abdomen. 0 = none; .5 = trace; 1 = lining furculum; 2 = filling furculum, flush with breast muscle; 3 = mounded in furculum and beginning to cover abdomen; 4 = mounded on breast and sides of abdomen; 5 = covering breast and abdomen (no or very little skin visible)
- k. \*Culmen - Bill measurement from the nares to the tip of the bill using calipers and recorded to the nearest tenth millimeter.

- l. \*Exposed Culmen - Bill measurement from the base of the feathering on the bill (not nostril or forehead feathering) to the tip using calipers and recorded to the nearest tenth millimeter.
- m. \*Tarsus - Leg measurement from the tarsal joint to the edge of the most distal scale before the toes emerge (following the description in Pyle 1997). Measure the right tarsus with calipers and record to the nearest tenth millimeter.
- n. Body Mass – Read from a digital scale tared to directly display the body mass of the bird and recorded to the nearest 0.10g .
- o. Time of processing – round down to the nearest 10-minute interval; record in military hours.
- p. The net where the bird was caught and the initials of the processor.
- q. Additional comments: Any physical abnormalities or other optional data. Rare species and unusual or interesting characteristics should be documented. Banding related injuries (e.g. wing strain) should also be recorded here.

### **Injured Birds**

Injured birds should be immediately brought to the attention of the Bander-in-Charge.

The Bander-in-Charge should be capable of making decisions regarding appropriate care of injuries. As responses vary, this protocol will not address specific injury related decisions. Treatment should **ONLY** be given by experienced personnel. Otherwise, attempts to “help” can often lead to further injury.

Recommended items for bird first aid include: ‘New skin’, disinfectant/sanitizer, super-glue. splinting materials (cut feather shafts from larger birds work well for passerines), ‘Quik-stop’

### **Closing Procedures**

Nets should be operated a minimum of 6 hours a day, weather permitting.

Depending on the location, nets may be left on the poles each day and furled tightly closed on the last net round of the day. This applies to island and remote mainland sites. To avoid vandalism, nets need to be taken down and put up each day at any site located within public access. All nets in public access areas also need to have the USGS permit and permit holder/operator contact information (protected from the elements) attached or clearly visible nearby.

To furl the nets: All loops should be placed together on the poles and the white (top) loop should be “locked” down over the other loops. The top trammel line is then pulled out towards the bander and the rest of the net is rolled as tightly as possible into the top shelf. This is best accomplished by starting at one end and rolling toward the middle of the net, watching the length of the net to be careful netting does not flip over the top trammel line as you are rolling. Then, complete the job from the other end of the net, making sure the direction of the roll is always from the same side of the net. After the netting is well rolled into the top pocket, flip the netting over the top trammel line a few times to draw the small gap between the top trammel and the rolled net closed.

This style of closing not only reduces the chance of a bird being caught accidentally in a closed net but also greatly facilitates the opening of nets in the morning, even when they are wet or frosted. Simply raise up the top trammel line unfurling the net

as necessary. Once the top trammel line snaps free, the rest of the net will fall out of the top bag easily when the other trammel lines are extended open.

### **Additional Information**

All unbanded birds should be recorded on a separate datasheet. This includes individuals that are observed hitting and bouncing out of the net, birds that escape while being handled before they are banded, and birds that may be released at the net unbanded (either because of weak condition or high volume). Record species, if known, and the net in which they were caught.

Every station is responsible for keeping record of banding related injuries AND mortalities in order to maintain that operations are being carried out to minimize these occurrences. Annual/seasonal mortalities should be < 1% of the total number of captures.

Effort - Banders are responsible for keeping track of net effort each day. The following information should be written down in order to calculate net effort:

- i. Time nets opened and closed
- ii. Which nets were opened and the total number of nets
- iii. Net hours (calculated by multiplying the number of nets open by the total number of hours nets were open) *Note: 6 - meter nets should be counted as half when calculating net hours.*

The following should be summarized at the end of each day and can be entered into respective Excel datasheets. Formatted Excel summary spreadsheets for the following are available upon request:

- i. Count of all individuals banded each day by species

- ii. Recaptures and unbanded birds are counted separately and are recorded simply as a total of each, not by species.
- iii. Number of birds captured in each net. Recaptures and unbanded birds should be included in this count.
- iv. The number of hours each individual net was open.

All banding records should be promptly entered and proofed for both recording and data entry errors.

### **Vegetation Characteristics and Net Lane Maintenance**

Net lane width should be less than one meter on either side of the net, as large disturbances to the vegetation around nets can create edge effects.

Net lanes should be kept clear of tall grasses, roots, vines, branches, etc. that may easily become entangled in the net and make extraction difficult or lead to bird injury.

Net placement should be standardized between sites to keep the general surrounding habitat as consistent as possible.

Photos should be taken of the vegetation in each net lane every year to document height and diversity of plant growth. Photos should be taken from the same vantage point and at the same angle twice each season, once in the beginning and once toward the end of the season.

Pictures should be saved in the following format: Location\_net#\_date  
(example) - Metinic\_Net15\_082810

Additional vegetative characteristic studies may be designed as needed.

Vegetation monitoring protocols, as used in National Park Service studies, are available in McCabe 2015.



## **Visitors**

It is at the discretion of each individual station how they handle visitors, however, bird welfare, handling time, and accuracy of the data should NEVER be sacrificed for education/demonstration purposes.

In general, we recommend not allowing visitors to participate in net runs or only using a small subset of nets to demonstrate the capture and extraction process.

Additional people on net runs can slow extraction time and progress, which compromises bird safety and welfare. Because most banding related injuries and mortalities occur in the net or during net extraction, it is also better to not open visitors up to the possibility of encountering one of these “sensitive” situations.

Visitors should NOT be allowed to walk net lanes unless led by qualified personnel. If visitors are taken to the nets, the group number should be kept to a minimum, as larger groups will increase the stress level for birds in nets. Personnel should also be sure to clear birds from bottom shelves before allowing visitors to approach the net to avoid birds accidentally getting injured or stepped on.

