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Stopover Ecology of Ruby-throated Hummingbirds (*Archilochus colubris*) During Autumn Migration

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STOPOVER ECOLOGY OF RUBY-THROATED HUMMINGBIRDS (*ARCHILOCHUS COLUBRIS*) DURING AUTUMN MIGRATION

by

Theodore Joseph Zenzal Jr.

A Dissertation
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and the Department of Biological Sciences
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

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ABSTRACT

STOPOVER ECOLOGY OF RUBY-THROATED HUMMINGBIRDS (ARCHILOCHUS COLUBRIS) DURING AUTUMN MIGRATION

by Theodore Joseph Zenzal Jr.

May 2016

The Ruby-throated Hummingbird (Archilochus colubris) is one of the smallest Nearctic-Neotropical migrants and the only species of hummingbird that breeds in Eastern North America, yet few studies have investigated the biology of Ruby-throated Hummingbirds when they stopover during migration. Given their small size, high metabolism, aggression, and specialized diet, hummingbirds may represent a migrant that operates on the physiological edge. Therefore it is important to understand the factors that influence their stopover as well as the decision to resume migration. Towards this end, Ruby-throated Hummingbirds were captured during autumn migration along the northern coast of the Gulf of Mexico to investigate (1) differences between age and sex classes during stopover, (2) resource use and defense during stopover, (3) the feasibility of using radio telemetry, and (4) the conditions influencing both an individual’s departure time and direction upon resuming migration. Data provided strong evidence of age-dependent migration and only weak evidence of sex-dependent migration. Older birds arrived earlier, had larger fuel loads, had shorter stopover durations, and longer estimated flight ranges than younger birds. In younger birds there was no effect of sex, but in older birds males arrived with larger fuel loads than females. When ages were combined, males were estimated to have longer flight ranges compared to females. During stopover, males tended to use aggressive behaviors in order to obtain priority access to resources. Resource use was influenced by defense, fuel load, conspecific density, and sex. Resource defense was influenced by conspecific density and fuel load. An aviary study to determine the influence of radio-tags on hummingbirds suggested that individuals are capable of carrying the additional weight; however, effects were less when tags were smaller. When birds departed coastal Alabama, the majority left between sunrise and noon and timing was dependent on both wind direction and wind speed. The distribution of departure bearings were uniformly distributed, although most individuals departed parallel with the coast line. Overall, these results suggest that the stopover and migration of Ruby-throated hummingbirds are influenced by the interaction of both intrinsic and extrinsic variables as they circumnavigate the Gulf of Mexico to tropical wintering grounds.

ACKNOWLEDGMENTS

This research could not have been completed without the help of many different individuals and organizations. The person deserving of the most recognition is my advisor, Frank Moore, without whom this work would not have been possible. Frank not only worked countless hours to see this research through, he also provided inspiration, optimism, and support during my career as a graduate student. Frank has not only been a mentor and a teacher, but also a friend, and I am grateful to have had the opportunity to work under his supervision. My committee members also provided unwavering support of this research from initiation to completion. Robb Diehl has been integral in the design and methods of some of this work as well as in my professional and personal development. Åke Lindström has provided constructive criticism and stimulating conversations about hummingbird migration; I appreciate him allowing me to carry out his project. Carl Qualls was a source of statistical guidance and gave me an appreciation of gene theory. Conversations with Jodie Jawor were essential in developing the methodology used during behavioral observations. Finally while not an official committee member, Jake Schaefer provided vast amounts of statistical advice and humor. I thank you all for the time you have invested in me.

I would also like to thank present and past members of the Migratory Bird Research Group. I am especially grateful to Will Lewis, Kristen Covino, Emijo Lain, Jaci Smolinsky, Zoltan Németh, Rachel Bolus, Michael Sellers, Emily Cohen, Kristina Paxton, Eben Paxton, Sheri Glowinski, and Jill Lafleur who

helped me both in and out of the field. Zoltan Németh also provided inspiration and advice throughout my time at USM. Rob Smith was an instrumental part of who I am today; without Rob seeing my potential as a student and a researcher I would likely not be completing this degree. I am fortunate to have been part of the Migratory Bird Research Group family.

I would also like to thank the different organizations that made this research possible. The Bon Secour National Wildlife Refuge, Dauphin Island Sea Lab, Fort Morgan State Historic Park, and Alabama DCNR allowed us to conduct work on their property. Funding was provided through the National Science Foundation (NSF), National Geographic, Birmingham Audubon Society, Alabama Ornithological Society, Wilson Ornithological Society, Louisiana Ornithological Society, Eastern Bird Banding Association, and a fellowship through the NSF GK-12 program “Molecules to Muscles”.

I would also like to thank collaborators for assistance in analyzing radio telemetry data, especially Mike Ward, Jill Deppe, Rachel Bolus, Tony Celis-Murillo, and Lynn Schofield. However, data collection would not have been possible without the USM graduate and undergraduate students that helped to set up and take down radio towers in exchange for pizza.

Finally, none of this work would have been possible without the hard work and dedication of my Fort Morgan field crews. Even though the days were long and sometimes intense, at the end of the season we were all rich in experience. Thank you for your dedication and passion.

DEDICATION

I dedicate this dissertation to my family and friends that have supported, inspired, and believed in me. My parents, Ted and Debbie Zenzal, have been a source of constant support throughout my life and without them I would not have been fortunate enough to pursue so many great opportunities that have made me who I am today. Emijo Lain has been my biggest supporter; words cannot describe the amount of gratitude I have for everything she has done for me. Thank you all.

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Introduction

Approximately two thirds of all birds breeding in Eastern North America are Nearctic-Neotropical migrants (Rappole 1995). While migratory distance can range from a few thousand kilometers to tens of thousands of kilometers, individuals rarely cover the whole distance in one flight, rather they stop *en route* and search for suitable habitat within which to rest and refuel (e.g., Moore et al. 2005a). It is estimated that upwards of 70% of time during migration is spent on stopover (Hedenström and Alerstam 1997), when energy expended is thought to be high relative to migratory flight (Wikelski et al. 2003). Traveling long distances across areas that vary in suitability comes with uncertainties, including unfamiliar habitat (Németh and Moore 2007), predation pressure (Cimprich and Moore 1999), competition (Lindström et al. 1990), and weather (Newton 2007). Consequently, the mortality associated with migration can be substantial (Sillett and Holmes 2002, Newton 2007, Paxton et al. 2007, Klaassen et al. 2014, Lok et al. 2015; but see Leyrer et al. 2013).

Obtaining food resources during stopover is crucial for birds because it allows them to resume migration in a timely manner. Access to food may be influenced by intrinsic factors such as an individual’s sex and age (Lindström et al. 1990, Carpenter et al. 1991, 1993a, 1993b, Moore et al. 2003). Sex-based differences may be due to sexual size dimorphism (e.g., Temeles 1986, Mulvihill et al. 1992, Székely et al. 2000, Hatch and Smith 2009), hormonal differences, especially testosterone (e.g., Geslin et al. 2004; Covino et al. 2015), or differences in aggression (e.g., Moore et al. 2003; Dierschke et al. 2005). Most studies testing sex-dependent asymmetries have found that males dominate females during migration, and thereby gain priority access to resources increasing fuel loads and fueling rates (Carpenter et al. 1991, 1993a, 1993b, Maitav and Izhaki 1994, Yong et al. 1998, Moore et al. 2003, Németh and Moore 2012). However, not all studies have found differences between sexes during migration (Otahal 1995, Izhaki and Maitav 1998).

Age-related asymmetries may also influence migration because younger, hatching year birds tend to be less efficient foragers and are often subordinate to older, after-hatching year birds (Gauthreaux 1978, Burger 1988, Wunderle 1991, Woodrey 2000). Banding records during migration are consistent with that expectation as young birds typically carry less fat, have lower mass, and stay longer during stopover (Morris et al. 1996, Woodrey and Moore 1997, Woodrey 2000); although an individual's fuel load may drive priority access to resources irrespective of age differences (Moore et al. 2003). In any case, many of the challenges that migrants encounter are likely magnified for young, inexperienced birds especially during their first migration in autumn.

The Ruby-throated Hummingbird (*Archilochus colubris*) is a Nearctic-Neotropical migrant and the only species of hummingbird that breeds in Eastern North America, yet surprisingly little is known about this species' migration and stopover ecology. Ruby-throated Hummingbirds, especially older males, are territorial during the breeding season but apparently less so during the remainder of the annual cycle (Weidensaul et al. 2013). In general, hummingbirds represent a unique system compared to other taxa due to their aggressive nature, small size, reverse sexual size dimorphism (Ridgeway 1911, Weidensaul et al. 2013), high metabolism (0.022 milliliters O_2 minute^{-1}; Lasiewski 1963), high energy assimilation efficiency when feeding on nectar (97-99%; Hainsworth 1974), and use of torpor for energy conservation (Weidensaul et al. 2013). From a strictly energetic standpoint, hummingbirds should have a larger fuel load capacity compared to most migrants as smaller birds in general can carry more fuel reserves relative to their fat-free mass (Hedenström & Alerstam 1992) and have larger fuel deposition rates (Lindström 2003).The ability to carry such high fuel loads may seem beneficial during migration, however in reality hummingbirds must cope with additional challenges compared to larger birds such as more frequent feeding and costs associated with maintaining a higher body temperature (Vogel 1988).

Ruby-throated Hummingbirds exhibit reverse sexual size dimorphism, as well as sex- and age-dependent wing morphologies (Stiles et al. 2005). Adult males have the shortest and most tapered wings compared to other age and sex classes. Immature males have slightly longer and less tapered wings compared to adult males. All females share a similar wing morphology, with longer, more rounded wings than males of either age class (Stiles et al. 2005). Short wings permit increased agility at the expense of increased energetic costs of flight due to high wing disc loading (WDL) (Feinsinger and Chaplin 1975, Norberg 1990); whereas long wings permit increased load bearing and lower WDL, though flight speed and agility are decreased (Norberg 1990). Sex and age dependent wing morphology could impact migration speed (but see Chai et al. 1999) as well as foraging behavior (e.g. Feinsinger and Chaplin 1975, Feinsinger and Colwell 1978) during stopover.

The first objective of this study was to provide basic information on the stopover biology of Ruby-throated Hummingbirds, including phenology, stopover duration, fuel deposition rate, arrival condition, and estimated flight ranges of individuals that had stopped along the northern coast of the Gulf of Mexico (GOM) in autumn. Our second objective was to evaluate the influence of sex and age on the stopover biology of Ruby-throated Hummingbirds during autumn migration. We hypothesized that males would differ from females during stopover because of differences in wing morphology (Stiles et al. 2005) and increased likelihood of territorial behavior in males (Weidensaul et al. 2013) We also hypothesized that adult birds would differ from young birds during stopover because adults are more experienced and socially dominant to juvenile year, at least in other hummingbird species (e.g., Stiles 1973, Ewald and Rohwer 1980). Specifically, we predicted that (1) males and adults would arrive earlier and in better condition than females and young birds respectively; (2) males would have larger fuel deposition rates than females; (3) stopover duration would be shorter in adults and males; 4) Females, with a more energetically efficient wing design, and adults would have longer flight ranges compared to males and young birds (cf. Pennycuick 2008).

Methods

Field Site and Data Collection

We captured Ruby-throated Hummingbirds (henceforth Hummingbirds) using 29-32 nylon mist nets (12 x 2.6 meters or 6 x 2.6 meters with 30 millimeter mesh) at the Bon Secour National Wildlife Refuge, Fort Morgan, Alabama (30°10’N, 88°00’W; Figure 1) during fall migration 2010 – 2014 (Table 1). Nets were open from approximately sunrise until noon (Central Daylight Time), daily weather permitting. Our study site was located 2 kilometers from the end of the Fort Morgan Peninsula and was dominated by slash pine (*Pinus elliottii*), sand live oak (*Quercus geminate*), myrtle oak (*Quercus myrtifolia*), hollies (*Ilex* spp.), saw palmetto (*Serenoa repens*), and greenbrier (*Smilax* spp.) (for a complete description see Zenzal et al. 2013). Netting effort was both passive and active. To increase capture efficiency we used artificial feeders and baited a subset of nets (2010: n = 11; 2011-2014: n = 4) within our overall netting array. Starting in 2011, we equipped 10 feeders with radio frequency identification (RFID) readers as part of a different project. These 10 feeders were distributed throughout the study site, and not always associated with nets. While the placement of feeders at nets was to increase sample sizes, we recognize this subsequently influenced other factors such as fuel deposition rates (FDR).

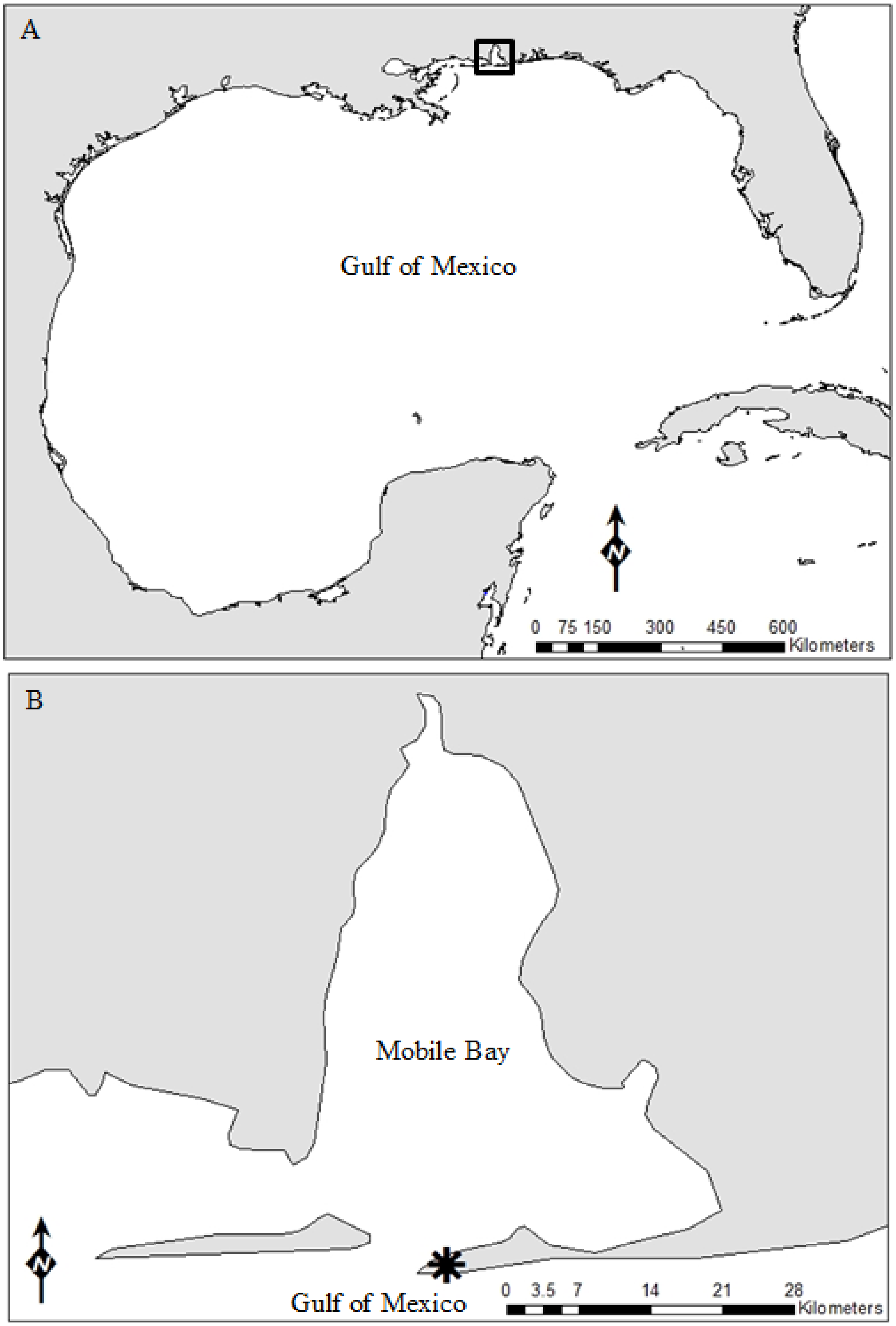


Figure 1. Map of Fort Morgan Study Site

(A) Gulf of Mexico region with Mobile Bay area enclosed by a square. (B) Fort Morgan peninsula in coastal Alabama, USA. Study site is represented by asterisk.

Table 1

Capture Effort of Ruby-throated Hummingbirds

Year	**Dates of operation**	**Net Hours**	**Capture Rate**
2010	31 August – 28 October	8427	8.72
2011	30 August – 30 October	7778	11.61
2012	2 September – 30 October	9910	2.76
2013	26 August – 31 October*	8575	3.69
2014	25 August – 1 November	9493	5.31

Note: Year of study, capture effort, and capture rate per 100 net hours (1 net hour = 12 m of net open for 1 hour) of Ruby-throated Hummingbirds during autumn migration in coastal Alabama. * We were unable to access our study site due to the U.S. government shutdown during October 1-13, 2013.

We banded Hummingbirds (n = 2,729) with a USGS aluminum leg band, aged as hatching year (HY; “young”) or after hatching year (AHY; “old”) and sexed according to Pyle (1997), estimated fat (Helms and Drury 1960), measured natural wing chord and mass (to the nearest 0.01 grams using an electronic balance), and took a wing photo when time permitted to determine wing span and wing area for flight range estimates. During 2011-2014, a subset of individuals received auxiliary markers either in the form of a radio-tag (~300 milligrams; n = 55; JDJC Corp., Fisher, Illinois, USA) or a passive integrated transponder (PIT) tag (~100 milligrams; n = 549; Cyntag, Cynthiana, Kentucky, USA). During 2012-2014 a subset of birds were auxiliary marked with back color tags (~30 milligrams; n = 446) as described by Kapoor (2012). Birds only received one type of auxiliary marker in addition to an aluminum leg band. All auxiliary marked birds were included in subsequent analyses since radio-tags, the marker type most likely to impact individuals due to weight and size, did not affect Hummingbirds (Zenzal et al. 2014). During 2010, a subsample of birds (n = 88) were held for an aviary study (see Zenzal et al. 2014), and those individuals were only included in our phenology and arrival condition analyses.

Stopover Variables

We assessed phenology using date of first capture, standardizing date across all years by converting calendar date to ordinal day. Data from 2013 were not used in our analyses of phenology because the U.S. government shutdown prohibited access to our study site (Table 1). Any calendar dates presented are based on non-leap years.

We corrected for size in our estimate of fuel load to control for sexual size dimorphism and variation in fat deposition among birds. Fat-free body mass was calculated based on regressions of mass and wing length of Hummingbirds captured at our site between 2010-2014 (see Ellegren 1992, Owen and Moore 2006). For each sex we regressed mass on fat score for individuals with the same wing chord (1 mm increments). The intercept from each wing chord class was then regressed by wing chord for each sex. The resulting equation from the second linear regression provided the size-specific fat-free mass of each wing chord class by sex (males: 2.83 ± 0.29 grams, females: 3.12 ± 0.10 grams; these and all other results are presented as median ± standard deviation unless otherwise indicated). Estimated fat-free mass was then subtracted from the mass of each bird at initial capture, the difference should then provide the fuel load carried by the individual upon capture.

We estimated minimum stopover duration (SD) by subtracting the last detection date (recapture, RFID reader, observed color marker, or radio transmitter) from the initial capture date (Cherry 1982). We acknowledge that each marker type likely differs in detection probability; however we believe using the most precise data provides an accurate portrayal of their stopover biology. Birds only captured once (transient birds; *sensu* Schaub et al. 2008) and not redetected by any other means were not included in the analysis of stopover duration. We compared age groups when years were pooled. Comparison between sexes was limited to HY birds due to low sample sizes of AHY birds captured each year.

Fuel deposition rate (FDR, grams day^{-1}) was estimated using methods described by Cherry (1982), this method provides a way to standardize the amount of time between initial capture and final capture since some birds have been found to increase mass over the course of the day (e.g. Woodrey and Moore 1997). We first determined the amount of fuel deposited per hour (0.02 ± 0.04 grams; mean ± standard deviation) using birds recaptured the same day (transient birds, n = 37) at least 3 hours from the initial capture (mean amount of time between captures [± standard deviation] 5.85 ± 2.17 hour). We chose a 3 hour time lapse because birds may continue to show a stress response to handling up to 1 hour after capture (Holberton et al. 1996). Individuals should have acclimated to handling and resumed refueling after 3 hours. We corrected the mass of all individuals used in this analysis to 12:00 using the mean hourly fuel deposition rate. FDR was determined by subtracting the corrected mass at initial capture from the corrected mass at final capture, and that value divided by the number of days elapsed between captures. We were only able to compare HY males and females that stopped over (non-transient birds) in the FDR analysis because of inadequate samples of recaptured AHY individuals (Males n = 2; Females n = 1). We also performed a simple linear regression to determine mass change of birds captured only once throughout the season (see Woodrey and Moore 1997). This approach allowed us to take advantage of our large dataset as we recaptured only ~11% of all birds banded and to examine refueling rates of each age and sex group. For this analysis we regressed arrival fuel load (see above) by time of day as a way to test the assumption that birds increased mass over the course of the day.

Finally, we used Pennycuick's (2008) program Flight 1.24 to estimate flight ranges from a random subsample of individuals from each age/sex group (n = 35 for all groups) using the same methods as Zenzal et al. (2014). For each age-sex class we randomly selected birds with wing photos across all years. The software utilizes wingspan, wing area, fat-free mass, and fuel load upon arrival (described above) to estimate flight range. Ideally we would use departure condition in flight models as opposed to arrival condition, but low sample sizes of AHY recaptures (n = 5) precluded use of departure condition for analysis. Only individuals with a wing photo and a positive body condition (above fat-free mass) were included in the analysis since both are required to meet the conditions of the model. We derived wingspan and wing area from photographs using ImageJ (Abramoff et al. 2004), and we assumed flight in still-air conditions at an altitude of 500 meters (air density of 1.17 kilogram meter^{-3}; based on Kerlinger and Moore 1989, Woodrey and Moore 1997). We used the default settings for all other parameters in the model.

Statistical Analysis

Data were checked for normality using a Shapiro-Wilk test (Shapiro and Wilk 1965). Potential flight range estimates were the only data to be normally distributed; therefore, we performed an analysis of variance on estimated flight ranges to determine an age or sex effect while grouping individual as a random factor within year. Since all other data were not normally distributed even after attempting standard transformations (log and square root), all two way comparisons used Mann-Whitney U tests (Mann and Whitney 1947). For each phenology and arrival condition we compared sexes of only HY birds for each year of the study (except 2013 for the phenology analysis) since sample sizes of AHY birds were low during each individual year. Subsequently these analyses would be considered multiple comparisons; therefore, we employed the Holm-Bonferroni correction (Holm 1979) to determine an adjusted alpha based on the number of comparisons for each stopover variable. In order to analyze differences between age groups we pooled data across years to compare overall patterns between AHY and HY birds. We also pooled all years to compare differences between AHY males and females in phenology and arrival condition, but not FDR or SD due to low sample sizes. Finally, a Spearman's rank correlation coefficient was used to look for a relationship between arrival condition and FDR or SD for male and female HY birds that were recaptured on a subsequent day after initial capture. All statistical analyses were performed using the R statistical language 3.1.3 (R Core Team 2015).

Results

Phenology

The overall passage (2010-2014) of Hummingbirds through Coastal Alabama spanned some 62 days, occurring between day 238 (August 26th) and day 300 (October 27th), with a mean passage date of 268 ± 11 (September 25th) capturing 0.12 birds per net hour. When examining individual age and sex classes we found differences in arrival timing between age groups, but not between sexes.

Older birds arrived earlier than younger birds when all years were pooled ($W = 79156$, $p < 0.001$, Cohen's $d = 0.60$; Figure 2). The phenology of older birds was more constrained, with all but one bird arriving over a period of 35 days (from day 247 to 282; Figure 3A) compared to HY birds which arrived over a period of 62 days (from day 238 to 300; Figure 3B).

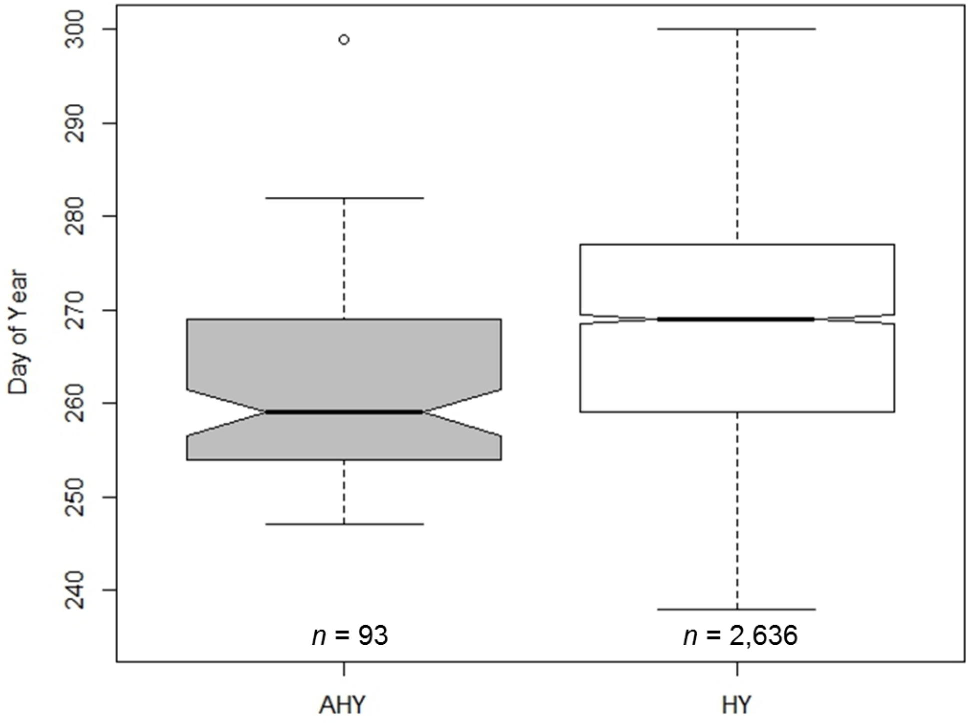


Figure 2. Passage Dates of After-hatch Year and Hatch-Year Ruby-throated Hummingbirds During Autumn Migration

Y-axis indicates ordinal date. Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicates interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers. Ordinal day 240 = 28 August.

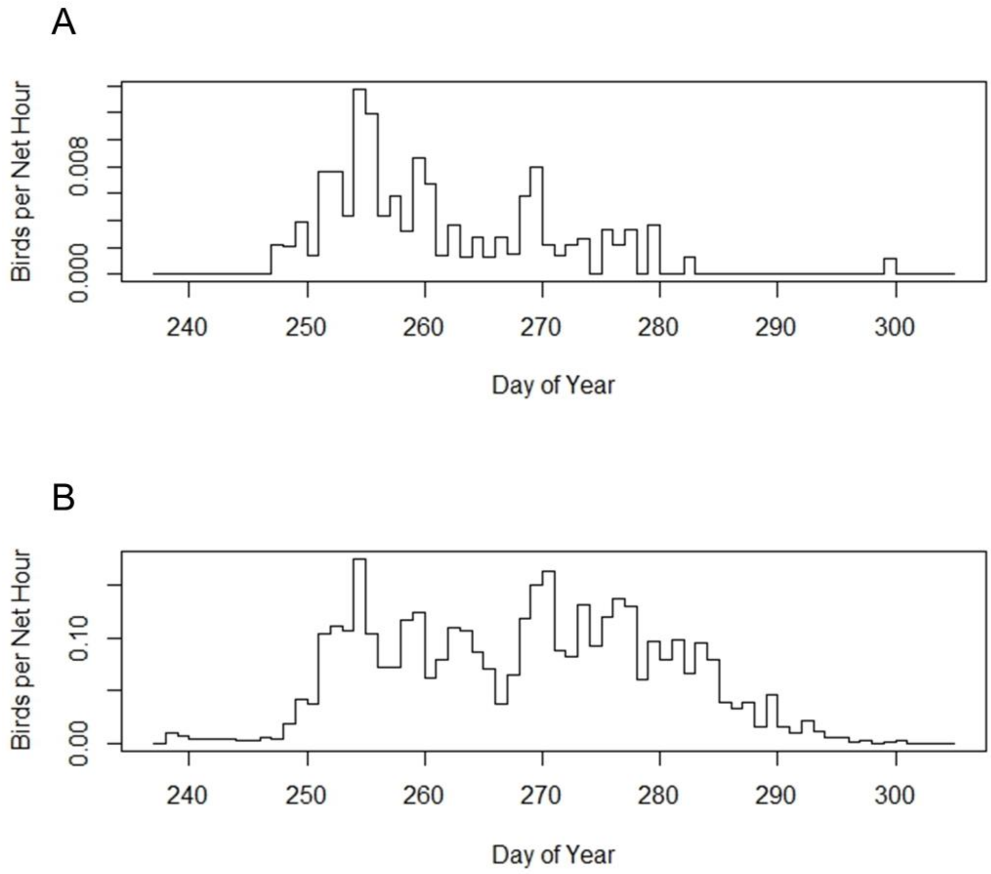


Figure 3. Phenology of Ruby-throated Hummingbirds Captured from 2010 to 2014

(A) Phenology of after hatch year birds. (B) Phenology of hatch year birds. X-axis shows day of year, Y-axis indicates the number of birds per net hour. Ordinal day 240 = 28 August.

In 2010 HY females arrived earlier than males by 4 days (W = 53916, $p < 0.001$, adjusted alpha = 0.01; Figure 4), however we found no difference in arrival timing during any of the subsequent years ($p > 0.14$; Figure 4). We also found no difference in the arrival timing of AHY males (n = 42) and females (n = 51) when all years were pooled (W = 1148.5, p = 0.55). Given the overall trend that supported our null hypothesis, evidence suggests Hummingbirds do not exhibit differential migration timing by sex in autumn.

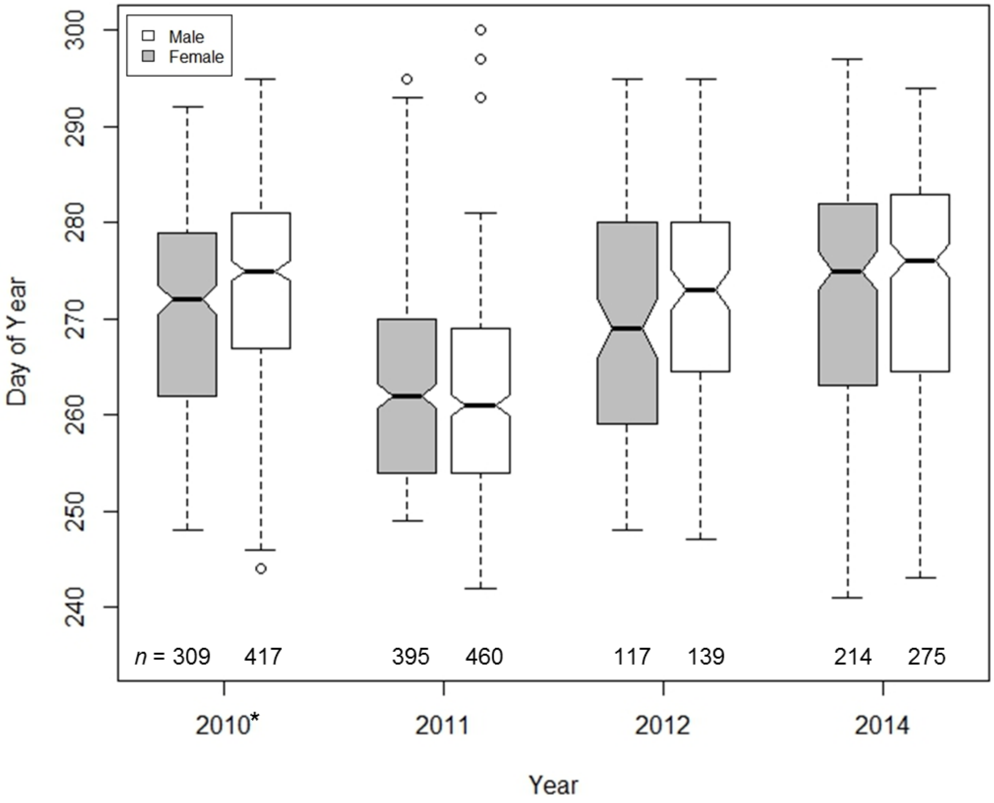


Figure 4. Passage Dates of Hatch-Year Ruby-throated Hummingbirds by Male and Female for 2010-2012 and 2014

Asterisk indicates a significant difference between sexes. Y-axis indicates ordinal date and X-axis shows year of study. Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicates interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers. Ordinal day 240 = 28 August.

Arrival Condition

Overall Hummingbirds arrived with substantial fuel loads, carrying an estimated 0.92 ± 0.53 grams (above lean body mass (LBM): 33% males, 29% females) of fat upon initial capture (Figure 5). Arrival condition ranged from 0.53 grams (below LBM: 19% males, 17% females) below fat-free body mass to 2.80

grams (above LBM: 99% males, 90% females) above fat-free body mass (Figure 5).

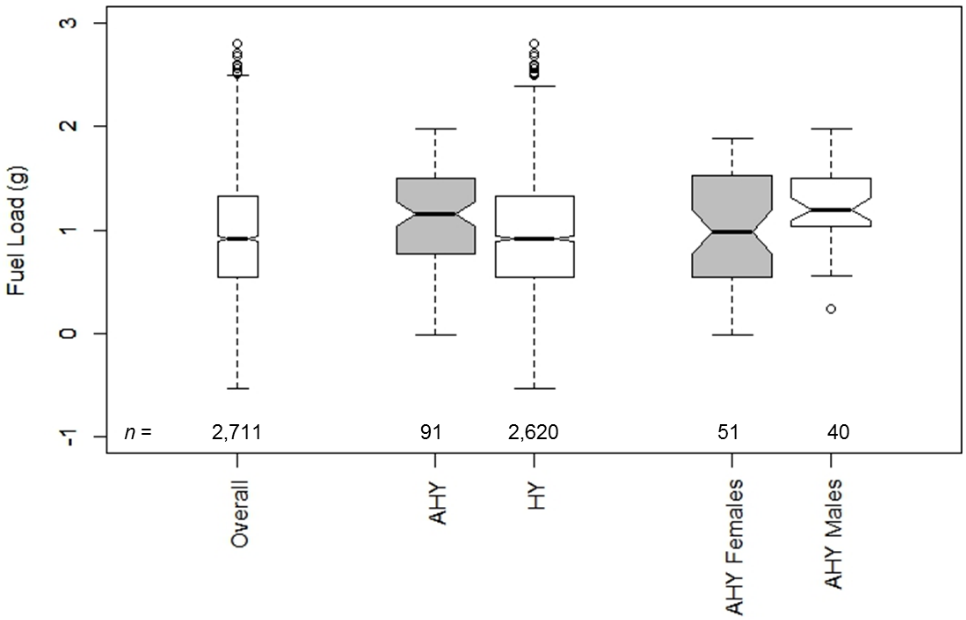


Figure 5. Fuel Load of Ruby-throated Hummingbirds at Initial Capture

Shown are overall pattern, comparison between age groups, and comparison between AHY males and females for all years pooled. Y-axis indicates amount of fuel (g) over fat-free body mass. Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicates interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

We found evidence of age-dependent arrival condition, but mixed results for sex-dependent effects. Older birds arrived in better condition than younger birds when data were pooled across years (W = 143,241, $p = 0.001$, Cohen's d = 0.33; Figure 5). We found no difference between sexes of HY birds ($p > 0.02$, adjusted alpha = 0.01; Figure 6) when we analyzed each year (2010-2014) separately. However, when years were pooled to analyze older males and females, we found that older males arrived with larger fuel loads compared to older females (W = 762, p = 0.04; Figure 5). Our results suggest stronger differences between sexes in older birds, but these differences are not reflected in younger birds.