## **Bird Handling Safety**

Wash hands often. Wash with soap and water for 15-20 seconds. If hand washing with soap is not an option – sanitizing with an alcohol-based hand sanitizer is an appropriate alternative.

Do not eat, drink, or smoke while handling wildlife.

Handle birds upwind to the extent practical to decrease the risk of inhaling aerosols such as dust, feathers or dander. Work in well-ventilated areas when working indoors.

Do not handle any birds that appear to be sick or injured unless you are going to dispatch the animal. If it is necessary to handle these birds, wear personal protection equipment and wash materials that have come in contact with the bird.

Freshly killed birds (by predator, building strike, banding casualty, etc) can be saved for mounting by state and federal agencies or universities. Wrap birds in paper to freeze in natural position (folded wings, legs outstretched, head back, feathers smoothed). Place in freezer safe Ziploc bag with label of species, date, collector, location, age/sex, and cause of death (if known).

Call state and/or federal wildlife authorities if you find more than a few dead birds within a 24-48 hour period and stop handling all birds. A large number of dead birds could indicate a disease outbreak and you should not handle or attempt to collect them. Early detection and removal of carcasses is critical to controlling disease outbreaks but full personal protection equipment is required (goggles, respirator, coveralls, boot protectors, nitrile gloves).

Refer to the Field Manual of Wildlife Diseases to aid in the identification of avian diseases.

Wash or disinfect hands thoroughly after handling any bird with symptoms of foot pox, scaly leg, or conjunctivitis. These conditions pose no threat to banders but are highly contagious between birds.

## APPENDIX B: CHAPTER 2 CANDIDATE

### MODEL RESULTS by SPECIES

Candidate models and AICc selection criteria for each individual species.  $K$  = number of estimated parameters, AICc = Akaike's Information Criterion with second-order bias correction for small sample sizes,  $\Delta AICc$  = difference in AICc relative to the most parsimonious model, and  $\omega_i$  and *Cum.*  $\omega_i$  denote AICc weight and cumulative weights, respectively. WPWA and HETH did not have enough age structure in the data to include candidate models. SS refers to conditions at sunset, SR conditions at sunrise, 'u' is the east/west wind component (where '0' is no wind, a negative value indicates winds from the east, and larger vector values indicate stronger winds), and 'v' is the north/south wind component (where '0' is no wind, a negative value indicates winds from the north, and larger vector values indicate stronger winds).

#### B.1 BLPW model

Model	$K$	AICc	$\Delta AICc$	$\omega_i$	<i>Cum.</i> $\omega_i$
Null model (Intercept only)	2	394.7	0.0	0.56	
SR u/v	4	397.3	2.6	0.15	0.71
Age + SR u/v	5	398.8	4.1	0.07	0.78
SS u/v	4	399.1	4.4	0.06	0.84
Passage Day + SR u/v	5	399.5	4.9	0.05	0.89
Age + SS u/v	5	400.3	5.6	0.03	0.92
Passage Day + Age + SR u/v	6	401.2	6.5	0.02	0.94
Passage Day + SS u/v	5	401.6	6.9	0.01	0.95
SS u/v + SR u/v	6	402.6	7.9	0.01	0.96
Passage Day + Age + SS u/v	6	402.8	8.1	0.01	0.97

## B.2 MAWA model

Model	$K$	$AIC_c$	$\Delta AIC_c$	$\omega_i$	<i>Cum. <math>\omega_i</math></i>
Passage Day + Age + SR u/v	6	441.1	0.0	0.54	
SR u/v	4	444.5	3.3	0.10	0.88
Age + SR u/v	5	444.7	3.6	0.08	0.96
SS u/v + SR u/v	6	447.6	6.4	0.02	0.98
Null model (Intercept only)	2	451.3	10.2	0.01	0.99
SS u/v	4	454.8	13.7	0.00	0.99
Age + SS u/v	5	455.4	14.3	0.00	0.99
Passage Day + SS u/v	5	456.6	15.4	0.00	0.99
Passage Day + Age + SS u/v	6	456.9	15.8	0.00	1.00

## B.3 MYWA model

Model	$K$	$AIC_c$	$\Delta AIC_c$	$\omega_i$	<i>Cum. <math>\omega_i</math></i>
Passage Day + Age + SS u/v	6	738.5	0.0	0.39	
Age + SS u/v	5	739.7	1.2	0.21	0.60
Passage Day + Age + SR u/v	6	739.7	1.2	0.21	0.81
Age + SR u/v	5	739.9	1.5	0.19	1.00
Null (Intercept Only)	2	749.8	11.3	0.00	
SS u/v	4	750.2	11.7	0.00	
SR u/v	4	751.2	12.8	0.00	
Passage Day + SS u/v	5	752.2	13.7	0.00	
Passage Day + SR u/v	5	753.4	14.9	0.00	
SS u/v + SR u/v	6	754.3	15.8	0.00	

#### B.4 YPWA model

Model	$K$	AICc	$\Delta AICc$	$\omega_i$	Cum. $\omega_i$
Age + SS u/v	5	428.7	0.0	0.24	
Null model (Intercept only)	2	429.1	0.4	0.20	0.44
SS u/v	4	429.7	0.9	0.15	0.59
Passage Day + Age + SS u/v	6	429.8	1.1	0.14	0.73
Age + SR u/v	5	430.7	2.0	0.09	0.82
Passage Day + SS u/v	5	431.2	2.5	0.07	0.89
Passage Day + Age + SR u/v	6	432.0	3.1	0.05	0.94
SR u/v	4	432.4	3.7	0.04	0.98
Passage Day + SR u/v	5	433.8	5.1	0.02	1.00
SS u/v + SR u/v	6	434.1	5.4	0.00	

#### B.5 WPWA model

Model	$K$	AICc	$\Delta AICc$	$\omega_i$	Cum. $\omega_i$
Null model (Intercept only)	2	212.7	0.0	0.65	
SR u/v	4	215.7	3.0	0.15	0.80
SS u/v	4	216.9	4.3	0.08	0.88
SS u/v + SR u/v	6	217.1	4.4	0.07	0.95
Passage Day + SR u/v	5	218.4	5.7	0.04	0.99
Passage Day + SS u/v	5	219.9	7.2	0.01	1.00