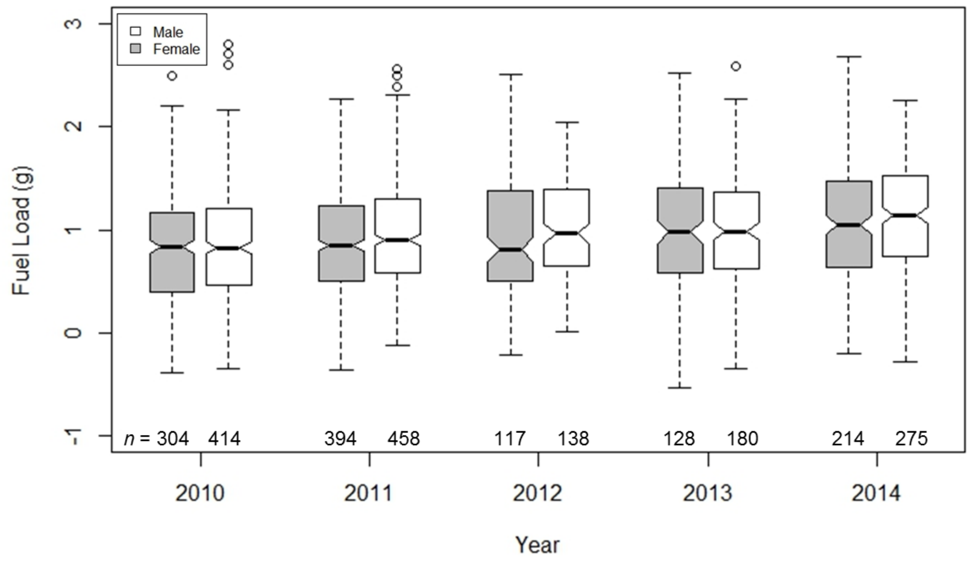


Figure 6. Fuel Loads of Hatch-year Ruby-throated Hummingbirds by Male and Female for 2010-2014

Y-axis indicates amount of fuel (g) over fat-free body mass and X-axis shows year of study. Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicates interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

Stopover Duration

The majority of birds captured (~89%) were transients, never detected again. For non-transient birds, overall length of stopover for birds recaptured at least one day after initial capture was 2 ± 2 days. SD of recaptured birds ranged from a minimum of 1 day to a maximum of 15 days (Figure 7). The majority of individuals (72%) that stopped over were redetected no more than 3 days from initial capture. We found no difference between sex (HY only, $p > 0.02$, adjusted alpha = 0.01; Figure 8), but found an effect of age (W = 213, $p = 0.05$, Cohen's d = 0.80; Figure 7) on SD. All AHY birds (n = 3) were only redetected 1 day after initial capture, while 62% of HY birds (n = 376) were redetected at least two days from initial capture. Unsurprisingly, stopover length in both HY males ($p < 0.001$, $r = -0.40$, n = 244) and females ($p = 0.003$, $r = -0.31$, n = 132) was inversely correlated with fuel load at initial capture.

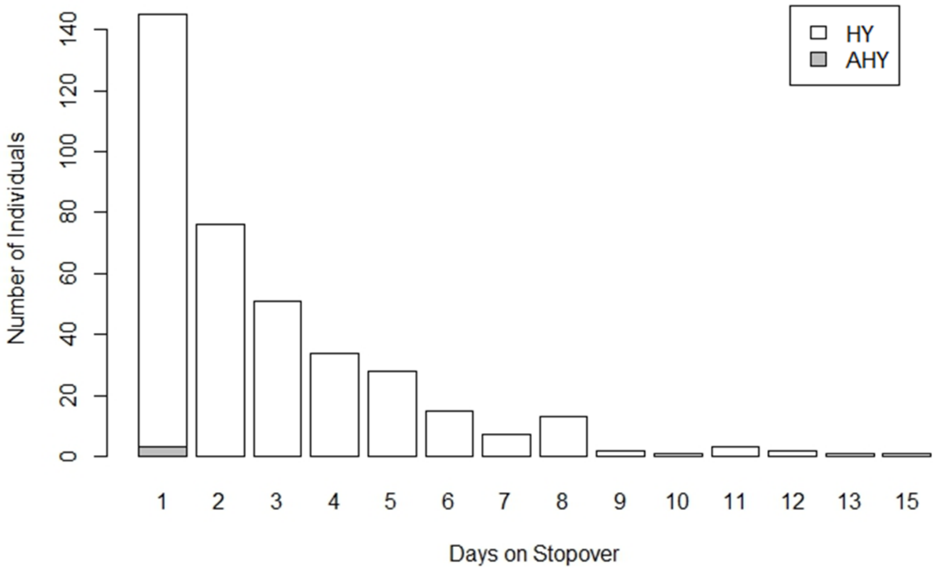


Figure 7. Distribution of Ruby-throated Hummingbird Stopover Durations

Age group distributions when all years are pooled. Y-axis indicates the number of individuals and X-axis shows minimum stopover durations.

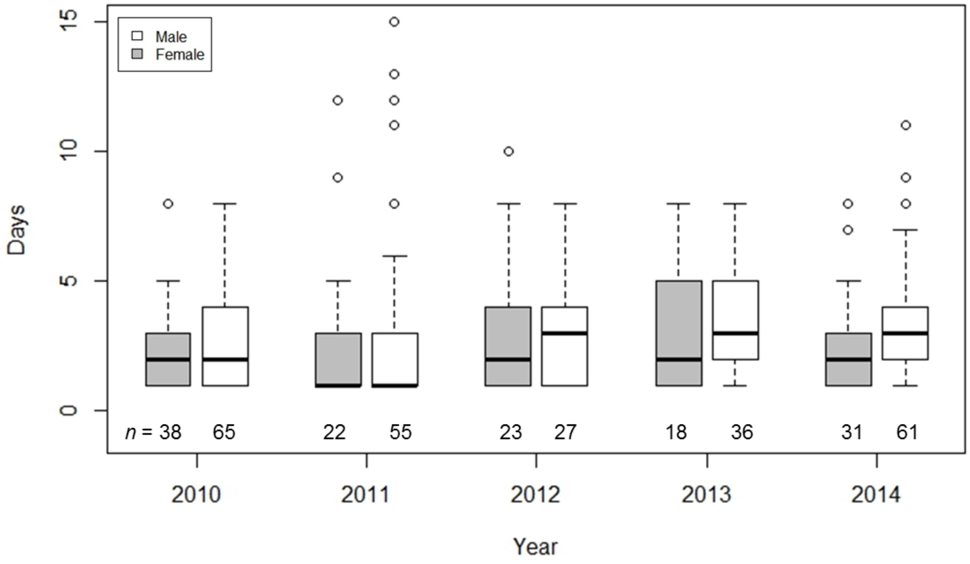


Figure 8. Stopover Duration of Hatch-year Ruby-throated Hummingbirds by Male and Female for 2010-2014

Y-axis indicates minimum stopover duration and X-axis shows year of study. Central black line indicates median, top and bottom of box indicates interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

Fuel Deposition Rate

The overall FDR of non-transient Hummingbirds was 0.10 ± 0.24 grams day-1 (increase to LBM: 4% males, 3% females), ranging from a negative rate of 0.94 grams day-1 (decrease to LBM: 33% males, 30% females) to a maximum of 1.04 grams day-1 (increase to LBM: 37% males, 33% females). HY birds make up the majority of these data, heavily influencing the overall results (HY: n = 271; AHY: n = 3). We found no evidence of sex (HY only, $p > 0.06$, adjusted alpha = 0.01; Figure 9) or age ($W = 419$, $p = 0.93$, Cohen's $d = 0.60$) influencing FDR during autumn migration. We also found no relationship between capture time and fuel load when analyzing data overall (p = 0.17, r = -0.03, n = 2711), by sex (HY only: males p = 0.11, r = -0.04, n = 1,463; females p = 0.76, r = -0.009, n = 1,158), and by age (AHY: p = 0.25, r = -0.12, n = 91; HY: p = 0.24, r = -0.02, n = 2,620). However, we did find that the arrival mass of HY males (p < 0.001, r = -0.29, n = 202) and HY females (p = 0.008, r = -0.28, n = 104) was inversely correlated with FDR.

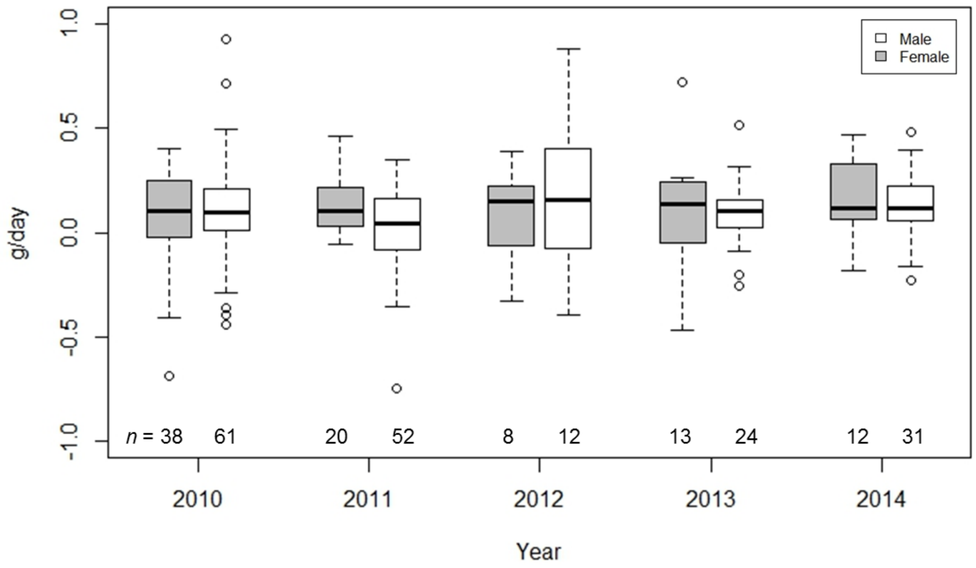


Figure 9. Fuel Deposition Rates of Hatch-year Ruby-throated Hummingbirds by Male and Female for 2010-2014

Y-axis indicates fuel deposition rate (g day-1) and X-axis shows year of study. Central black line indicates median, top and bottom of box indicates interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

Flight Models

Overall estimated flight range was 2,261.63 ± 1,152.94 kilometers with a minimum of 16 kilometers and maximum of 4,960 kilometers. We found that both age ($F_{1,117} = 10.87$, $p = 0.001$) and sex ($F_{1,117} = 4.25$, $p = 0.04$) affected range estimates. Older birds and males were estimated to be able to fly further than younger birds and females respectively (Figure 10). We found no age by sex interaction ($F_{1,117} = 1.30$, $p = 0.26$). A visual sensitivity analysis of the models found that fuel load was the most influential factor of these flight range calculations.

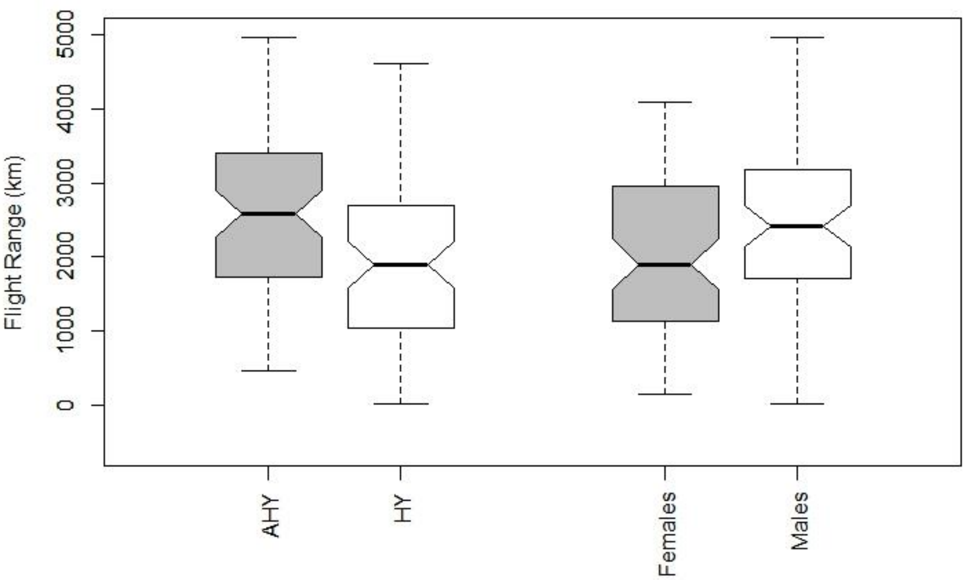


Figure 10. Potential Flight Ranges of Ruby-throated Hummingbirds by Age and Sex Groups

Y-axis indicates range (km). Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicates interquartile range, and whiskers indicate total range.

Discussion

Our study fills a huge gap in the natural history of Ruby-throated Hummingbird migration by providing some of the first information on the temporal pattern of arrival, as well as on arrival condition, stopover biology (FDR and SD), and departure (flight range) of Ruby-throated Hummingbirds as well as reporting on age and sex dependent effects. Much of the information available on hummingbird migration has depended on work with Rufous Hummingbirds in western North America (e.g., Gass et al. 1976, Kodric-Brown and Brown 1978, Gass 1979, Carpenter et al. 1991, 1993a, 1993b, 1993c). Rufous Hummingbirds exhibit age and sex dependent migration as well as social dominance during stopover (Carpenter 1993a and references therein). While we expected similarities between species, each faces unique challenges during migration. Rufous Hummingbirds move over a continuous land mass, confront many inhospitable arid areas, and find suitable stopover habitat at small alpine meadows, skipping (*sensu* Piersma 1987) from one to the next (Gass et al. 1976). Ruby-throated Hummingbirds negotiate one large inhospitable area (Gulf of Mexico [GOM]), and otherwise have access to largely contiguous hospitable areas during passage (La Sorte et al. 2014). Moreover, the two species experience different competitive interactions: Ruby-throated Hummingbirds face interspecific competition on the wintering grounds (Weidensaul et al. 2013), whereas Rufous Hummingbirds encounter interspecific competition throughout their annual cycle (e.g., Wolf and Hainsworth 1971, Powers and McKee 1994, McCaffrey and Wethington 2008). The two migration systems likely reflect distinct ecological processes (*sensu* Kelly and Hutto 2005).

Overall Stopover Biology

Ruby-throated Hummingbirds migrate through the northern Gulf coast from late August through late October, with peak migration occurring from early

September through early October. Our estimates are consistent with an earlier peak passage reported from stations at higher latitudes in North America (Mulvihill and Leberman 1987, Willimont et al. 1988, Weidensaul et al. 2013) and later arrival in the tropics (Deppe and Rotenberry 2005). Arrival condition varied widely among birds captured at our coastal study site, with some birds having almost no body fat, and others with fuel loads that were nearly twice their lean body mass. Our recapture data showed that birds that were leaner upon arrival tended to have a higher FDR and longer SD compared to the birds that arrived with larger stores. This suggested that the birds that we recaptured refueled during stopover. That said most birds that stopped along the Gulf coast were never redetected. We also found a lack of relationship between capture time and arrival fuel load. Not finding a relationship between mass and time of day might suggest that birds are arriving at our study site over the course of the day as they migrate, but more study is needed.

Although we are uncertain whether Ruby-throated Hummingbirds fly around or over the GOM, the average bird captured at our study site could make the ~1,000 km flight across the GOM in still air conditions. Our mean potential flight range was similar to those of Ruby-throated Hummingbirds sampled during migration using different estimation methods (Odum et al. 1961); however, our range was protracted compared to potential flight ranges from Odum et al. (1961). Nevertheless, even birds with adequate fuel loads may opt to move around the GOM because atmospheric conditions favorable for a trans-gulf flight do not occur with any regularity until late autumn (Able 1972; Kranstauber et al.

2015). Prevailing weather during migration surely influences the flight energetics of hummingbirds more than larger landbird migrants known to make trans-Gulf flights (see Ravi et al. 2015). It is also important to keep in mind that flight simulations may overestimate range since hummingbirds have higher metabolic rates compared to other migrants used to develop the models. In any case, the modeling software provides a metric to evaluate differences in wing morphology and condition between different groups within the same species.

Age-dependent Migration

Older birds arrive earlier than younger birds during fall passage, a pattern found in many species of passerines (e.g., Woodrey and Chandler 1997, Woodrey and Moore 1997, Jakubas and Wojczulanis-Jakubas 2010). Adult Ruby-throated Hummingbirds leave more northern areas earlier in the season than younger birds, possibly because males provide no parental care (Mulvihill and Leberman 1987, Peterjohn 1989, Weidensaul et al. 2013), which may explain earlier arrival at our stopover site. Moreover, molt occurs primarily on the wintering grounds (Baltosser 1995). Even if adults and young birds departed the breeding grounds at the same time, differential passage may reflect the fact that younger birds travel slower than adults (e.g., spend longer at each stopover site or make additional stops *en route* or take a less direct migratory route), which would increase travel time and might explain the disparity we observe between the number of old and young birds at our study site.

Older birds arrived with larger fuel loads and tended to stay for a shorter time at our site than younger birds, both of which can be due to less efficient foraging, social subordinacy, or disorientation, compared to older birds. Our findings are also consistent with evidence that older birds are more efficient at foraging (Burger 1988, Wunderle 1991, Woodrey 2000) and typically gain priority access to resources (Gauthreaux 1978, Woodrey 2000). While we were not able to assess differences in FDR between age groups, we would not be surprised if older birds had higher FDRs given differences in fuel load upon arrival. Larger arrival fuel loads would ensure that older birds had longer potential flight ranges, which is what we found. Others have reported age dependent fuel load and mass in other landbird migrants (e.g., Veiga 1986, Morris et al. 1996, Woodrey and Moore 1997, Jakubas and Wojczulanis-Jakubas 2010). Moreover, stopover duration was negatively correlated with fuel load in young Ruby-throated Hummingbirds, which has been reported in other landbird migrants (Pettersson and Hasselquist 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Yong and Moore 1994).