## B.6 HETH model

Model	$K$	$AICc$	$\Delta AICc$	$\omega_i$	<i>Cum.</i> $\omega_i$
SS u/v	4	359.3	0.0	0.32	
SR u/v	4	359.5	0.2	0.29	0.61
Null model (Intercept only)	2	360.6	1.3	0.17	0.78
Passage Day + SS u/v	5	361.8	2.5	0.09	0.87
Passage Day + SR u/v	5	362.0	2.7	0.09	0.96
SS u/v + SR u/v	6	363.3	4.0	0.04	1.00

## B.7 SWTH model

Model	$K$	$AICc$	$\Delta AIC$	$\omega_i$	<i>Cum.</i> $\omega_i$
Passage Day + SS u/v	5	276.7	0.0	0.64	
Passage Day + Age + SS u/v	6	279.8	3.1	0.14	0.78
SS u/v	4	279.9	3.3	0.13	0.91
Age + SS u/v	5	282.8	6.1	0.03	0.94
SS u/v + SR u/v	6	283.5	6.8	0.02	0.96
Passage Day + SR u/v	5	284.1	7.5	0.02	0.98
Null model (Intercept only)	2	284.3	7.6	0.01	0.99
SR u/v	4	285.6	9.0	0.01	1.00
Passage Day + Age + SR u/v	6	287.2	10.5	0.00	
Age + SR u/v	5	288.5	11.8	0.00	

## B.8 DEJU model

Model	$K$	$AIC_c$	$\Delta AIC_c$	$\omega_i$	<i>Cum.</i> $\omega_i$
Age + SR u/v	5	618.8	0.0	0.27	
Age + SS u/v	5	618.3	0.5	0.21	0.48
Passage Day + Age + SR u/v	6	620.3	1.4	0.13	0.61
SS u/v	4	620.4	1.6	0.12	0.73
Passage Day + Age + SS u/v	6	620.8	2.0	0.10	0.83
SR u/v	4	621.3	2.5	0.08	0.91
Passage Day + SS u/v	5	622.8	4.0	0.04	0.95
Passage Day + SR u/v	5	623.6	4.8	0.02	0.97
Null model (Intercept only)	2	624.2	5.4	0.02	0.99
SS u/v + SR u/v	6	625.5	6.7	0.01	1.00

**APPENDIX C**  
**CHAPTER 3 SPECIES SAMPLE SIZES by SITE**

Proportion of young (HY) birds and sample sizes (in parentheses) for each species by site

Species	Great Duck Island	Metinic Island	Petit Manan Point	Seawall	Total N
American Goldfinch	1.00 (1)	0.00 (1)	0.93 (14)	0.83 (12)	28
American Redstart	0.86 (21)	0.95 (37)	0.67 (72)	0.69 (13)	143
American Robin	1.00 (6)	NA	1.00 (2)	0.81 (21)	29
Baltimore Oriole	1.00 (8)	1.00 (19)	1.00 (4)	1.00 (1)	32
Black-and-White Warbler	1.00 (9)	0.93 (27)	0.64 (33)	0.67 (6)	75
Blue-headed Vireo	1.00 (21)	0.97 (37)	0.86 (29)	1.00 (7)	94
Blackpoll Warbler	0.81 (21)	0.85 (192)	0.72 (116)	0.74 (43)	372
Black-throated Blue Warbler	0.80 (10)	0.84 (19)	0.94 (18)	1.00 (8)	55
Black-throated Green Warbler	1.00 (3)	1.00 (12)	0.78 (18)	1.00 (2)	35
Canada Warbler	0.50 (2)	1.00 (3)	0.83 (6)	1.00 (1)	12
Chipping Sparrow	NA	1.00 (11)	1.00 (2)	NA	13
Cape May Warbler	0.00 (1)	0.82 (11)	1.00 (2)	NA	14
Common Yellowthroat	0.92 (36)	0.88 (173)	0.78 (199)	0.83 (24)	432
Chestnut-sided Warbler	1.00 (3)	1.00 (4)	1.00 (6)	1.00 (3)	16
Eastern Phoebe	1.00 (6)	NA	1.00 (1)	0.75 (4)	11
Golden-crowned Kinglet	1.00 (24)	0.71 (7)	1.00 (39)	0.96 (24)	94
Gray-cheeked Thrush	1.00 (8)	1.00 (7)	0.75 (4)	1.00 (3)	22
Gray Catbird	0.92 (12)	0.83 (12)	0.95 (19)	0.91 (57)	100
Hermit Thrush	0.97 (31)	1.00 (21)	0.80 (46)	0.92 (26)	124
Indigo Bunting	1.00 (3)	1.00 (4)	1.00 (1)	NA	8
Least Flycatcher	1.00 (5)	1.00 (7)	0.93 (14)	0.86 (7)	33



Species	Great Duck Island	Metinic Island	Petit Manan Point	Seawall	Total N
Lincoln's Sparrow	1.00 (7)	1.00 (16)	0.83 (12)	1.00 (4)	39
Magnolia Warbler	0.62 (13)	0.74 (31)	0.50 (54)	0.38 (8)	106
Mourning Warbler	1.00 (3)	1.00 (9)	0.88 (8)	NA	20
Myrtle Warbler	0.94 (105)	0.92 (668)	0.95 (187)	0.92 (104)	1064
Nashville Warbler	1.00 (9)	0.90 (20)	0.91 (23)	0.86 (7)	59
Northern Parula	1.00 (3)	0.96 (25)	0.95 (19)	0.83 (6)	53
Northern Waterthrush	0.87 (39)	0.89 (64)	0.63 (24)	0.60 (5)	132
Ovenbird	1.00 (5)	1.00 (7)	1.00 (8)	NA	20
Palm Warbler	0.90 (21)	0.93 (70)	0.80 (35)	0.69 (13)	139
Philadelphia Vireo	1.00 (4)	1.00 (12)	1.00 (8)	1.00 (2)	26
Rose-breasted Grosbeak	1.00 (9)	0.67 (3)	NA	NA	12
Ruby-crowned Kinglet	0.88 (8)	1.00 (3)	0.93 (14)	1.00 (3)	28
Red-eyed Vireo	0.97 (99)	0.95 (196)	0.97 (133)	0.98 (40)	468
Savannah Sparrow	0.82 (33)	1.00 (9)	0.94 (16)	1.00 (7)	65
Dark-eyed Junco	0.98 (48)	0.94 (48)	0.97 (33)	0.89 (19)	148
Scarlet Tanager	1.00 (5)	0.83 (6)	1.00 (3)	1.00 (1)	15
Song Sparrow	0.96 (46)	0.97 (38)	1.00 (14)	0.85 (74)	172
Swamp Sparrow	0.93 (28)	0.83 (23)	0.85 (26)	0.94 (34)	111
Swainson's Thrush	0.63 (24)	0.75 (16)	0.71 (24)	0.91 (22)	86
"Traill's" Flycatcher	1.00 (12)	1.00 (16)	0.96 (25)	1.00 (24)	77
White-crowned Sparrow	1.00 (4)	1.00 (2)	1.00 (2)	1.00 (4)	12
Wilson's Warbler	1.00 (14)	1.00 (27)	1.00 (27)	1.00 (1)	69
Winter Wren	1.00 (2)	1.00 (2)	1.00 (3)	NA	7
White-throated Sparrow	0.93 (68)	0.87 (53)	0.87 (90)	0.78 (32)	243
Yellow-breasted Chat	1.00 (6)	1.00 (12)	1.00 (1)	0.82 (11)	30
Yellow-billed Cuckoo	1.00 (4)	1.00 (3)	1.00 (2)	1.00 (2)	11

Species	Great Duck Island	Metinic Island	Petit Manan Point	Seawall	Total N
Yellow-bellied Flycatcher	1.00 (13)	1.00 (3)	1.00 (17)	1.00 (1)	34
Yellow-bellied Sapsucker	1.00 (26)	1.00 (2)	0.50 (2)	1.00 (3)	33
Yellow Warbler	0.88 (17)	1.00 (26)	0.89 (19)	0.85 (13)	75

## **APPENDIX D: NORTHEAST REGIONAL MIGRATION**

### **MONITORING NETWORK AREA SEARCH**

#### **SURVEY PROTOCOL**

The information outlined in this protocol offers some basic standardized guidelines for network participants to follow when conducting surveys. However, because aspects of each site (i.e. habitat, proximity to water – which amplifies sound and affects detectability, personnel qualifications, etc.) vary so much among locations, and specific research goals vary among sites, operating procedures beyond those provided here should be tailored to fit the individual demands and resources at each respective site.

The guidelines and restrictions outlined here are also specific to conducting landbird surveys. We encourage network participants to also record shorebird, seabird, and raptor sightings independent from area search surveys, as the optimum time for surveying these other groups of birds will vary and recording additional behavioral observations (e.g. activity, hunting/foraging) may be beneficial.

There are a number of resources available that offer detailed field methods for monitoring landbird migrants and from which these guidelines were drawn. Network participants are encouraged to use these references in establishing new sites or incorporating surveys into existing monitoring efforts. A list of suggested readings is provided at the end of this document.

#### **Daily Surveys**

##### **Dates and Times**

Seasonal - Surveys are to accompany migration banding efforts and are to be completed daily, even in inclement conditions. This ensures continued sampling even on

days when weather precludes banding (see Additional Considerations section below). Actual dates will vary by site location and personnel available. The following dates (same as banding protocol) are offered as a guideline.

*Spring Season* - 30 April - 7 June

*Fall Season* ~ 20 August - 1 November

Daily - Surveys are to be conducted within two hours of local sunrise. For example, if sunrise is at 0530, surveys should be completed by 0730. Crews are expected to make adjustments accordingly as each season progresses. Surveys are 30 minutes long and should not be compromised for banding. If need be, banding efforts should be adjusted to allow for a crew member to leave and conduct the survey.

## **Location**

No site should have more than two independent survey areas.

Survey sites should be independent of the banding area, or as much as possible, to minimize sampling overlap. However, because the same crew is often managing all monitoring activities, distance from the banding area will also be an important consideration. At a minimum, we recommend survey sites be 50-100 meters away from the banding area (Figure 1). This will also help ensure disturbance caused during one activity does not affect results of the other (i.e. survey activity could disperse birds from net lanes if the two areas overlapped).

Sites with only one survey area should select survey habitat independent of the banding site. In other words, we recommend the survey site/habitat be chosen as if the banding area does not exist.

Sites with two survey areas should select one with comparable habitat to the banding area and one with more diverse vegetative characteristics. For surveying migrant activity, bear in mind that a relatively open site where the vegetation is not too dense and birds can still be seen easily is best (Hussell and Ralph 2005).

Sites should be between 1.5 and 1.75 acres in size. This is a manageable area to survey within the allotted 30 minutes. Metinic Island survey sites are shown in Figure 1 as an example.

The boundaries of survey sites should be *clearly* marked with flagging or otherwise denoted by landscape characteristics (i.e. shoreline or tree line) so observers count birds *only* within the defined area.

### **Survey Guidelines**

Apart from an initial training/orientation period, only one observer should be present in the survey area during the 30-minute survey period.

Only birds seen or heard within the boundaries of the survey area are to be counted. Birds heard or seen upon approaching or departing the survey area or observed outside of the 30-minute survey period should **NOT** be included. These can, however, be recorded among other incidental bird sightings for the day.

Observers may move freely within the defined survey area during the count period. These are *not* to be conducted as fixed-point count surveys. However, observers should budget their time so the entire area is covered during the 30-minute period. If extra time allows, an observer can always revisit a “hot spot”. Essentially, observers are “birding” within the boundaries of the survey area for 30 minutes and recording what they see or hear.