The ratio of AHY: HY Ruby-throated Hummingbirds captured at our study site was highly skewed (1:28), well beyond what you would expect (1:1 – 1:3) assuming two broods per breeding season and 100% survivorship (see Peck and James 1983). In other migrant landbirds, inland sites tend to have a more balanced age ratio than coastal sites (Robbins et al. 1959, Ralph 1971, 1978, 1981), and our migration station is on the immediate coast of the GOM. Young birds on their first migration may not recognize the GOM as an ecological barrier until over the water and then reorient to the closest landmass (e.g., Diehl et al. 2003). It is also possible that young birds stop along the coast to obtain enough fuel for a Gulf crossing (e.g., Woodrey and Moore 1997), while adults depart from locations further inland. Some young migrants arriving at our site may be disoriented (Ralph 1978) or follow a migratory route different from adults (Hake et al. 2003, Agostini 2004); maybe older birds depart inland sites and to make trans-Gulf flights while younger birds follow the coast around the GOM.

Sex-dependent Migration

We found little evidence of sex-dependent migration during autumn, contrary to the pattern in spring passage (Németh and Moore 2012). Males and females of both age classes showed similar phenology of passage on the northern Gulf coast. During autumn there may be little pressure for a particular sex to minimize time spent on migration compared to spring (Smith and Moore 2004 and references therein), but we know little about the wintering ecology of Ruby-throated Hummingbirds. The need to arrive early in order to acquire feeding areas may be diminished because the generalist foraging strategy of Ruby-throated Hummingbirds helps them adapt to changes in resource density (Lara 2006) and/or reduced energetic demands during winter. More study is needed to connect patterns found during autumn migration with the biology of birds on the wintering grounds (*sensu* Marra et al. 2015).

Among young birds, sexes did not differ in fuel load upon initial capture, amount of time on stopover, or FDR. Young males and females also exhibited a similar relationship between arrival fuel load and SD as well as FDR. While we may have expected differences due to morphology and behavior, it is possible that performance differences are minimized when solely analyzing young birds.

Young of both sexes are expected to have equivalent levels of experience when facing the challenges of migration such as resource acquisition, habitat selection, and predator avoidance. Further, differences in wing morphology between young males and females are not as strong as found in older individuals (Stiles et al. 2005), which might lessen any differences in aerodynamic performance.

Although there was no difference between sexes of young birds, older males arrived with larger fuel loads compared to older females. The strong differences in wing morphology and WDL (Stiles et al. 2005) could impact not only the ability for individuals to obtain resources, but also the manner in which individuals acquire resources (Feinsinger and Chaplin 1975). Wing morphology is known to influence foraging behavior; males attempt to monopolize resources whereas females use a traplining strategy (Feinsinger and Chaplin 1975, Feinsinger and Colwell 1978, Norberg 1990; but see Altshuler et al. 2004). It is also possible that Ruby-throated Hummingbird adult males are socially dominant over females as in other hummingbird species (e.g., Feinsinger and Colwell 1978, Kodric-Brown and Brown 1978, Carpenter et al. 1993a). Note that gorget coloration of older males may provide a competitive advantage if used to convey dominance as in other hummingbird species (Stiles 1973, Ewald and Rohwer 1980).

Although we expected longer potential flight ranges in females because of their more efficient wing design, we found the opposite to be true. However, adult males arrive with larger fuel loads, which were found to override any differences attributable to wing morphology in the calculations. Although female wing design may yield lower energetic costs of flight (Norberg 1990), the ability to obtain resources to fuel flight is likely more important for extended flight bouts.

Conclusions

Our study describes the autumn migration of Ruby-throated Hummingbirds along the northern coast of the GOM. We found evidence of age-dependent migration in phenology, arrival mass, stopover duration, and potential flight ranges, consistent with older birds having a competitive edge during migration. We also found an interaction between sex and age; male and female hatching year birds did not differ in their stopover biology, but older males had larger fuel loads upon arrival than did older females. When age classes were pooled, males had longer potential flight ranges than females. The disparity between the number of old and young birds captured might suggest differences in migration routes or habitat use along the Gulf coast. Young birds may also rely on the coast for orientation as a leading line (*sensu* Mueller and Berger 1967), whereas older birds might take a more direct route. Our results differ from those reported on age and sex dependent stopover biology of Rufous Hummingbirds, possibly indicating a more structured social hierarchy in Rufous Hummingbirds during migration. The short stopover durations of Ruby-throated Hummingbirds might prohibit social hierarchies from forming minimizing differences between ages and sexes in how they spend their stopover time.

CHAPTER II – RESOURCE USE AND DEFENSE BY RUBY-THROATED HUMMINGBIRDS (*ARCHILOCHUS COLUBRIS*) DURING AUTUMN MIGRATION

Introduction

Migration is a part of the annual cycle for many species of birds and during migration the majority of their time and energy is spent at stopover sites (Hedenström and Alerstam 1997; Wikelski et al. 2003). A successful stopover depends on access to food or food resources that allow an individual to deposit fuel and continue migration (Blem 1980). Individuals on stopover benefit if they are able to select suitable habitat in which to rest and refuel in a timely fashion while successfully negotiating challenges, such as predation, competition, and weather (Moore et al. 2005a). If individuals are unable to obtain enough energy during stopover, they may experience a delayed migration, which could have negative effects on the next phase of the annual cycle (Smith and Moore 2003; Norris et al. 2004), while individuals in the poorest condition may starve. The ability to obtain high quality food resources influences mass gain and stopover duration (Bibby and Green 1981, 1983; Carpenter et al. 1983; Lindström et al. 1990). Demand for resources to fuel continued migratory flight may lead to adjustments in foraging behavior (Wang and Moore 2005) or adjustments in diet (Parrish 1997), and when resources are limited competition among migrants can be expected (Moore and Yong 1991). Therefore, understanding how migratory birds behave during stopover is largely a matter of identifying how they react to resources, competition, and predation (e.g. Paton & Carpenter 1984; Alerstam and Lindström 1990).

Although the selection of stopover habitat is largely scale dependent with extrinsic factors having greatest influence at broader spatial scales (Moore et al. 2005b; Buler et al. 2007), once a migrant settles in a local area, movements should be influenced by the availability and quality of resources (Smith et al. 2007; Cohen et al 2012). Migrant density is likely to increase with resource abundance, and density-dependent competition can negatively influence fueling rates of birds during stopover (e.g. Moore and Yong 1991; Kelly et al. 2002), which may retard the speed of migration (Erni et al. 2002; Schaub et al. 2008; but see Holmgren et al. 1993; Yosef and Chernetsov 2004). When food becomes a limiting factor, defense of resources (e.g., Brown 1964; Lott 1984; Carpenter 1987) may be advantageous (Kodric-Brown and Brown 1978; Hixon 1980; Carpenter 1987). Resource owners gain exclusive use of food sources, which should translate to increased mass gain (Carpenter et al. 1983) and a quicker resumption of migration, but resource defense should be abandoned when the costs to hold the resource outweighs the benefits of exclusive exploitation (e.g., Southwood 1977; Lott 1984; Carpenter 1987).

Understanding how migratory birds respond to variation in food resources is best studied by experimental manipulation of resources (e.g. Kodric-Brown and Brown 1978; Carpenter et al. 1983; Lindström et al. 1990; Fransson and Weber 1997; Fransson 1998a, 1998b; Bayly 2006). Toward that end, hummingbirds represent an excellent study system because resources can easily be manipulated using commercial feeders and sugar water solution to test predictions about resource use (e.g. Kodric-Brown and Brown 1978; Powers and McKee 1994; McCaffrey and Wethington 2008). The Ruby-throated Hummingbird (RTHU; *Archilochus colubris*) is an abundant Nearctic- Neotropical migrant found throughout Eastern North America (Weidensaul et al. 2013) and their migration is thought to follow the phenology of flowering plants (Bertin 1982). Given their high metabolism and body temperature (Lasiewski 1963; Vogel 1988), energy demands during migration are likely exacerbated for hummingbirds. Furthermore, the need to obtain energy within the patchy distribution of nectar resources may cause RTHU to display aggressive behaviors vis-à-vis defense of resources (Rousseu et al. 2014), similar to the territorial social system they exhibit during the breeding season (Pitelka 1942; Weidensaul et al. 2013).

RTHU exhibit reverse sexual size dimorphism (Weidensaul et al. 2013), which may influence the foraging strategy used by each sex (cf. Feinsinger and Chaplin 1975). Males, while smaller than females, are generally more aggressive and territorial than females during the breeding season (Weidensaul et al. 2013). One reason males are more successful when defending space during the breeding season is a wing design that favors increased maneuverability at the cost of higher energy requirements, versus the wing design of females which favors flight efficiency (lower energy costs) at the expense of maneuverability (Norberg 1990; Stiles et al. 2005). These differences may affect the individual’s foraging strategy and the quality of resources an individual is able to exploit. However, resource defense dynamics depend on both the sex of the defender as well as the competitor (Rousseu et al. 2014). Priority access to resources (*sensu* Moore et al. 2003) is not always dictated by morphological characteristics or sex. Lindström et al. (1990) demonstrated that dominance may differ throughout the annual cycle; additionally, numerous studies have shown that tradeoffs between food and danger may cause energy deprived individuals to be bolder and take more risks to acquire resources (Metcalfe and Furness 1984; Lindström et al. 1990; Moore 1994; Fransson and Weber 1997; Dierschke 2003).

The energy demand of migration coupled with unpredictable food quantity and quality, as well as variable conspecific density, can influence how an individual uses resources during stopover. The objective of this study is to determine the influence of intrinsic (sex, body condition, and behavior) and extrinsic factors (competitor density and resource quality) on the use and defense of resources by Hummingbirds. I measured resource use through the feeding rates, how often a RTHU drank from an artificial feeder, and resource defense through chase rate, how often a chase occurred at an artificial feeder. Specifically, I expect: 1) males to have higher feeding and chasing rates compared to females; 2) leaner birds to have higher feeding and chasing rates compared to fatter birds ; 3) density to have a negative relationship with feeding rate but a positive relationship with chase rate; 4) birds initiating chases to have higher feeding rates compared to birds being chased or not involved in chases; and 5) high quality feeders (1:2 sucrose solution) to have higher chase rates and lower feeding rates compared to standard quality feeders (1:4 sucrose solution; Pyke and Waser 1981; Ornelas et al. 2007).

Methods

Study Site and Experimental Setup

My study was carried out at the Bon Secour National Wildlife Refuge (NWR) in Fort Morgan, Alabama (30°10’N, 88°00’W) during the 2012-2014 autumn migration seasons. The Fort Morgan Peninsula, buttressed between Mobile Bay and the Gulf of Mexico, provides possibly the last stopover habitat for large numbers of southbound landbird migrants, including hummingbirds (e.g. Woodrey and Moore 1997; Kelly et al. 1999; Woltmann and Cimprich 2003; Deppe et al. 2015; Zenzal and Moore 2016). The study site is dominated by three species of tree: Slash Pine (*Pinus elliottii*), Sand Live Oak (*Quercus geminate*), and Myrtle Oak (*Quercus myrtifolia*). Common shrubs and vines include: Inkberry (*Ilex glabra*), Yaupon (*Ilex vomitoria*), Greenbrier (*Smilax* spp.), Muscadine (*Vitis rotundifolia*), Wax Myrtle (*Morella cerifera*), Red Bay (*Persea borbonia*), Saw Palmetto (*Serenoa repens*), and Sand Heath (*Ceratiola ericoides*). The study site is primarily composed of scrub/shrub habitat bordered by pine forest (Zenzal et al. 2013). While herbaceous plants are common within our study site, typical hummingbird pollinated flowers (e.g., *Campsis radicans*) are rarely found (Zenzal, personal observation), which explains low capture rates of RTHU during previous banding sessions (Moore, unpublished data).

Given the low abundance of natural nectar sources for hummingbirds, we experimentally manipulated resources by adding 5 pairs (n = 10) of artificial feeders (HummZinger® Ultra 12 ounce, Aspects, Inc. ®, Warren, Rhode Island, USA) across the study site (Figure 11). For each pair, one feeder contained a high quality (1:2) sucrose solution, which has been found to be preferred by hummingbirds and maximizes instantaneous rates of energy intake (Tamm and Gass 1986), while the other feeder contained a standard quality (1:4) sucrose solution similar to concentrations found in hummingbird pollinated flowers (Pyke and Waser 1981; Ornelas et al. 2007). Each feeder was equipped with a radio frequency identification (RFID) reader and antenna (e.g., Brewer et al. 2011; Hou et al. 2015; Rousseu et al. 2014) in order to log visits of tagged individuals (see below). The RFID antenna encircled one feeding port on each feeder; the other three ports were covered with red vinyl electrical tape (Scotch®) and the attached perch was removed to encourage birds to perch on the antenna (Figure 12). Individual feeders at each station were ~8 meters apart to allow observation of both feeders for when RTHU attempted to defend both feeders, while each feeding station was 75 meters apart (Figure 11) running parallel with the coast line. This spatial arrangement, size, and lone available feeding port made it possible for a single individual to defend space around a feeder.

Figure 11. Location of Feeding Station and Banding Tent

Feeding stations are represented by stars and the banding tent is represented by a triangle. The study site was located within the Bon Secour National Wildlife Refuge in Fort Morgan, Alabama, USA.

Figure 12. Artificial Feeder used at Feeding Stations

The radio frequency identification reader antenna encircles the only open port on the feeder. Feeders contained either a standard quality sucrose solution (1:4) or a high quality sucrose solution (1:2). Photograph by T.J. Zenzal Jr.

Banding Effort

At the Bon Secour NWR, we captured Ruby-throated Hummingbirds using nylon mist nets during autumn migration (see Zenzal and Moore 2016 for a complete description of capture effort). Capture effort was both active and passive, baiting a subset of nets (n = 4) with artificial feeders; these feeders were not associated with the experimental array described above (minimum distance between feeders at nets and feeding stations ~20 meters). Once captured, we banded each individual with a USGS aluminum leg band, aged (hatch year or after hatch year) and sexed them according to Pyle (1997), estimated fat (Helms and Drury 1960), and measured both unflattened wing chord (to the nearest 0.01

millimeters using electronic calipers) and mass (to the nearest 0.01 g using an electronic balance).

Each year of the study, a subset of individuals received an auxiliary marker in order to identify individuals visiting artificial feeders. Auxiliary-marked birds received one of the following in addition to the aluminum leg band: a radio-tag (~300 milligrams; female n = 24, male n = 25; JDJC Corp., Fisher, Illinois, USA), passive integrated transponder (PIT) tag (~100 milligrams; female n = 190, male n = 214; Cyntag, Cynthia, Kentucky, USA), or back color tag (~30 milligrams; female n = 189, male n = 257; Kapoor 2012). We do not expect tags to influence the behaviors recorded during the short behavioral sampling periods (3.83 ± 7.43 minutes; this and all subsequent results given as mean ± SD) since radio-tags, the heaviest tag and most likely to influence flight, were not found to influence Ruby-throated Hummingbirds during 7 minute trials in an aviary throughout autumn migration (Zenzal et al. 2014). Furthermore, when manufacturing back color tags we excluded shades of red, orange, and pink from our color combinations to limit any non-intended influence of the marker on behavior (reviewed by Calvo and Furness 1992; but see Carpenter et al. 1993a), given that the red gorget of the Ruby-throated Hummingbird might act as a badge to signal dominance (*sensu* Rohwer 1982).

Behavioral Observations

Each season, feeding stations were set up the first week of September with observations starting shortly thereafter (Table 2) and concluding on 26 October by which time the majority of hummingbirds had passed through the study site (Zenzal and Moore 2016). Each morning, artificial feeders were observed from approximately 30 minutes after local sunrise (CDT) until either all 10 feeders were observed or other circumstances prohibited observations from taking place (e.g., unfavorable weather). In an attempt to equalize observation effort among all feeders and avoid a temporal bias, observations began at a different feeding station every day. Each season a single hired technician collected all behavioral data; for two seasons (2013-2014) the same individual collected all behavioral data. The total amount of time spent at an individual feeder during a particular season ranged from 7.75 – 13.58 hours, with 10.97 (± 2.07) hours being the mean observation time across all seasons (Table 2).

Table 2

Effort of Behavioral Observations

Year	Start date	End date	Mean	Standard deviation	Minimum	Maximum	Total
2012	9/9	10/26	12.14	0.65	11.33	13.33	121.40
2013[a]	9/7	10/26	8.22	0.37	7.75	8.67	82.22
2014	9/6	10/26	12.56	0.72	11.25	13.58	125.58

The year of study, dates observations were conducted, as well as the mean (± SD), minimum, and maximum number of hours spent observing artificial feeders (n = 10) are displayed. [a]We were unable to access our study site because of the U.S. Government shutdown during October 1 – 13, 2013.

For each observation period, the observer waited 5 minutes before collecting data to allow birds to acclimate to their presence. After the acclimation period, the technician made observations in 15 minute increments. During each

15 minute sampling period observers recorded the number of hummingbirds observed within 10 meters of the feeder. These samples provided an estimate of density (competition) during a particular observation. In addition to counts during each 15 minute sampling period, focal sampling was also performed, which included recording the total amount of time the focal individual was observed, the number of times the focal subject fed (dipped bill tip into the feeder), the number of chases conducted, and the chase status of the focal subject (i.e., being chased, doing the chasing, or no chasing), and the focal hummingbird's auxiliary marker if present. If a different individual usurped control of the feeder from the observed individual, a new observation was conducted on the new focal individual. The maximum amount of time spent observing a single feeder was 1 hour. If no focal bird was present at a feeder at the end of a 15 minute sampling period or the total sampling period equaled 1 hour, we concluded the observation with a one minute census of individuals within 10 meters of the feeder before moving to the next feeder. Each feeder was only observed once a day and all observations were audio recorded in the field and later transcribed by the observer.