Importantly, counts are to be made conservatively and require the observer being aware of individual bird behavior, as to not count any individual twice. Thus, in recording the number of birds observed, the suggested approach is to record the maximum # of individuals of a given species seen at any one time. This ensures numbers of birds observed are independent of one another. For example, if you hear a Song Sparrow sing in spot A, observe it fly towards spot B, then observe a Song Sparrow in spot B later on in the survey and cannot confirm this as a different bird, the total Song Sparrow count should be 1, not 2.

“Pishing” is not allowed during the survey *unless* it is done very quietly and only to attract a target individual into sight for identification purposes. It is not to be used for detection purposes. “Pishing” or making noise of any kind is NOT allowed near the survey perimeter as this could influence movements of birds in and out of the survey area.

Observers should look for and document any banded birds included in the survey count to confirm if survey site data are reliably independent from banding data.

### **Data Collection**

The following information is to be collected as part of the daily surveys:

Location (if there is more than one survey area at a given site, e.g. Metinic has a coast and field survey site)

Start and end times, recorded in military hours

Brief weather description at time of survey, noting, specifically, conditions that could influence visibility or detectability of bird (e.g. wind, fog, drizzle).

Total number of individuals observed (this alone is the highest priority in terms of data collection) by species

If species cannot be identified, observers should record birds in general taxonomic groups (i.e. unknown warbler, unknown sparrow, etc.) or simply as ‘unknown’.

Lastly, when possible, documenting a bird’s age or sex may help distinguish individual birds observed throughout the survey period. For example, a surveyor may observe a Scarlet Tanager at two different points throughout a survey. Following the suggested protocol above, this should only be recorded as one since we cannot be certain it was just the same individual observed twice. However, knowing the first was a male and the second a female would enable us to confidently count them as two separate individuals.

### **Additional Considerations**

Weather certainly will affect the activity, as well as detectability, of birds during a survey. However, during inclement weather, surveys are our only source of information about migrant activity on the ground. Thus, as mentioned above, it is important for surveys to continue regardless of weather and especially important for observers to record weather conditions during the survey. Weather conditions should then be factored into data analysis of survey totals where necessary.

Inter-observer variability is often inevitable in bird surveys. Ideally, the same observer should conduct the surveys throughout each season and from year to year. Because this is often not the case, especially when conducting a multi-year study, it may be best to have a variety of qualified observers conduct surveys. This would help dampen the effects of between-year biases that arise from relying on a single observer,

especially if one particular observer had superior skills. Ultimately, this decision will be made on a site-by-site basis.

Survey data are to be analyzed separate from banding data. Count totals are not to be included in a 'Daily Estimated Total', as is done at some other migration monitoring sites (see References below).

### References

NRMMN survey protocol was adapted from area search censusing as described in:

Field protocol for migration monitoring at Rocky Point Bird Observatory. 2008.

Gahbauer, M.A. and M.A.R. Hudson, 2008. Field Protocol for migration monitoring program. McGill Bird Observatory.

Dunn, E. H., D. J. T. Hussell, C. M. Francis, and J. D. McCracken. 2004b. A comparison of three count methods for monitoring songbird abundance during spring migration: banding, census, and estimated totals. Pp. 116-122 *in* C. J. Ralph and E. H. Dunn (editors) *Monitoring Bird Populations Using Mist Nets*. *Studies in Avian Biology* 29.

Dunn, E. H. and D. J. T. Hussell. 1995. Using migration counts to monitor landbird populations: review and evaluation of current status. p 43-88 *in* D. M. Power (editor). *Current Ornithology*, Vol. 12. Plenum Press, News York, NY.

Hussell, D. J. T. and C. J. Ralph. 2005. Recommended methods for monitoring change in landbird populations by counting and capturing migrants. *NABB* 30: 6-20.

Ralph, C. John; Geupel, Geoffrey R.; Pyle, Peter; Martin, Thomas E.; DeSante, David F. 1993. Handbook of Field Methods for Monitoring Landbirds. Gen. Tech. Rep. PSW-GTR-144-www. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 41 p.



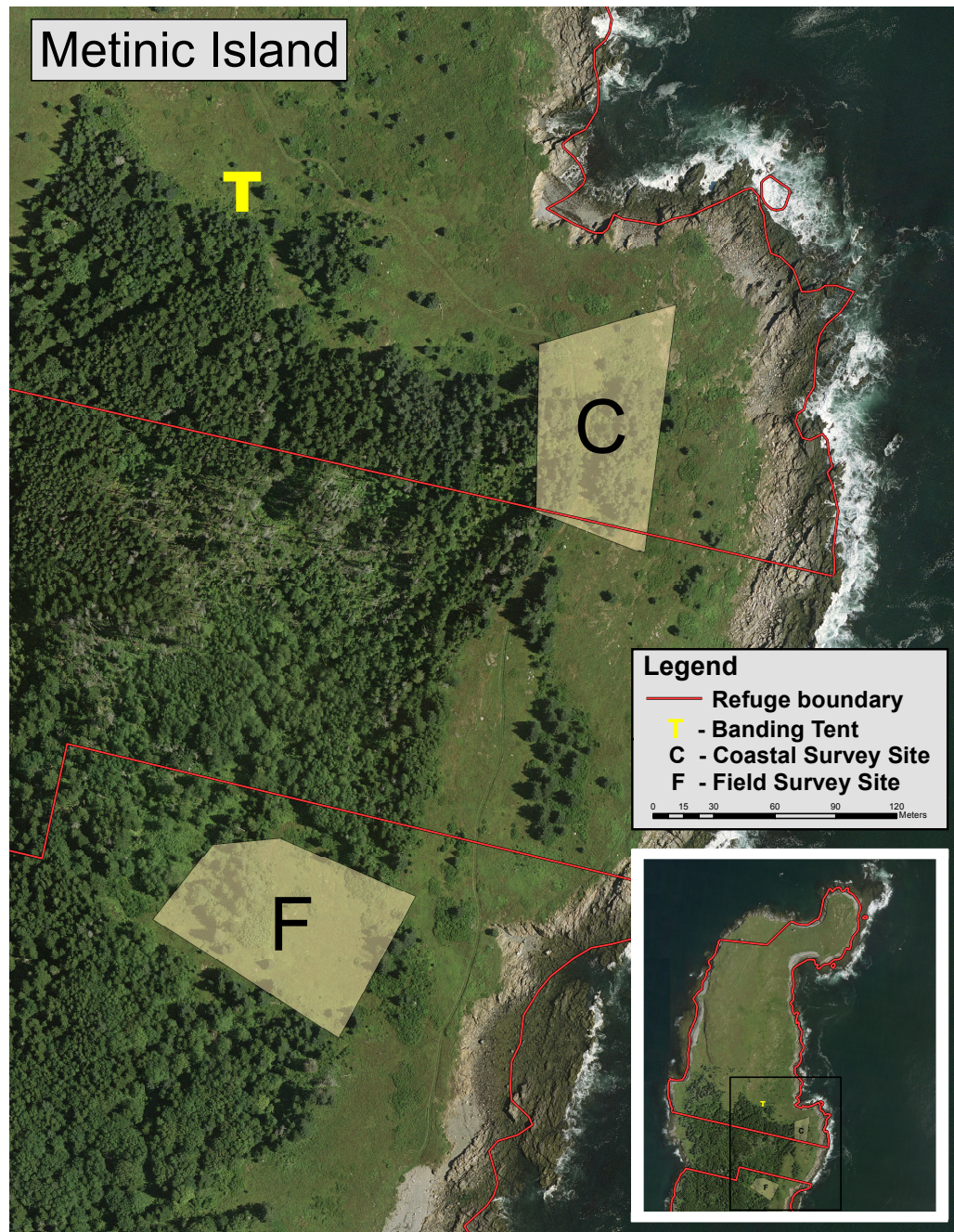


Figure D.1. Map showing the north end of Metinic Island, banding area, and two survey sites. Note the size and location of each site in relation to the other and to the banding station. Map produced by Michael Langlois, Maine Coastal Islands NWR.

## APPENDIX E: CHAPTER 4 SAMPLE 'R' SCRIPT

```
## examine variation in fat/trig/glyc using species, age, julian, time of day, origin, mig
dist
## fall migrants

library(lattice)      #graphics
library(lubridate)     #time/date handling
##### MASS models #####
library(lme4)
library(effects)
library(vegan)
library(MuMIn)
library(multcomp)
library(bbmle)
library(car)
####for plotting effects with interaction terms
library(interplot)
####plotting multiple regression lines with colors
library(sjPlot)
#### misc. packages for lmm and AICc ####
library(ggplot2)
library(grid)
library(nlme)
library(ordinal)

# bring in the data
trig.pass=read.csv(file.choose())
del.pass=read.csv(file.choose())
str(trig.pass)
names(trig.pass)
is.na(trig.pass)

# remove unnecessary variables...(keep just the ones you want to work with)
x = subset(trig.pass, select = c(Species, Mig.Dist, Mass, Julian, Forage, Year,
Capture.Time, pass.day, Age, Fat, Tmmol.L))
x2 = subset(del.pass, select = c(Species, Mig.Dist, Forage, Year, Capture.Time, pass.day,
Del.Value, Age, Fat, Tmmol.L))
str(x2)

#change year to factor
year=as.factor(x$Year)
as.factor(year)

#del should already be numeric
```

```

del=as.numeric(x2$Del.Value)
del

#evaluate Fat and transform
hist(x$Fat)
hist(log10(x$Fat+1))

#####
# an example of selecting specific data within a file. Using a master file with all species
#and specifying set of values for a variable
mawa = subset(x, Species == "MAWA" & Tmmol.L>1 & Gmmol.L>1)

# subset but not restricted to a set of values
mawa = subset(x, Species == "MAWA")
ypwa = subset(x, Species == "YPWA")
wpwa = subset(x, Species == "WPWA")
mawa = subset(x, Species == "MAWA")
mywa = subset(x, Species == "MYWA")
swth = subset(x, Species == "SWTH")
heth = subset(x, Species == "HETH")
scju = subset(x, Species == "SCJU")
blpw = subset(x, Species == "BLPW")

###show table of categorical variable values
table(x2$Fat, x2$Age)

###show above table as proportions (length divides by total in dataset)
table(x$Fat, x$Age)/length(x$Fat)

###calculate mean for TRIG and fat scores by species
mean(blpw$Tmmol.L)
mean(mawa$Tmmol.L)
mean(mywa$Tmmol.L)
mean(wpwa$Tmmol.L)
mean(ypwa$Tmmol.L)
mean(heth$Tmmol.L)
swth2=na.omit(swth)
mean(swth2$Tmmol.L)
mean(scju$Tmmol.L)

###for se(x) function
library(sciplot)
###calculate SE (+/-) for TRIG and fat scores by species
se(blpw$Tmmol.L)
se(mawa$Tmmol.L)
se(mywa$Tmmol.L)

```

```

se(wpwa$Tmmol.L)
se(ypwa$Tmmol.L)
se(heth$Tmmol.L)
swth2=na.omit(swth)
se(swth2$Tmmol.L)
se(scju$Tmmol.L)
min(blpw$Tmmol.L)
max(blpw$Tmmol.L)

#####
year=as.factor(ypwa$Year)
year=as.factor(wpwa$Year)
year=as.factor(mywa$Year)
year=as.factor(swth$Year)
year=as.factor(heth$Year)
year=as.factor(scju$Year)
year=as.factor(blpw$Year)

mean(Tmmol.L,na.rm=TRUE)
sd(Tmmol.L)

#frequency fat classes for all and by species
hist(x$Fat, col="grey")
hist(mawa$Fat, col="grey")
hist(ypwa$Fat, col="grey")
hist(wpwa$Fat, col="grey")
hist(mywa$Fat, col="grey")
hist(swth$Fat, col="grey")
hist(heth$Fat, col="grey")
hist(scju$Fat, col="grey")
hist(blpw$Fat, col="grey")

# if wanted to throw out data, look at just 2011 delta values
subset(x, Year=="2011")
#####

# look at distribution of variables, frequency plots (evaluated fat above)
hist(x$HCT, col="grey")
hist(sqrt(x$HCT))
hist(x$Tmmol.L, col="grey")
hist(log10(x2$Tmmol.L))

plot(Tmmol.L~Forage, data=x, col = "gray", xlab = "Foraging Guild",
      ylab = "Tmmol.L")
names(x)
#ab line will only work if you specify the slope and intercept, or tell it which lm