The observer attempted to accurately identify any auxiliary-marked bird being observed by focal sampling. For radio-tagged birds observed at feeders (n = 6), we identified individuals using a handheld receiver and Yagi antenna. Color marked birds observed at feeders (n = 51) were identified by color combinations of back tags; any observed color combination was confirmed by banding records of deployed color combinations. For PIT tagged birds observed at feeders (n =

27), we corroborated the time, date, and visitations of RFID data at a particular feeder with behavioral observations to identify individuals. We limited statistical analyses to known individuals in order to investigate intrinsic factors that may influence resource use and defense during stopover. The majority of focal individuals (99%) observed were hatch year individuals.

Statistical Analysis

In order to carry out our objectives, we computed new variables based on data collected in the field. We calculated the mean density of individuals at each feeder for every date based on censuses performed during behavioral observations (see above). Given the importance of fuel load on motivation (Moore et al. 2003), we also estimated the bird's fuel load on the day it was observed using daily fuel deposition rates (FDR; grams day-1) of hummingbirds described by Zenzal and Moore (2016) since few birds (n = 23) were observed the same day of capture. We estimated FDR in two ways: 1) if an individual was recaptured during the season on two different days, we calculated the actual FDR of that individual (0.15 ± 0.15 g; n = 21); 2) if an individual was only captured once (n = 49), only recaptured on the same day as initial capture (n = 2), or the adjusted mass based on the actual FDR was not within the normal mass of a RTHU (n = 1), we applied a standard sex-specific FDR based on recapture data from our study site (females: 0.09 ± 0.23 grams, n = 92; males: 0.08 ± 0.25 grams, n = 182; Zenzal and Moore 2016). To adjust masses, we multiplied the FDR (either actual or standard) with the number of days between capture date and observation date, then added that value to the capture mass of each individual. We then subtracted the lean body mass, based on wing length regressions described in Zenzal and Moore (2016), from the adjusted mass to determine estimated fuel loads to account for sexual size dimorphism. We also calculated feeding and chase rates for each observation based on the actual amount of time the bird was observed. We removed a single individual from the analysis that was observed using multiple feeders on the same day.

To examine the influence of intrinsic and extrinsic factors on resource use and defense we used a boosted regression tree (BRT) approach following methods described in Elith et al. (2008). The advantages of BRT, which include (1) only one assumption, (2) a choice of error distributions, and (3) the possibility to fit a variety of functions (curvilinear, linear, non-linear; see Elith et al. 2008 for a general overview), have attracted attention in the area of ecology (e.g., Leathwick et al. 2006, De'ath 2007, Elith et al. 2008, Tanneberger et al. 2010). Instead of providing p-values to describe relationships between dependent and independent variables, the BRT uses decision trees and machine learning algorithms to output the relative influence of independent variables based on a dependent variable. Relative influences are presented as percentages, totaling 100, where independent variables with high percentages show a strong relationship with the dependent variable. The model also produces partial dependence plots which illustrate the relationship between the dependent and independent variables.

To carry out the BRT, we first confirmed that our independent variables are not collinear using correlation tests between continuous variables

(Spearman’s Rank), meeting the lone assumption of the BRT. We then followed the BRT script supplied by Elith et al. (2008) using a Gaussian distribution, tree complexity of 2, bag fraction of 0.5, and attuned the learning curve of each model to generate approximately 1,000 trees (feeding rate: 0.001; chase rate: 0.0005). To analyze resource use, we used feeding rate as the dependent variable while sex, fuel load, resource quality (1:2 or 1:4 sucrose solution), density, and chase status as independent variables (n = 84); we removed one observation where an individual was both chased and chasing during the same sampling period prior to analysis. To analyze resource defense, we used chase rate as the dependent variable with sex, fuel load, resource quality, and density as independent variables (n = 84).

While the BRT describes the relationship between the resource use and defense of individuals at feeders in relation to intrinsic and extrinsic variables, it does not describe which individuals are gaining priority access to food resources. Since priority access likely influences the ability for an individual to use and defend resources (e.g., Moore et al. 2003), we performed Pearson’s Chi-squared tests (Zar 2010) on sex, resource quality, and chase behavior to determine which individuals are gaining access to food resources. Finally, we performed a Kruskal-Wallis rank sum test (Kruskal and Wallis 1952) to explore the relationship between conspecific density and chase status since conspecifics likely influenced the behavior of focal individuals (n = 84). All statistics were performed in the R statistical language (version 3.2.3; R Core Team 2015) utilizing packages “gbm” (Ridgeway et al. 2015), “dismo” (Hijmans et al. 2016), and “pgirmess” (Giraudoux 2016).

Results

Feeding Rate

We used feeding rate (number of times the focal subject dipped bill tip into the feeder divided by time) as a measure of the ability for individuals to satisfy energetic demands. The model showed that feeding rate was most strongly influenced by chase status (38.50% relative influence) and fuel load (36.81% relative influence). Conspecific density (17.30% relative influence) exerted about half of the influence of the aforementioned variables on the model, while resource quality (5.03% relative influence) and sex (1.84% relative influence) had weak associations relative to the other variables. Birds not involved in agonistic behavior had the highest feeding rate, while aggressive individuals that chased conspecifics had the lowest feeding rate. Leaner birds had higher feeding rates than birds with higher fuel loads. Feeding rate differed little between different conspecific densities, feeder quality, and sex (Figure 13).

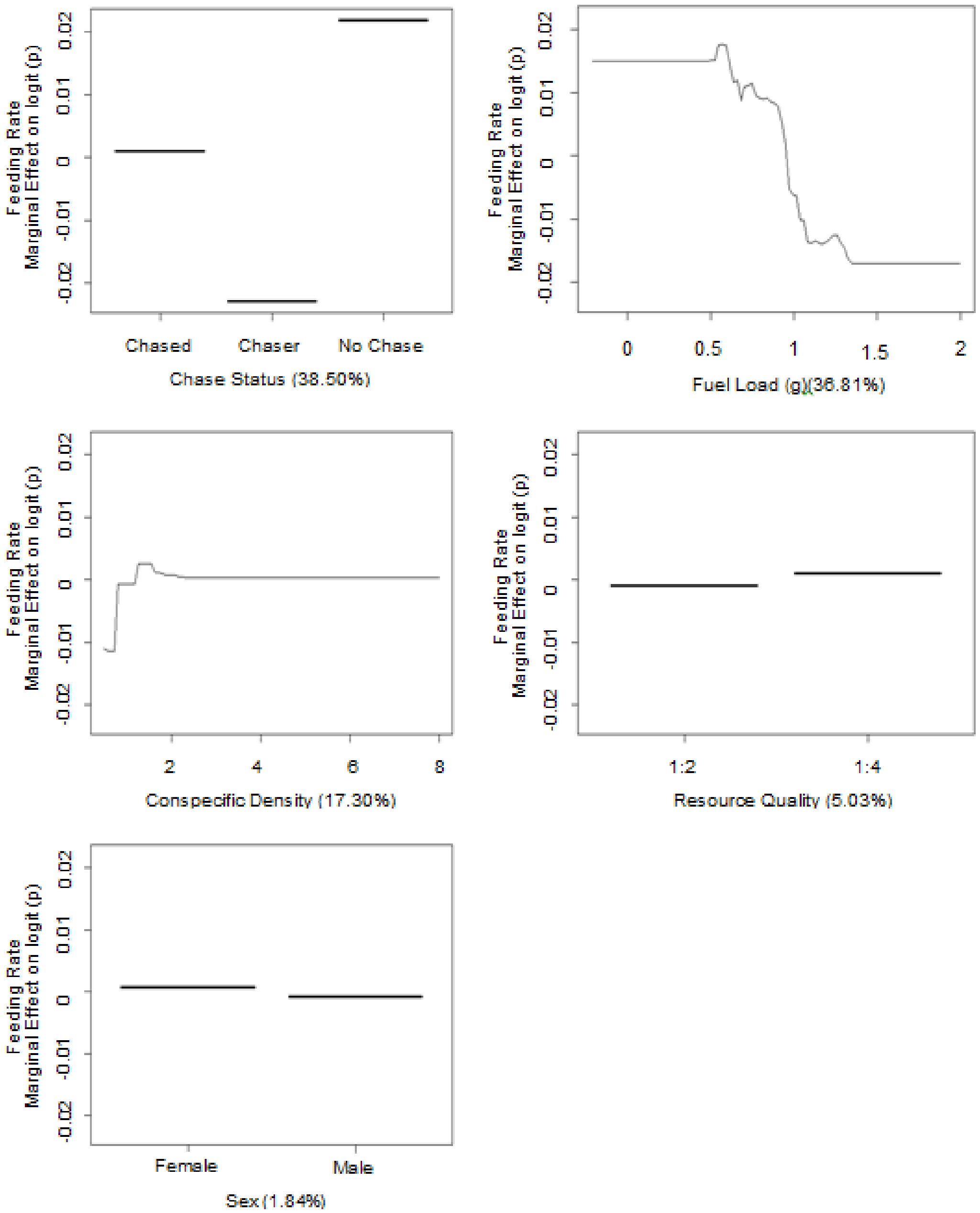


Figure 13. Partial Dependence Plots for Predictor Variables in the Model for Ruby-throated Hummingbird Resource Use.

Positive values on y-axis indicate a positive influence on feeding rate. Y-axes are on a logit scale and are centered to have a zero mean over the data distribution. Percentages after variable names indicate the relative influence.

Chase Rate

Hummingbirds engaged in agonistic behavior, chasing or being chased, when defending resources; we measured these agonistic behaviors as the chase rate (number of chases divided by time). Conspecific density (51.33% relative influence) was the independent variable that had the strongest influence on chase rate. The model shows that chases increased with conspecific density (Figure 14). Furthermore, the Kruskal-Wallis rank sum test indicated a significant effect of density on chase status ($\chi2 = 20.90$, df = 2, $p < 0.001$) and a post-hoc analysis revealed that conspecific density differed between birds not involved in chases compared to birds either chasing or being chased. Birds tended be non-agonistic during low conspecific density (0.46 ± 0.64 birds), but were either chasing or being chased during higher conspecific densities (1.65 ± 0.88 and 2.57 ± 2.07 birds, respectively). The combined results of the BRT model and Kruskal-Wallis rank sum test indicate that hummingbirds first changed their behavior to defend resources when competition increased, then increased the number of agonistic behaviors as conspecific density increased.

Fuel load (42.60% relative influence) also had a relatively strong influence on chase rate. The relationship between chase rate and fuel load was non-linear; birds carrying moderate fuel loads (between 0.5-1 g over lean body mass) had the highest chase rates (Figure 14). Both resource quality (5.74% relative influence) and sex (0.33% relative influence) had little influence on the model in relation to the other variables. Chase rate was similar between resource qualities and sexes.

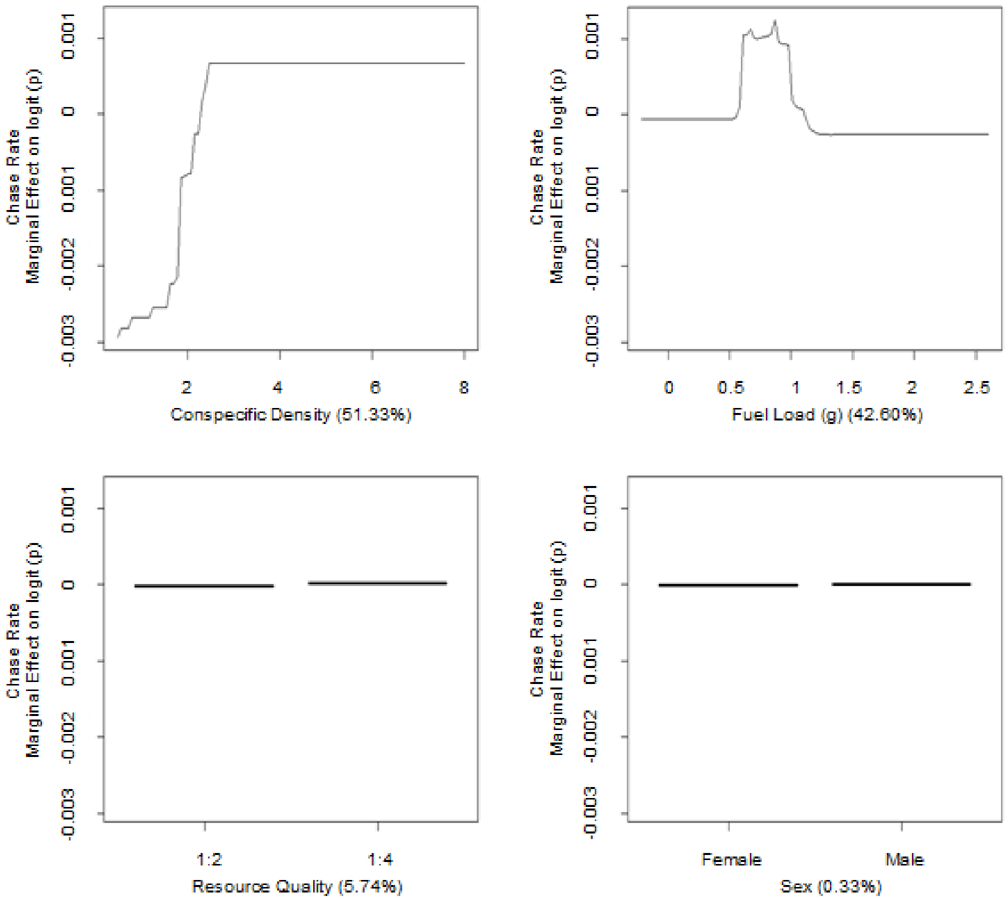


Figure 14. Partial dependence plots for predictor variables in the model for Ruby-throated Hummingbird Resource Defense

Positive values on y-axis indicate a positive influence on chase rate. Y-axes are on a logit scale and are centered to have a zero mean over the data distribution. Percentages after variable names indicate the relative influence.

Priority Access

To determine priority access to feeders, which can help to better understand resource use and defense, we performed a number of Chi-squared tests. More males (n = 63) were the focal subjects compared to females (n = 22) during behavioral observations ($\chi2 = 19.78$, df = 1, $p < 0.001$). We also found that chase status is dependent on sex ($\chi2 = 13.45$, df = 3, $p = 0.004$). Males were either not involved in a chase (n = 28) or performing a chase (n = 27), whereas females were either not involved in a chase (n = 14) or were being chased from a feeder (n = 6; Table 3). However, we did not find overall differences between the frequencies of focal subjects displaying agonistic behaviors (n = 43) versus not behaving agonistically (n = 42; $\chi2 = 0.01$, df = 1, $p = 0.91$); but out of observations that included agonistic behaviors, we found the majority of individuals were performing chases (n = 28), compared to birds being chased (n = 14), or both chasing and being chased during the same observation (n = 1; $\chi2 = 25.44$, df = 2, $p < 0.001$). Finally, we found no differences in the numbers of birds exploiting high quality sucrose solution feeders (n = 48) compared to standard quality sucrose solution feeders (n = 37; $\chi2 = 1.42$, df = 1, $p = 0.23$).

Table 3

Agonistic Behavior in relation to Sex

	Female	Male
No agonistic behavior	14	28
Chaser (aggressive)	1	27
Chased (submissive)	6	8
Both (chaser and chased)	1	0

Behaviors observed by males and females during individual sampling periods (n = 164). Behaviors were dependent on an individual's sex ($\chi2 = 13.45$, df = 3, $p = 0.004$).

Discussion

The ability for birds to meet the energetic demands of migration is directly tied to their ability to exploit resources (Moore and Yong 1991; Smith et al. 2007; Cohen et al. 2012) and our study provides hard to come by information on resource use and defense during the stopover of a migratory landbird using patchily distributed resources. We determined how intrinsic (sex, fuel load, and behavior) and extrinsic (conspecific density and resource quality) factors influence foraging and agonistic behavior of Hummingbirds during stopover. Our results suggest that intrinsic factors have stronger associations with resource use and priority access to food, while extrinsic factors are more strongly associated with resource defense.

Priority access to resources is influenced by the sex of the individual (e.g., Moore et al. 2003; Dierschke et al. 2005; Arizaga and Bairlein 2011), likely mediated by a set of interrelated factors including sexual size dimorphism (e.g., Temeles 1986; Hakkarainen et al. 1996), sex-dependent hormone levels (e.g., Geslin et al. 2004), or social dominance (Moore et al. 2003; Dierschke et al. 2005). During the breeding season, male RTHU defend food resources separate from the female’s territory, which is typically limited to the nest (Saunders 1938; Pitelka 1942; Weidensaul et al. 2013; but see Bolles 1894; Saunders 1936) and male dominance seems to carryover to stopover. We found sex ratios to be highly skewed at artificial feeders with the majority (74%) of behavioral observations collected on males, even though males only made up 55% of captures over the same time period, suggesting that male Hummingbirds have priority access at our study site. Defense of feeders was also dependent on sex, with males tending to chase conspecifics when behaving agonistically, whereas females that did engaged in agonistic behaviors tended to be chased. These findings, primarily on hatch year birds, are similar to studies on hatch year

Rufous Hummingbirds (*Selasphorus rufus*) during stopover (Kodric-Brown and Brown 1978; Carpenter et al. 1991, 1993a). Furthermore, differences between exploitation and dominance at feeders may reflect differences in foraging behavior between sexes. Males typically defend resources through aggressive chases, whereas females tend to use traplining—flying from flower to flower without defending space—as their foraging strategy (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Norberg 1990).

Although we found both behavior and priority access to feeders to be sex-dependent, resource use and defense by birds exploiting feeders as measured through feeding and chase rate, respectively, were only weakly influenced by sex relative to other variables. Analyses revealed little difference between the chase rate and feeding rate of males and females. The weak influence of sex suggests that, though males tend to have priority access to feeders, both sexes behave similarly when using and defending feeders. While capable of exploiting high quality resources, female hummingbirds seem to be more selective when deciding to defend resources and do so only when the benefits greatly outweigh the costs, since they are more able to successfully exploit resources when non-territorial. Male hummingbirds may choose to defend resources more frequently, even when costs approach the benefits, since they tend to lose mass when non-territorial (Carpenter et al. 1993b). These results are similar to studies of migrant Rufous Hummingbirds and support a sex-dependent foraging strategy where females adapt their strategy to meet the energetic demands of migration (e.g., Kodric-Brown and Brown 1978; Carpenter et al. 1991, 1993a, 1993b).