```

```

#model it should be based on
abline(col = "red")
y=lm(log10(Tmmol.L)~log10(Mass), data=x)
plot(y)
hist(log10(x$Mass))
summary(y)
plot(y)
#####

# test for multicollinearity, na.omit means leave out any (na) values, c3,6,7 identifies
# which columns of data to include in the collinearity plot
str(x)
pairs(na.omit(x[c(1,2)]),lower.panel=panel.smooth,
      upper.panel = NULL)

names(x2)
plot(Tmmol.L~Julian, data=x, col = "green", main="All")
plot(log10(Tmmol.L)~Del.Value, data=x2, pch= 16,
      ylab = "Tmmol.L", xlab="Del")
plot(Tmmol.L~Mass, data=x, pch= 16,
      ylab = "Tmmol.L")
plot(Tmmol.L~Fat, data=x, pch= 16,
      ylab = "Tmmol.L")
plot(Gmmol.L~Fat, data=x, pch= 16, xlab = "Fat",
      ylab = "Gmmol.L")

# this helps you to evaluate interactions visually,
# the pattern visible is usually reversed for two interacting variables, inconsistent
patterns,
#looking to tell if the distribution of the results for one variable is dependent upon the
other
boxplot(Age~Species, data=x2, col = "green")

#scatterplots
plot(fatty~Julian, data=fresh, pch= 16, xlab = Julian,
      ylab = "Fat")

##### Trig models All Birds #####
#Univariate tests for partial calculated R2
na.omit(x)

t.1=lm(scale(log10(Tmmol.L))~Mig.Dist+year+Capture.Time, data=x)
plot(t.1)
plot(effect("Mig.Dist",t.1), cex=3,cex.lab=5)
summary(t.1)
anova(t.1) #does not give r2 value, maybe try Anove

```

```

t.1b=lm(scale(sqrt(HCT))~Mig.Dist, data=x)
summary(t.1b)

t.2=lm(scale(log10(Tmmol.L)~Age+year+Capture.Time+Species, data=x))
anova(t.2)
summary(t.2)
interplot(m=t.2,var1="Tmmol.L",var2="Age")
plot(effect("Age",t.2))
t.2a=lm(scale(log10(Tmmol.L))~year+Capture.Time+Species, data=x)
summary(t.2a)

###get effects values to make a separate file for ggplotting
summary(effect("Age",t.2))
qplot(Age, log10(Tmmol.L),
data=x,method="lm",aes(group=1),formula=y~x,xlab="Age", ylab="Tmmol.L")

#investigate sex relationship for kicks
t.2b=lm(scale(log10(Tmmol.L)~Sex+year+Capture.Time+Species, data=x))
anova(t.2b)
summary(t.2b)
plot(effect("Sex",t.2b))

#back transform log10 trig values into an interpretable number
10^0.11
10^0.12
t.2c=lm(scale(log10(Tmmol.L))~year+Capture.Time+Species, data=x)
summary(t.2c)

t.3=lm(log10(Tmmol.L)~Forage+year+Capture.Time+Species+Forage:Capture.Time,
data=x)
t.3=lm(log10(Tmmol.L)~Forage+year+Capture.Time+Species, data=x)

## to test forage ability changed across the season
t.3b=lm(log10(Tmmol.L)~Forage+year+Capture.Time+Species+Forage:pass.day+pass.d
ay, data=x)
anova(t.3)
plot(effect("Forage:pass.day",t.3b))
summary(effect("Forage:pass.day",t.3b))
?exp
summary(effect("Forage",t.3))
# backtransform TRIG
10^0.26
exp(0.6)
10^0.002

t.3a=lm(scale(log10(Tmmol.L))~year+Capture.Time+Species, data=x)

```

```

summary(t.3a)

t.4=lm(log10(Tmmol.L)~pass.day+Species+Capture.Time+pass.day:Capture.Time,data=
x)
t.4=lm(log10(Tmmol.L)~pass.day+Species+Capture.Time+Species:pass.day,data=x)
anova(t.4)
t.4
10^0.07
10^0.16
summary(t.4)
summary(effect("pass.day:Species",t.4))
plot(effect("Species:pass.day",t.4))

t.5=lm(log10(Tmmol.L)~del+year+Capture.Time+Species,data=x2)
10^0.01
10^0.4
anova(t.5)
plot(effect("del",t.5))
summary(effect("del",t.5))
summary(t.5a)

t.6=lm(log10(Tmmol.L)~Capture.Time:Foraging+year+Species, data=x)
summary(t.6)
anova(t.6)
plot(effect("Capture.Time",t.6), cex=1.5,cex.lab=2.0)
(10^0.01)+0.25
(10^0.4)+0.25

#evaluate quadratic
t.4a=lm(scale(log10(Tmmol.L))~scale(pass.day)+I(scale(pass.day)^2)+scale(Capture.Ti
me)+Species+pass.day:Species,data=x)
anova(t.4)
summary(effect("Julian",t.4a))
plot(effect("pass.day",t.4))
#####
##get graphing specs
par()

#multi species plot made from summary effects/species csv (no confidence intervals),
# make ggplot from csv file like other effect plots for categorical variables.
# code below is just from other ways I found to try
# Species intx factor
x$pass.day
t.4=lm(log10(Tmmol.L)~pass.day*Species+Species+pass.day+Capture.Time+pass.day:C
apture.Time,data=x)
eff=effect("pass.day*Species", t.4)