Arguably the most important constraint on birds during migration is the need to acquire sufficient nutrients to meet energetic requirements (Blem 1980). Both fuel stores and availability of resources at a stopover site can influence the way animals use and defend resources (e.g., Sealy 1989; Loria and Moore 1990; Moore et al. 2003). For example, we found a negative relationship between fuel load and feeding rate; hummingbirds increased their foraging rate to meet energetic demands not unlike lean Red-eyed Vireos (*Vireo olivaceus*) who increased foraging rate and agonistic behaviors in order to obtain more food during stopover (Loria and Moore 1990; Moore et al. 2003; but see Lindström et al. 1990). The association between fuel load and chase rate, however, is not as straightforward. Hummingbirds with very low fat stores and very high fat stores tend to have lower rates of agonistic behaviors, while birds with moderate fuel stores tend to have the highest rates of agonistic behaviors. Hummingbirds in poor energetic condition might not have the capacity to defend resources through energetically expensive chasing behavior, and RTHU in much better condition may be risk averse, only feeding when gaining the most reward (see Moore and Simm 1986). Surprisingly, individuals defending feeders through chases had the lowest feeding rates. While this result likely reflects the costs of priority access (e.g., Vogel 2005), aggressive individuals may have had priority access to feeders during times of high competition. This explanation is further supported by our findings that agonistic behaviors were a result of high levels of conspecific densities.

Conspecific density is an important extrinsic variable in relation to food acquisition (Moore and Yong 1991; Kelly et al. 2002). Feeding rates can be depressed during competition because (1) high volumes of birds decrease the overall availability of food (Goss-Custard 1980, 1984; Hansson and Pettersson 1989; Moore and Yong 1991) and (2) competing for food is energetically expensive, takes time away from foraging, and competitively inferior individuals may be excluded from feeding (Goss-Custard 1980, 1984; Carpenter et al. 1993a; Vogel 2005). We found a positive relationship between conspecific density and chase rate, but feeding rate did not appear to change with density. Furthermore, density influenced the behavior of hummingbirds with agonistic behaviors being more prevalent at higher conspecific densities. The behaviors we observed might explain the negative relationship between migrant density and mass gain during stopover found in previous studies using banding data (Moore and Yong 1991; Kelly et al. 2002); however, our results are limited to patchy resource distributions where interference competition is possible (e.g., flower patches, fruiting trees/shrubs).

Given the energetic demands of migration, we would expect individuals to maximize caloric intake and minimize energy expenditure by exploiting the most profitable food sources (e.g., Moore and Simm 1985). Contrary to our expectations, the quality of food sources had little influence on feeding and chase rates of hummingbirds during stopover studied here, and individuals did not show a preference for feeder quality. Given that our high quality sucrose solution had double the sucrose concentration of the standard quality solution, which approximates hummingbird pollinated flowers (Pyke and Waser 1981; Ornelas et al. 2007), we expected a higher proportion of individuals to be exploiting the more profitable resource (see work with captive individuals Tamm and Gass 1986) and chase rates to be greater at the more profitable feeder. Our data show that chase rates and frequencies at feeders were similar between both resource qualities, which may suggest that individuals are willing to defend an inexhaustible resource regardless of the quality. Moreover, defense of an artificial feeder is likely more economical than defense of flower patches, which vary in size and floral density (e.g., Carpenter et al. 1983, 1993a), but we expect our findings on resource defense to be similar in natural settings where food resources are patchily distributed (e.g., Moore 1977, 1978; Carpenter et al. 1983, 1993a).

Our study reveals that both intrinsic and extrinsic factors influence the stopover ecology of migrant RTHU. Specifically, intrinsic factors seem to be of greater influence on resource use, whereas extrinsic factors are more important on resource defense. For Ruby-throated Hummingbirds we found sex, fuel load, density, and behavior to be strongly associated with the ability of individuals to exploit and defend resources throughout our study site. Our results are consistent with Johnson and Sherry’s (2001) hypothesis that migrants use a combined free and despotic distribution based on extrinsic and intrinsic factors, similar to distributions of migrants they found on the winter grounds. This hypothesis is reasonable considering the dynamic nature of stopover in which the behavioral plasticity of migrants is expected (Moore et al. 1995). Furthermore using Hummingbirds as a model, we were able to manipulate resources and collect information on known individuals, which has allowed us to reveal the behavioral mechanisms that mediate priority access to resources, filling an essential gap in our knowledge of the relationship between migrants and resource use during stopover.

CHAPTER III – THE IMPACT OF RADIO-TAGS ON RUBY-THROATED HUMMINGBIRDS (*ARCHILOCHUS COLUBRIS*)

Introduction

Radio telemetry has advanced our understanding of wildlife biology in lock step with advances in technology. Using radio telemetry as a way to study birds started in the early 1960s (e.g., Lord et al. 1962; Southern 1964; Graber and Wunderle 1966) and is now widely used to remotely collect movement data of free-ranging birds. Advances in technology have allowed for miniaturization of radio-tags, which has enabled researchers to radio-tag smaller and smaller animals, including hummingbirds (e.g. Hadley and Betts 2009) and arthropods (e.g. Wikelski et al. 2006, 2010). The usual limitation in the use of radio-tags in avian biology is the weight of the radio-tag in relation to total body mass, which is recommended to remain <3-5% (Cochran 1980; Gustafson et al. 1997; Fair et al. 2010). The added weight of a radio-tag may decrease the probability of nesting and increase energetic expenditure (Barron et al. 2010), yet field studies have found that tags up to 5% of the bird's total body weight do not meaningfully affect survival or movements of small (< 20 g) birds (Naef-Daenzer et al. 2001; Hadley and Betts 2009).

Some research on passerines has shown that radio-tags negatively affect survival (Dougill et al. 2000; Mattsson et al. 2006), while other studies on large, mostly flightless birds suggest negative impacts based on increased energy expenditure (Osborne et al. 1997; Godfrey et al. 2002; Guthery and Lusk 2004). However, most studies investigating direct impacts of radio-tags on survival rates have found negligible effects, if any (Powell et al. 1998; Naef-Daenzer et al. 2001; Hernández et al. 2004; Terhune et al. 2007; Anich et al. 2009; Townsend et al. 2012). The detrimental effects of radio-tags described by Dougill et al. (2000) were due to tag design, while Mattsson et al. (2006) found decreased survival when outfitting nestlings with radio-tags. Long-term survival of radio-tagged birds does not seem to be impeded by tags, as long as tags are well designed and attached after fledging. Additionally, temporary radio-tags, in which the tag eventually falls off, would likely affect survivorship the least (e.g. Raim 1978, Sykes et al. 1990; Naef-Daenzer 1993; Naef-Daenzer et al. 2001; Anich et al. 2009; Hadley and Betts 2009; Smolinksky et al. 2013).

Even if there is no increased likelihood of mortality or reduced reproductive success while wearing a radio-tag, other influences might handicap organisms during particular times of their annual cycle. While Barron et al.'s (2010) meta-analysis on the effects of radio telemetry found no significant effect on flight ability, a radio-tag externally mounted to the back of a bird will necessarily increase body drag (Obrecht et al. 1988; Pennycuick et al. 2012). The main variable in telemetry effect studies is the ratio of the equipment weight to body; arguably the additional drag created by the radio tag has a larger impact on flying animals than the increase in weight. An increase in body drag has been estimated (all things being equal) to reduce long-distance flight ranges, such as during migration (Obrecht et al. 1988; Powell et al. 1998; Pennycuick 2008; Pennycuick et al. 2012). Additionally, the extra weight of a radio-tag may exacerbate energy expenditure of flight, an especially difficult problem for migrating birds that are already carrying increased fat loads. Nonetheless, most investigators make no attempt to determine any impacts of the device before implementing a radio tracking study.

The impact of radio-tags on birds is usually not tested prior to application on free-flying birds, especially for drag. If flight performance is affected by the weight of a radio-tag, then we would expect birds with the heaviest radio-tags to experience the largest effect. Drag, however, varies with transmitter and antenna size, not with mass (Pennycuick et al. 2012). Differing antenna lengths could have a disproportionate impact on the transmitter center of gravity imposing increased energetic costs per unit flight time on individuals outfitted with a longer antenna than individuals outfitted with a shorter antenna. Individuals with the longer antenna will either compensate energetically to the increased flight costs or fly less.

We analyzed the impact of radio-tags on the flight performance and behavior of Ruby-throated Hummingbirds (*Archilochus colubris*), a long-distance, migrant (likely both trans-Gulf and Circum-Gulf) traveling between breeding and wintering destinations (Weidensaul et al. 2013), and the smallest bird to our knowledge to be outfitted with a radio-tag. We used a pairwise study design on individuals in a controlled setting to examine three different radio-tag packages varying in weight and antenna length during fall migration, a time when individuals are accumulating additional mass via fat stores in order to fuel migratory flights. Our two main objectives a priori were: 1) quantify the flight time of birds with and without a radio-tag, and 2) estimate the flight range of birds with and without a radio tag from a mechanical model of weight and drag (Pennycuick 2008). A secondary objective a postori was to determine if preening behavior differed between treatments.

Methods

Study Site and Field Methods

We captured Ruby-throated Hummingbirds using nylon mist nets at the Bon Secour National Wildlife Refuge, Fort Morgan, Alabama (30°10'N, 88°00'W), between sunrise and noon from September 3 – 16, 2010. Netting effort was both active, baiting 10 nets with artificial feeders, and passive. We banded hummingbirds with a USGS aluminum band, aged and sexed them (Pyle 1997), estimated fat (Helms and Drury 1960), measured wing chord and mass, and took a wing photo to determine wing span and wing area for flight range estimates.

Aviary Routine and Radio-tag Attachment

We randomly selected a sub-sample of hatch year birds (n = 35; mass = 3.80 ± 0.73 grams for males (n = 20) and 3.76 ± 0.46 grams for females (n = 15) [these and following results are reported as mean ± SD]). We individually placed birds selected for experimentation into a field aviary (2.43 meters X 1.31 meters X 1.94 meters) with a perch and a feeder without a perch. We used a pairwise study design in which all individuals received, in random order, the control treatment (no radio-tag) and one of three experimental treatments (with faux radio-tag, Figure 15). In each experimental treatment the faux radio-tag varied by antenna length and/or mass. The first experimental group (n = 15) received a heavy radio-tag (240 milligrams; total body mass: 6.00% females, 6.32% males) with a long antenna (length: 12.7 centimeters; diameter: 0.229 millimeters). The second experimental group (n = 10) received a light radio-tag (220 milligrams; total body mass: 5.50% females, 5.79% males) with a long antenna (length: 12.7 centimeters; diameter: 0.152 millimeters). The third experimental group (n=10) received a light radio-tag (220 milligrams; total body mass: 5.50% females, 5.79% males) with a short antenna (length: 6.35 centimeters; diameter: 0.152 millimeters). Radio-tag design and two faux transmitters were provided courtesy of Sparrow Systems.

Figure 15. Ruby-throated Hummingbird with a faux radio-tag

Photograph by T.J. Zenzal

We attached radio-tags using a modified version of Raim's (1978) method. Radio-tags were first sewn to a piece of cloth the size of the radio-tag, then a second piece of cloth similar in size to the one sewn to the radio-tag was glued to the back of the bird using Revlon® Fantasy Lengths® eyelash adhesive. The cloth sewn to the radio-tag was glued to the cloth on the bird (Figure 15). Cloth, thread, and glue were not included in the radio-tag weight. We removed radio-tags by clipping feathers under the cloth. Treatment order was randomized between individuals to eliminate any effect of order on subsequent analysis. Each individual tested only one radio-tag. After being prepared for the appropriate treatment (with or without radio-tag), individuals were placed in the aviary, allowed to acclimate for 10 minutes before the treatment was recorded, and then videotaped (Panasonic PV-GS65) at 1/4000 frames per second for 7 minutes to score behaviors and time spent in various activities. We then prepped the same individual for the next treatment (attachment or removal of radio-tag), allowed another 10 minutes for acclimation, and then videotaped for another 7 minutes. After a bird completed both treatments, we released it without a radio-tag.

Flight Time

Flight time was quantified from the total 14 minutes (7 minutes for control treatment and 7 minutes for experimental treatment) of video recording. We defined flight as any period an individual was not perched, not distinguishing hovering flight (including feeding) from forward flight. Body condition was determined for two reasons: 1) birds were randomly selected during migration, differing in the amount of fat carried, and 2) this species exhibits reverse sexual-size dimorphism (Weidensaul et al. 2013). We calculated body condition (fat) based on mass and wing length of Ruby-throated Hummingbirds captured on the

Bon Secour NWR following Ellegren (1989, 1992) and Owen and Moore (2006). For both sexes, we determined fat free masses by regressing body mass on fat score for individuals in the same wing chord class (1 millimeter increments). The intercept of the regression provided an approximation of fat free mass for a sex-specific wing chord class. After performing regressions on all wing chord classes of individuals included in the study, we executed a second linear regression by regressing the intercepts on each related wing chord class for each sex. The resulting equation from the second regression allowed an estimation of size specific fat free masses for each hummingbird.

Restricted maximum likelihood (REML) models were used to assess the influence of radio-tags on flight time data using JMP statistical software (v.10, SAS Institute 2013). We performed a preliminary analysis on a subset of individuals balanced by experimental order (n = 14 for each group) to determine if the order in which treatments were applied had an effect on flight time. Flight time (square root transformed) was the response variable in a repeated measures mixed model with radio-tag type, experimental order, and presence/absence of radio-tag as fixed factors and individual as a random nested blocking factor. We removed experimental order from subsequent analysis (see Results). We then analyzed flight time data using a repeated measures mixed model with radio-tag type, sex, body condition (described above), and presence/absence of radio-tag as fixed factors and individual as a random nested blocking factor. To determine the impact of each radio-tag type, we reran the analysis for the three radio-tags separately and interpreted p-values using the Holm-Bonferroni adjustment method for multiple comparisons (Holm 1979). Body condition failed to meet the assumptions of normality (Shapiro-Wilk; p = 0.02), even after attempting all standard transformations. Therefore, we ran each analysis with and without body condition included as a covariate. To further explore the relationship between body condition and activity budget, we used a Spearman's rank correlation between flight time and body condition.

Preening Behavior

We quantified the number of preening occurrences from the video analysis of each bird. Preening is defined as each time an individual's bill made contact with its feathers. We analyzed preening occurrences using a generalized linear mixed-effects model fit by maximum likelihood with a quasi-Poisson distribution (O'Hara and Kotze 2010) in the R statistical language (R Core Team 2015), package "MASS" (Venables and Ripley 2002). The fixed factors of this model included radio-tag type, experimental order, body condition, and presence/absence of radio-tag, with individual as a random nested blocking factor. We excluded sex in this model since we did not believe there is any biological significance of sex on preening. We did however include experimental order because observations suggested that birds receiving the experimental treatment first may preen more after the back feathers were clipped to remove the transmitter. To further explore interactions we performed two additional tests in the R statistical language: First, a Nemenyi post-hoc test (Hollander and Wolfe 1999) from package "coin" (Hothorn et al. 2006, 2008) was performed on significant effects of the model. Second, a Spearman's rank correlation was used to determine a relationship between preening occurrences and flight time.

Flight Range Estimates

We used Program Flight 1.24 to estimated flight range of birds with and without radio-tags. Simulations were based on wing area, fat free mass, and body condition (Pennycuick 2008), for each bird (n = 31) with and without a radio-tag. We obtained fat free masses and body conditions of Ruby-throated Hummingbirds using methods described above. However, three of the individuals fell below the average fat free mass and according to the conditions of the model were not able to migrate. Therefore, two females and one male were eliminated from analysis due to lean body condition; additionally, a third female was removed because she had no associated wing photograph. We quantified wing span and wing area as described in Pennycuick (2008), although we photographed rather than hand traced wings. We modified Pennycuick's (2008) wing area quantification by using ImageJ (Abramoff et al. 2014) to determine the exact wing area (partial wing area plus rootbox) from a digital tracing of an individual's semi-span instead of using a grid to quantify area as performed with hand tracings. We assumed trans-Gulf flight in still-air conditions and an altitude of 500 m (air density of 1.17 kilograms meter^{-3}; Kerlinger and Moore 1989; Woodrey and Moore 1997). When an individual was simulated with a radio-tag, a payload mass was determined for the appropriate radio-tag size (220 milligrams or 240 milligrams) with a drag factor of 1.5 (Pennycuick et al. 2012). We determined differences between simulated flight ranges (square root transformed) for individuals with and without a radio-tag using a REML repeated measures mixed model. Radio-tag type, sex, and presence/absence of radio-tag were set as fixed factors and individual as a random nested blocking factor. This statistical analysis was performed using JMP statistical software (v.10, SAS Institute 2013).

Results

Flight Time

We found mixed evidence of experimental order impacting flight time of hummingbirds, due to a significant interaction between experimental order and presence/absence of a radio-tag ($F_{1,55} = 21.12$, $p = 0.0001$). Individuals decreased flight time during the second treatment regardless of treatment order. There was, however, much individual variation which clouds the interpretation of the results but illustrates that attachment of a radio-tag will not elicit the same response from every individual. Individuals receiving the control treatment first had an 80.00 ± 167.59 second decrease when the radio-tag was attached, while individuals with a radio-tag attached first had a 5.95 ± 148.26 second decrease during the control treatment. A bird undergoing the control treatment second had feathers clipped which possibly explains why there was decreased flight time during the control treatment. The decrease in the subsequent treatment is likely a result of preening and possibly acclimation to captivity (see below). However, the main effect of experimental order did not affect flight time ($F_{1,55} = 0.32$, $p = 0.58$). Based on the main effect test, large amount of inter-individual variation, and the a priori effort to randomize treatment order, we concluded that experimental order did not meaningfully impact activity budgets and excluded it as a factor from the subsequent analysis.

Flight time was about 8% less with a radio-tag attached ($F_{1,69}$ = 7.36, p = 0.01 without body condition as a factor; $F_{1,69}$ = 6.00, p = 0.02 with body condition as a factor). Flight time without a radio-tag (182.94 ± 121.72 s) was greater than when a radio-tag was attached (149.6 ± 104.39 s, averaged across all models). However, size of the radio-tag did not have a significant effect on flight time in either model ($F_{2,69}$ = 0.98, p = 0.39 without body condition as a factor; $F_{2,69}$ = 1.83, p = 0.18 with body condition as a factor). Further analysis using multiple comparison testing between radio-tag types using the Holm-Bonferroni adjustment (Holm 1979) revealed that the only radio-tag to have a significant decrease (~11%) in flight time between the treatment and the control was the heavy tag ($F_{1,29}$ = 15.06, p = 0.002 without body condition as a factor; $F_{1,29}$ = 13.27, p = 0.004 with body condition as a factor; adjusted α = 0.017), while flight time in both of the light tag treatments did not differ from controls (long antenna tag: ~8% decrease, $F_{1,19}$ = 1.76, p = 0.22 without body condition as a factor; $F_{1,19}$ = 2.32, p = 0.18 with body condition as a factor; adjusted α = 0.025; short antenna tag: ~6.5% increase, $F_{1,19}$ = 0.05, p = 0.83 without body condition as a factor; $F_{1,19}$ = 0.06, p = 0.82 with body condition as a factor). Mean flight time decreased predictably from the light weight short antenna tag having the most flight time (210.70 ± 127.14 seconds), followed by the light weight long antenna tag (148.40 ± 74.93 seconds), while the heavy weight long antenna tag had the least flight time (137.00 ± 107.92 seconds; Figure 16). Although wing morphology of Ruby-throated Hummingbirds is sex-dependent (Stiles et al. 2005), neither model showed an effect of sex on flight activity ($F_{1,69} = 2.31$, $p = 0.14$ without body condition as a factor; $F_{1,69} = 1.24$, $p = 0.28$ with body condition as a factor) nor an interaction between sex and the presence of a radio-tag ($F_{1,69} = 0.21$, $p = 0.65$ without body condition as a factor; $F_{1,69} = 1.49$, $p = 0.24$ with body condition as a factor). Finally, body condition did not impact flight time ($F_{1,69} = 1.35$, $p = 0.26$), and a Spearman's rank correlation showed no relationship between flight time and body condition (with radio-tag Spearman's rho= -0.01, p = 0.94, n = 35; without radio-tag: Spearman's rho = -0.18, p = 0.30, n = 35).

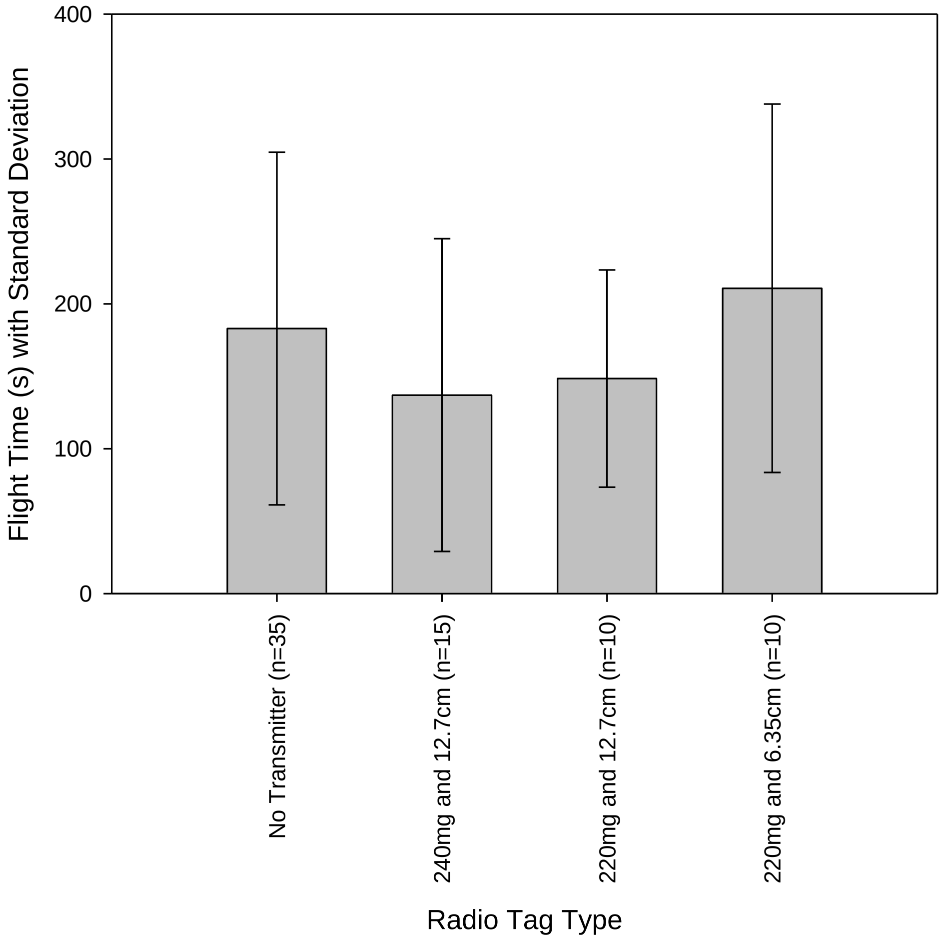


Figure 16. Flight Time of Ruby-throated Hummingbirds with Radio-tag

Mean flight time (s) of Ruby-throated Hummingbirds per 7 min treatment with (240mg: n=15; 220mg: n=10) and without (n=35) radio-tags attached. Radio-tags are separated by mass (mg) and length of antenna (cm). Standard deviation is shown as vertical bars.

Preening Behavior

As expected, initial analysis revealed that preening occurrences had a significant negative correlation with flight time (with radio-tag: Spearman's rho = -0.39, p = 0.02, n = 35; without radio-tag: Spearman's rho =-0.38, p = 0.02, n = 35), which is not surprising given preening and flying are mutually exclusive behaviors. Preening occurrences did not differ between the presence/absence of a radio-tag (t = 0.18, df = 23, p = 0.86, n = 35). However, experimental order did have a significant effect on the number of preening occurrences (t = 2.43, df = 23, p = 0.02, n = 35). Birds receiving the control treatment first (n = 16) had a mean of 25.31 ± 42.53 preening occurrences which increased to 37.63 ± 55.15 preening occurrences when the radio-tag was attached. Birds that first received the experimental treatment (n = 19) increased preening occurrences from 27.84 ± 35.06 to 30.26 ± 40.71 after the radio-tag was removed. However, given the close means and significant effect of preening on experimental order, a Nemenyi post-hoc test (Hollander and Wolfe 1999) was performed on the number of preening occurrences by order which yielded a non-significant effect (Z = 0.31, p = 0.76, n = 35). Although the number of preening occurrences does not differ significantly while an individual has a radio-tag attached, the number of preening occurrences are greater when a radio-tag is attached (32.31 ± 35.38) compared to when no radio-tag is attached (28.00 ± 41.01) averaged across treatments.

There is much individual variation between subjects regardless of treatment. When a radio-tag was attached preening occurrences ranged from 0 to 184 instances over 7 minutes, individuals without a radio-tag attached showed a similar range from 0 to 157 instances over the same time frame. This analysis further explains the significant interaction between presence/absence of a radio-tag and experimental order for flight time.

Flight Range Estimates

Flight modeling provided an estimate of how a radio-tag affects flight range. The presence of a radio-tag significantly affected simulated flight ranges ($F_{1,62} = 135.26$, $p < 0.0001$), reducing an individual's flight range by ~340 kilometers on average (without radio-tag: 1512.26 ± 1188.65 kilometers; with radio-tag: 1172.00 ± 916.86 kilometers). There was no effect of sex on flight range ($F_{1,62} = 0.48$, $p = 0.49$), nor was there an effect of radio-tag mass ($F_{2,62} = 1.08$, $p = 0.36$).

Discussion

Hummingbirds are challenging to study because their size and speed of movement makes detection of birds difficult by visual means. The ability to continually track and record the behavior of radio-tagged hummingbirds would measurably enhance our understanding of migratory movement, dispersal, resource use, home range activity, and habitat use. For example, the first published application of a radio-tag on a hummingbird determined the movement patterns of Green Hermits (*Phaethornis guy*) in Costa Rica (Hadley and Betts 2009). To our knowledge, the Green Hermit is the smallest bird (5.8 ± 0.09 g;

Hadley and Betts 2009) that has been radio-tagged prior to our study of Ruby-throated Hummingbirds. The miniaturization of transmitters has allowed others to track flying arthropods, much smaller than most hummingbirds, which provided insight to questions that would be difficult to answer using other means (e.g., Wikelski et al. 2006, 2010; Pasquet et al. 2008; Hagen et al. 2011).

Activity budgets of Ruby-throated Hummingbirds are influenced by the presence of a radio-tag, although only the heaviest radio-tag showed a significant decrease (~11%) in flight time from the control treatment. The light radio-tags had less influence in flight time with the long antenna tag decreasing flight time by ~8%, and the short antenna tag increasing flight time by ~6.5%. These radio-tags at 220 milligrams, just over 5% total body mass of a Ruby-throated Hummingbird, did not seem to pose a significant handicap on activity, similar to other studies using radio-tags at a comparable percent body weight (Naef-Daenzer et al. 2001; Hadley and Betts 2009). However, it is difficult to extrapolate the small differences found in flight activity that might be an artifact of a seven minute experimental period in an aviary to actual migratory flight.

Free ranging animals may behave differently when in captivity (see Clubb and Mason 2003). The size of the aviary or simply being placed in an aviary may have limited the activity of the hummingbirds once they determined there was no way out. Although time of day was not included as a factor in analysis, most birds were tested in the late morning or early afternoon when they are typically inactive (Zenzal, personal observation) or migrating (Hall and Bell 1981; Willimont et al. 1988). The length of time allotted for birds to acclimate to the radio-tag may have been too short, affecting the outcome; most birds receiving any sort of marker (e.g. band, radio-tag) spend an unpredictable amount of time reacting to the tag (preening or attempting to remove the marker) before resuming normal behaviors.

Preening increased in individuals that received the experimental treatment compared to the control treatment. Increases in comfort behavior (as described by Delius 1988; i.e. preening, wing flapping, head shaking) would necessarily increase the amount of time spent perching, while decreasing time spent in flight. While preening explains some of the variation found during flight activity, particularly between the different experimental orders which may be due to attaching radio-tags directly to feathers or clipping back feathers to remove the radio tag, caution is recommended when making interpretations from this analysis as handling birds seemed to increase the likelihood of birds preening. Although we found no significant effect of a radio-tag on preening, other studies have shown that preening did increase with the attachment of a transmitter (Hooge 1991; Pietz et al. 1993; Sykes et al. 1990).

The apparent effect of the radio-tag on activity might be influenced by attachment method, since the radio-tag was glued directly to back feathers instead of skin for easy removal after the experiment was complete. The most common adhesive attachment method requires feathers to be clipped in order to create a strong bond between the radio-tag backing and the skin of the bird or feather shaft (e.g., Raim 1978; Sykes et al. 1990; Naef-Daenzer 1993; Naef-Daenzer et al. 2001; Anich et al. 2009; Hadley and Betts 2009; Smolinksky et al.

2013). The effects of this attachment method are negligible on small birds compared to other attachment methods tested (Sykes et al. 1990). Furthermore, field studies showed no decrease in survivorship when this attachment method was used compared to non-radio-tagged birds (Naef-Daenzer et al. 2001; Anich et al. 2009).

The percent body mass and size of radio-tags, but not the antenna length, appeared to affect the activity budget; however much variation existed between and within treatments. Our findings are consistent with the influence of drag of the device (Barron et al. 2010; Pennycuick et al. 2012) rather than the weight of the radio-tag viz. energetic expenditure. The light radio-tag with the short antenna had the highest amount of flight time, likely due to decreased drag of the antenna. However, large individual variation across all the variables explored make it difficult to suggest any hard-and-fast rules for radio-tagging hummingbirds, besides selecting a radio-tag that has the smallest weight and drag available. A valuable follow-up study to the one described would determine the amount of drag different radio-tag designs have on free-flying hummingbirds, similar to Pennycuick et al.’s (2012) study of external device drag on Rose-coloured Starlings (*Pastor roseus*), with the use of a wind tunnel.

Predicted flight range was affected by the presence of a radio-tag but did not vary with size of the radio-tag or sex of the individual. Individuals able to fly farther by virtue of larger fat loads experienced larger decreases in distance when radio-tagged compared to individuals with shorter flight ranges. Although flight simulations showed a decrease in flight ranges, most studies on survival and return rates of radio-tagged long-distance migrants fail to show an effect of radio-tags on survival (Powell et al. 1998; Cardinal 2005; Anich et al. 2009; Townsend et al. 2012; however see Samuel and Fuller 1996). In two of these studies, a subsample of birds tagged were recaptured a year later (in one case 2 years later, Powell et al. 1998) with radios still attached (Powell et al. 1998; Townsend et al. 2012).

Hummingbird behavior is potentially affected by the presence of a radio-tag, so caution should be exercised when selecting individuals to tag, which will depend on season, sex, and condition. For example, a radio-tag is likely to impede nest construction in female hummingbirds (see Weidensaul et al. 2013). That said, observations of free flying Ruby-throated Hummingbirds during stopover revealed that individuals with radio-tags behave similarly to marked individuals without radio-tags in stopover duration, foraging, competitive interactions, and seasonally appropriate departure directions (Zenzal, personal observation). One of these free flying radio-tagged birds was detected, wearing its tag, at an artificial feeder in Corpus Christi, Texas (~950 km from Fort Morgan, Alabama) two weeks after being tagged (USGS Bird Banding Laboratory, personal communication).

CHAPTER IV – YOUNG RUBY-THROATED HUMMINGBIRDS (ARCHILOCHUS COLUBRIS) DO NOT CROSS THE GULF OF MEXICO DURING AUTUMN MIGRATION

Introduction

Most migratory bird species are faced with at least one ecological barrier during migration (Alerstam 1981). In eastern North America, the majority of breeding birds that winter in Central and South America must cope with the Gulf of Mexico (GOM). Birds that elect to fly across the GOM require stores of fat sufficient to meet the energetic demands of a trans-Gulf flight (Sandberg and Moore 1996; Smolinsky et al. 2013; Deppe et al. 2015); and the majority of those reserves are obtained during stopovers (e.g. Woodrey and Moore 1997; Zenzal and Moore 2016). Habitats along the northern coast of the GOM provide the last possible stopover before migrants engage in a non-stop flight of at least 900 km, and evidence suggests that landbird migrants may not begin to build large fuel loads until they encounter barriers (see Odum et al. 1961, Caldwell et al. 1963). Alternatively, individuals encountering this barrier may elect to move along the coastline consistent with circum-Gulf flight (Sandberg and Moore 1996, Alerstam 2001). Whether migrants fly around or over this ecological barrier, they face several important decisions (Deppe et al. 2015), notably when to depart a stopover site and in what direction to travel, which will have repercussions on other parts of the annual cycle (e.g. Smith and Moore 2003). Both intrinsic and extrinsic factors have been found to impact these decisions (e.g. Sandberg and Moore 1996; Smolinsky et al. 2013, Deppe et al. 2015).

Intrinsic factors such as age, sex, or fuel load may influence an individual's decision to depart and in what direction. Age is known to influence decision making (e.g., Thorup et al. 2003; Smolinsky et al. 2013; McKinnon et al. 2014; Dossman et al. 2016; but see Deppe et al. 2015). For example, less experienced hatch-year (HY) birds may be inadequately prepared to negotiate the GOM (Woodrey 2000) and/or more prone to orientation errors (Moore 1984; Able and Bingman 1987). The role of sex on departure decisions has received less attention. Although Helbig (1991) found no differences in migratory directions between male and female Blackcaps (Sylvia atricapilla), sex can influence access to resources (Moore et al. 2003) or wing morphology (Stiles et al. 2005), both of which may influence an individual's departure decisions (e.g., Sandberg and Moore 1996; Bowlin 2007; Smolinsky et al. 2013; Deppe et al. 2015). While age and sex have been found to influence departure behavior, fuel stores exhibit the strongest influence on the departure decisions of migrants. A migrant's fuel stores largely determine the distance a migrant is able to travel (Pennycuick 2008), influencing how an individual negotiates an ecological barrier (Sandberg and Moore 1996; Smolinsky et al. 2013, Deppe et al. 2015; Sjöberg et al. 2015; Dossman et al. 2016). Individuals with sufficient fuel stores are able to traverse a barrier, while individuals with insufficient fuel stores may choose to spend time fueling on stopover, reorient in search of better habitat, or if possible circumnavigate a barrier (Nilsson and Sjöberg 2015; Deppe et al. 2015). Rarely do these intrinsic factors act alone, for example young migrants are often in leaner condition compared to adult birds (Woodrey and Moore 1997; Zenzal and

Moore 2016), suggesting that these factors likely interact to influence departure decisions.

Extrinsic factors in the form of atmospheric conditions influence the decisions made during migration, especially when preparing for overwater flights (Richardson 1978, 1990; Deppe et al. 2015; Kranstauber et al. 2015). Weather can have either beneficial or detrimental effects on birds during migration. Migrants taking advantage of supportive winds may decrease the costs of transport (Liechti and Brunderer 1998; Kranstauber et al. 2015). Conversely, opposing winds, turbulence, or low visibility increase transport costs (e.g. Richardson 1978; Liechti and Brunderer 1998). Beneficial or not, studies have found that large scale weather patterns affect the departure decisions of individuals migrating along the northern GOM coast (Able 1972; Deppe et al. 2015).

The Ruby-throated Hummingbird (*Archilochus colubris*) is an intercontinental migrant that travels between breeding grounds in eastern North America and wintering grounds in Mexico and Central America (Weidensaul et al. 2013), primarily using nectar to fuel this migratory flight. We suspect that the GOM presents a formidable barrier to hummingbirds because of their small size (~3 grams) likely increases the susceptibility to unfavorable weather while aloft (Ravi et al. 2015). Although Ruby-throated Hummingbirds (hereafter “RTHU”) theoretically carry more than enough fuel stores to cross the GOM under still air conditions (Zenzal and Moore 2016), calculations based on the oxygen consumption of hovering flight suggest a hummingbird with 2 grams of fat would have a maximum flight range of 1050 kilometers (Lasiewski 1962) which would decrease under unfavorable atmospheric conditions. Given that hummingbirds increase wing beat frequency in turbulent conditions (Ravi et al. 2015); encountering unfavorable winds after departing over the GOM could dangerously increase the energetic cost of flight. Therefore, the decisions of migrants departing a coastal stopover site may reflect the importance of energetic condition and weather for a migratory bird, especially hummingbirds.