```

```

plot(eff)
##pub quality figure
p=qplot(Capture.Time, log10(Tmmol.L),data=x,
geom=c("point","smooth"),method="lm",
xlab="\nCapture Time", ylab="log10(Tmmol.L)\n")

#OR

p=ggplot(x, aes(Capture.Time, log10(Tmmol.L)))

#check variables
summary(p)
p+ geom_point()+ geom_smooth(method="lm", colour="black")+
xlab("\nCapture Time")+ ylab("log10(Tmmol.L)\n") #\n moves text away from axis

####create layers for plot
p + theme_bw() + #black and white
theme(panel.grid.minor=element_blank(), #remove grid lines
axis.text.x = element_text(colour="black", size=15),axis.text.y =
element_text(colour="black",size=15))+
theme(axis.title.x = element_text( size=20))+
theme(axis.title.y = element_text( size=20))+
geom_smooth(method="lm", colour="black")

#####Fat analyses#####
# w/ species - does not work well
#test for multicollinearity first
pairs(na.omit(x[c(6,7,8,12)]),lower.panel=panel.smooth,
upper.panel = panel.cor)

#Make fat ordered factor and confirm
fat.o=as.ordered(x$Fat)
is.ordered(fat.o)
fatty=as.numeric(x$Fat)
str(x)
fatty
is.numeric(fatty)
hist(log10(fatty))
#using clm and lm
f.1=lm(log10(fatty+.25)~scale(Mig.Dist)+year+Capture.Time, data=x)
anova(f.1)
summary(f.1)
f.1b=clm(as.factor(Fat)~scale(Mig.Dist)+year+scale(Capture.Time), data=x)
summary(f.1b)
anova(f.1b)

```



```

f.2=lm(log10(fatty+.25)~Age+year+Capture.Time+Species, data=x)
anova(f.2)
summary(f.2)
summary(effect("Age", f.2))
##10^effect -.25 to back transform
f.2b=clm(as.factor(Fat)~Age+year+scale(Capture.Time)+Species, data=x)
summary(f.2b)

hist(x$Mass)
f.3=lm(log10(fatty+0.25)~Forage+year+Capture.Time+Species+Capture.Time:Forage,
data=x)
f.3mass=lm(log10(Mass)~Forage+year+Capture.Time+Species+Capture.Time:Forage,
data=x)
f.3=lm(log10(fatty+0.25)~Forage+year+Capture.Time+Species, data=x)
anova(f.3)
summary(f.3mass)
plot(effect("Forage:Capture.Time",f.3mass))
summary(effect("Forage:Capture.Time", f.3))
summary(effect("Forage", f.3))
boxplot(fatty~Forage, data=x)
boxplot(log10(Tmmol.L)~log10(fatty+.25), data=x)
(10^-0.05)-0.25
(10^-0.1)-0.25
f.3b=clm(as.factor(Fat)~Forage+year+scale(Capture.Time)+Species, data=x)
summary(f.3b)

f.4=lm(log10(fatty+.25)~pass.day+Capture.Time+I(scale(pass.day)^2)+Species+Capture.
Time:pass.day, data=x)
f.4a=lm(log10(fatty+.25)~pass.day+Capture.Time+Species, data=x)
anova(f.4a)
summary(f.4a)
plot(effect("pass.day",f.4a))
(10^0.27)+0.25
(10^-0.1)+0.25

f.4b=clm(as.factor(Fat)~scale(pass.day)+scale(Capture.Time)+Species, data=x)
summary(f.4b)
summary(effect("pass.day:Species",f.4a))
plot(effect("pass.day",f.4a))

f.5=lm(log10(fatty+.25)~del+year+Capture.Time+Species,data=x2)
anova(f.5)
f.5b=clm(as.factor(Fat)~del+year+scale(Capture.Time)+Species, data=x2)
summary(f.5b)

f.6=lm(log10(fatty+.25)~Capture.Time+Species+year,data=x)

```

```
summary(f.6)
plot(effect("Capture.Time", f.6))
anova(f.6)
(10^0.15)+0.25
(10^-0.15)+0.25

f.6b=clm(as.factor(Fat)~scale(Capture.Time)+Species+year, data=x)
summary(f.6b)
```

## **BIOGRAPHY OF THE AUTHOR**

Adrienne Jo Leppold was born and raised in Pittsburgh, Pennsylvania and graduated as a band geek from Penn Hills Senior High School in 1997. After graduation, she knew she wanted to work with wild animals, so she pursued a degree in wildlife biology at California University of Pennsylvania (CalU). Originally preparing for a career path that would land her in a zoo (that was the extent to which this city girl thought she could work with wildlife), she soon came to understand through coursework and friends that there was such a thing as a “field biologist”. Her experience as a wildlife biology major in undergrad set her on the path she has pursued ever since, quickly transforming her from band geek to bird nerd. She received her B. S. degree in wildlife biology from CalU in May 2001.

She promptly turned down many well-paying, seasonal field technician positions following graduation and instead decided to “volunteer” for a project working with the Alaska Peninsula/Becharof National Wildlife Refuge (to be fair, she made \$3.00/day). This position broadened her experiences and even expanded into well-paying positions the following two years. Combine her experiences in Alaska with volunteering at one of the largest scale, longest running bird banding laboratories in the country (Powdermill Nature Reserve in southwestern PA - training fee paid in grunt data entry labor), and thus, a field ornithologist was born. She continued traveling as a field technician while also working at Powdermill. She ultimately took over the banding program at Powdermill but only after first trying to talk her boss out of giving her the job. Thankfully, others saw in her what she didn’t see in herself. Eventually, though, she reached her limits there and decided to pursue graduate school.

While her experiences have focused on passerines, near passerines, and seabirds, she is also experienced with raptors and shorebirds. Her graduate work has made groundbreaking strides in understanding the movement of landbirds through the region and led to the creation of an international, multi-agency initiative to study bird migration in the Gulf of Maine. She is a candidate for the Doctor of Philosophy degree in Biological Science from The University of Maine in August 2016.