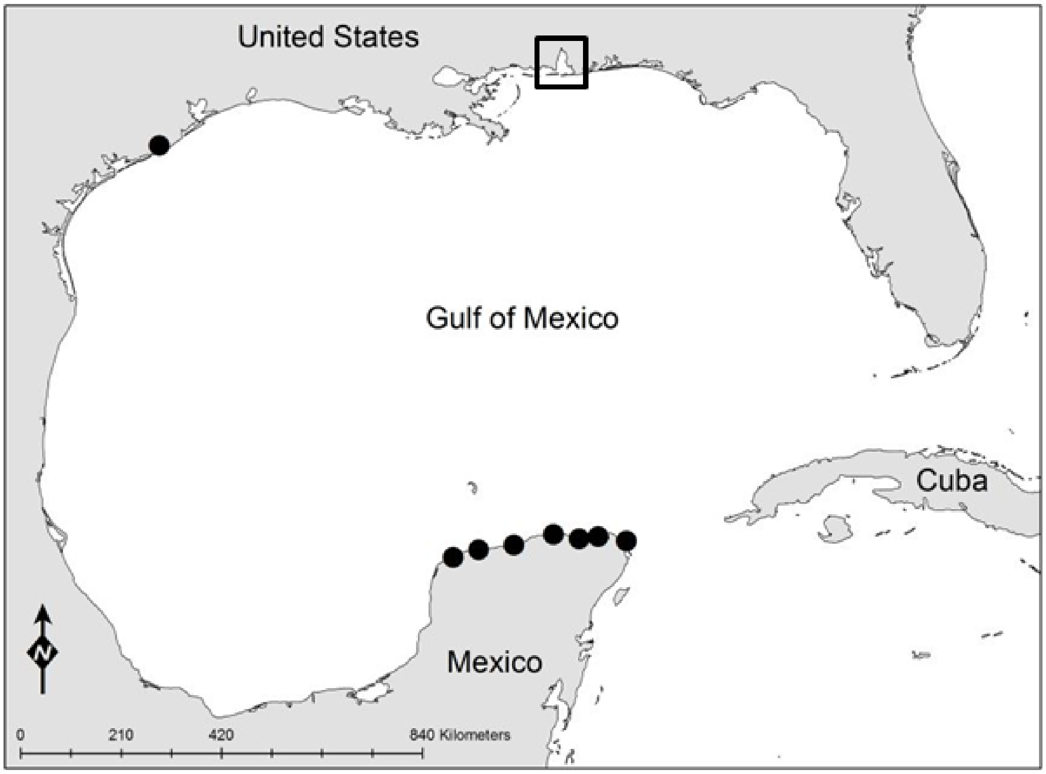
In this study, we examine how intrinsic and extrinsic factors impact the departure decisions of RTHU on their first migration by tracking the movements of radio-tagged individuals during stopover along the northern coast of the Gulf of Mexico. We focus on HY birds for two main reasons: 1) we capture a high abundance at our study site compared to adult birds (see Zenzal and Moore 2016) allowing for adequate sample sizes, and 2) HY birds may behave differently from adult conspecifics due to a lack of experience during migration (Woodrey 2000), which may be reflected as orientation errors (Ralph 1978; Moore 1984; Able and Bingman 1987), foraging inefficiencies (Burger 1988; Wunderle 1991), or different migratory routes (Hake et al. 2003; Agostini 2004). Research on our focal species has identified that their stopover biology is age-dependent with HY birds being disadvantaged – adult birds arrive in better condition and have higher fueling rates compared to HY birds (Zenzal and Moore 2016). Studying the departure decisions made by young migrants might increase understanding of migratory strategies based on endogenous programming or factors experienced *en route*.

Our main objective was to determine what factors influence the departure decisions of HY RTHU. We hypothesized that RTHU would behave similar to songbirds moving along the Gulf coast (Sandberg and Moore 1996, Smolinsky et al. 2013, Deppe et al. 2015), that is: (1) departure direction depends on both energetic condition and weather variables, and (2) the time of departure depends on weather variables. A secondary objective of this study is to determine the extent to which we can generalize what we know about songbird migration to RTHU.

Methods

Study Site and Capture Methods

Ruby-throated Hummingbirds were captured at a long-term study site (30°10’N, 88°00’W; Figure 17) on the Bon Secour National Wildlife Refuge (NWR) in Fort Morgan, Alabama. The location includes some of the last available habitat along the Gulf coast before a decision must be made in relation to crossing the GOM. The site was composed of scrub-shrub habitat and pine forest with Slash Pine (*Pinus elliottii*), oaks (*Quercus* spp.), hollies (*Ilex* spp.), Greenbreir (*Smilax* spp.), and Saw Palmetto (*Serenoa repens*) as the dominant species (for a complete description see Zenzal et al. 2013).


United States
Gulf of Mexico
Cuba
Mexico
N
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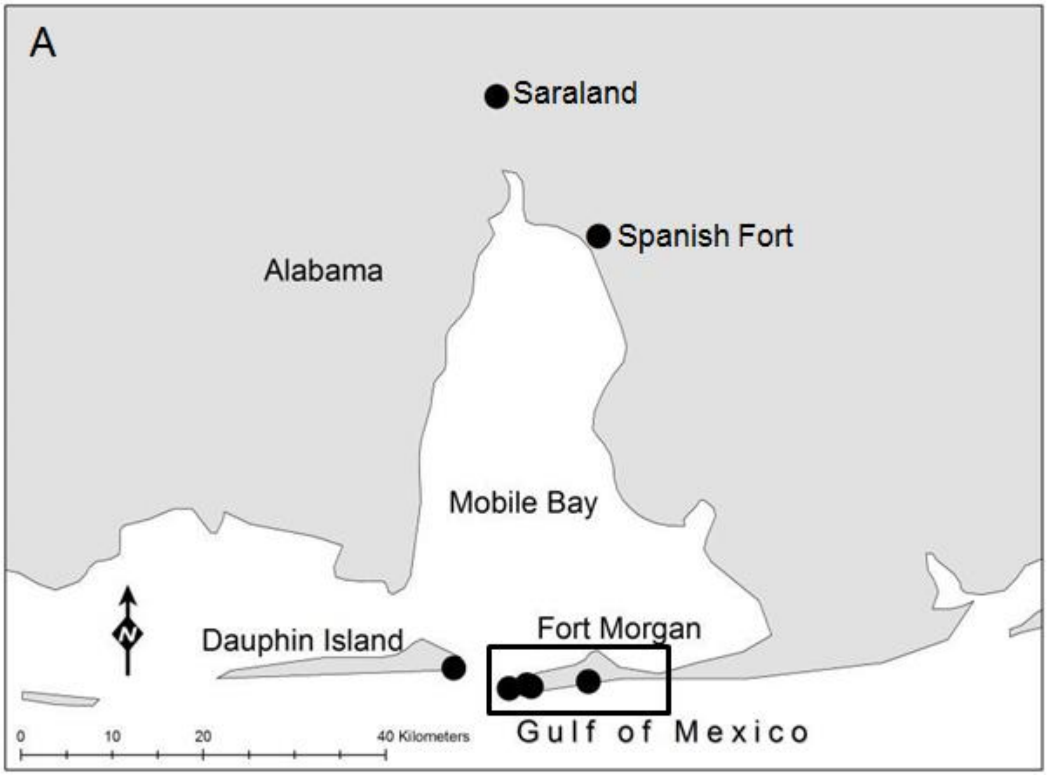
210
420
840 Kilometers


A
Saraland
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Gulf of Mexico

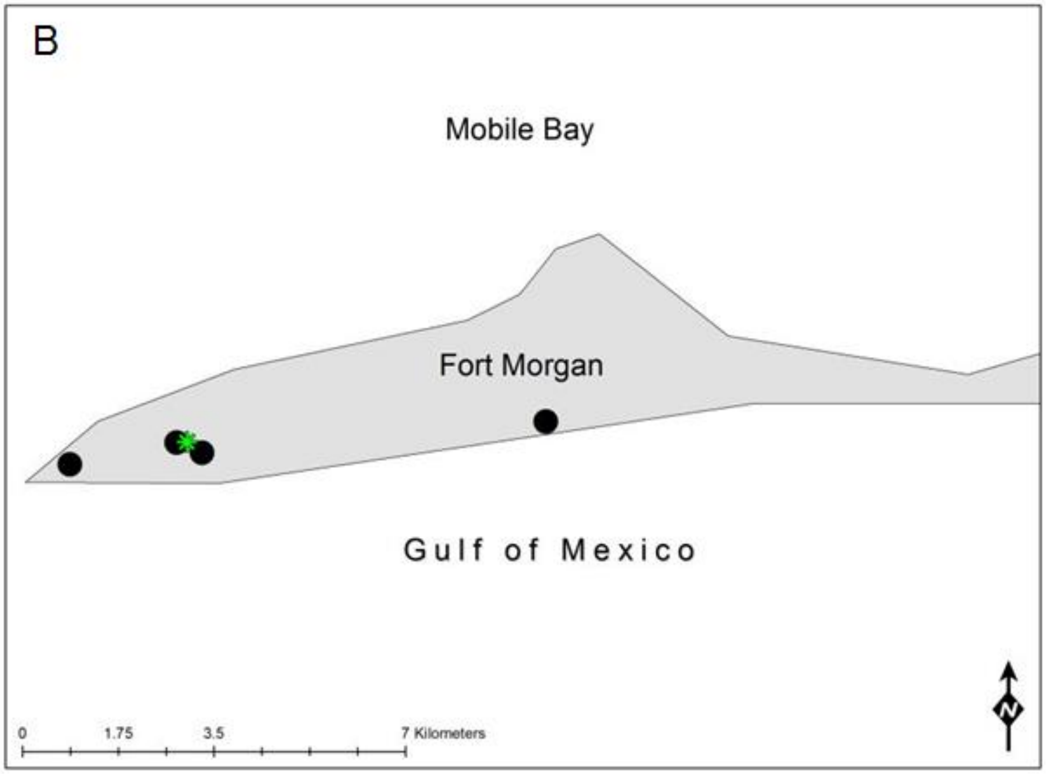


Figure 17. Locations of Radio Telemetry Towers and Study Site

Locations of radio telemetry towers (circles) around the Gulf of Mexico and study site (box). (A) Automated radio telemetry network around Mobile Bay in Alabama. (B) Telemetry towers (black circles) and banding station (green asterisk) on the Fort Morgan Peninsula in Alabama.

We captured RTHU using nylon mist nets (n = 29-32; 12 meters or 6 meters x 2.6 meters with 30 millimeter mesh) from approximately 25 August to 1 November 2011-2014 (see Zenzal and Moore 2016). We typically operated mist nets from sunrise until noon (Central Daylight Time), depending on weather conditions or capture rates. We supplemented resources on the study site with 14 artificial feeders. Ten of the feeders were part of a separate study and not associated with netting locations; the remaining four were used to increase Hummingbird capture probability, otherwise the majority of the netting effort was passive. We banded RTHU with a US Geological Survey (USGS) aluminum leg band, aged and sexed according to Pyle (1997), estimated visible subcutaneous fat (Helms and Drury 1960), and measured natural wing chord and mass (nearest 0.01 gram using an electronic balance).

Radio Telemetry Attachment

A subsample of HY RTHU (n = 55) received a small, pulsed radio-tag (0.28 ± 0.06 grams with glue and cloth [all results are presented as mean ± standard deviation]; ~10 day lifespan; JCJD Corp. Fisher, Illinois, USA) which was 6.9% of the average total body mass for the birds used in this study (4.14 ± 0.61 grams). We used radio-tags because: 1) they were not found to have a significant influence on hummingbirds in an aviary during autumn migration (Zenzal et al. 2014) and 2) we were able to take advantage of an existing international automated radio-tracking network (Deppe et al. 2015; see below). Each radio-tag had a unique frequency between 163.929-165.297 MHz with pulse intervals that ranged between 525-836 milliseconds and pulse widths that ranged from 14-16 milliseconds. We attached radio-tags using the modified Raim (1978) attachment method developed by Smolinsky et al. (2013), which allows radio-tags to fall off the bird in three to four weeks. Once a bird was selected, we cut feathers on the dorsal side to reveal a patch of skin and affixed the radio-tag to this patch using eyelash adhesive (Revlon brand) and cyanoacrylate glue (Loctite brand) at the bird’s approximate center of gravity. Birds were held for ~5 minutes after attachment to allow the adhesive to dry and to ensure that tag attachment did not impede movement.

Radio Telemetry Network

We used a network of automated radio-tracking towers (see Deppe et al. 2015) located in coastal Alabama and Texas (USA) as well as along the northern coast of the Yucatan Peninsula, Mexico to track RTHU (Figure 17). In Alabama, we operated three tracking systems on the Fort Morgan Peninsula to estimate the date, time, and direction of Hummingbird departures. Over the course of the study we changed the particular location of one tower prior to data collection in 2012, moving it ~ 1.5 kilometers east, in order to obtain better departure estimates. We added additional towers over the course of the study: in 2012 on Dauphin Island, Alabama (7.5 kilometers west of the study site), in 2013 on Spanish Fort, Alabama (50 kilometers north of the study site) where the Mobile-Tensaw Delta enters Mobile Bay, and in 2014 near Saraland, Alabama along the Mobile-Tensaw Delta (65 kilometers north of the study site; Figure 17A). In 2011, we equipped all towers with six three-element directional Yagi folded-dipole antennas (JDJC Corp., Fisher, IL). From 2012-2014 we equipped the eastern tower on Fort Morgan as well as the two towers north of Mobile Bay with four high-gain stacked directional antennas (designed by W.W. Cochran); all other towers used the directional Yagis described above. To continuously monitor radio-tagged birds we used automated receiving units (ARU; JDJC Corp., Fisher, Illinois, USA) programmed to search each tag frequency at 2.5-6 minute intervals. At each search interval the pulse width, pulse interval, noise, and signal strength of each radio-tag was recorded from each antenna by the ARU.

We used high-gain stacked antennas (similar to those described above) along the northern coast of the Yucatan Peninsula where we constructed a “telemetry fence” to detect the arrival of RTHU after a trans-Gulf flight (Figure 17B). In 2011, each radio-tracking tower (n = 7) was equipped with two sets of stacked antennas parallel to the coast, whereas from 2012-2014 each tower was equipped with a stacked antenna in each cardinal direction. In 2014 we added an additional tracking tower with four high-gain stacked antennas near Cedar Lake, Texas to perhaps detect RTHU engaged in circum-gulf movement. The ARU search interval was 4.25-6 minutes and recorded the same variables (pulse width, pulse interval, noise, and signal strength) for each radio-tag on each antenna (see Deppe et al. 2015 for a complete description of the telemetry network).

Radio Telemetry Processing

To process the automated radio telemetry data, we used R (R Core Team 2015) and Python scripts to detect radio-tagged individuals based on six criteria: 1) the individual had to be detected during at least three successive sampling periods, 2) detected frequency (MHz) had to be within two one-thousandths of the known radio-tag frequency, 3) pulse interval had to be within 50 ms of the radio-tag’s interval or a multiple thereof, 4) pulse width had to be within 2 ms of the radio-tag’s width provided by the manufacturer, 5) noise level under -130 dBm, 6) signal strength over -122 dBm. See Deppe et al. (2015) for a complete description of scripts and data processing techniques.

To determine the departure track and direction of an individual with signals > -122 dBm from the closest towers, we followed the same approach used by Smolinsky et al. (2013) and Deppe et al. (2015) that estimated a bird’s departure track and direction through biangulation or triangulation. Location of a Signal (L.O.A.S.) Software (Ecological Software Solutions, LLC, Sacramento, CA, USA) estimated the track of each individual using a sequence of UTM locations, a locally weighed regression (LOESS) allowed us to create a smoothed, predicted departure track. The last five predicted coordinates of the track determined the bird's departure time and bearing. If an adequate amount of high-quality signals were not obtainable to use the L.O.A.S.-LOESS method, we estimated departure direction from vanishing bearings according to data from the tower receiving the greatest signal. Along the YP we detected individuals using peak signal strength from one or two of the east/west oriented antennas.

We were unable to obtain any data on five tagged individuals due to problems with radio transmitters, radio towers or electromagnetic noise. Also, we were unable to determine the exact departure bearings on five other tagged birds due to electromagnetic noise; however, we were able to determine their cardinal departure direction (e.g., north). Therefore, we excluded these latter birds from any analysis requiring precise departure bearings.

Weather Variables

Weather data were obtained from two nearby weather stations since we were unable to gather all variables of interest from a single station. From the Bon Secour NWR station (BONA1; 30° 15' N, 87° 48' W) we obtained relative humidity (%) and precipitation (cm) during the hour the bird departed. From the Dauphin Island station (994420; 30° 15' N, 88° 4' W) we obtained wind direction, wind speed (meters•second-1), temperature (°C), and barometric pressure (hPa).

We selected data recorded within an hour of the bird's departure in order to relate atmospheric conditions to departure decisions. All variables were attained from surface level readings since hummingbirds likely fly at low altitudes (Kerlinger and Moore 1989).

Statistical Analysis

We used descriptive and information theoretic approaches to understand the departure decisions of RTHU. First, we used circular statistics to calculate the mean direction and resultant length (r), which represents the concentration of data, followed by a Rayleigh test of uniformity on departure time (n = 50) and direction (n = 45; Fisher 1993; Pewsey et al. 2013). We selected Akaike's information criterion corrected for small sample sizes (AIC_c; n = 50; Burnham and Anderson 2002) to determine what variables might influence an individual's departure time and direction. We performed the following data transformations in order to fit circular variables to linear models. We transformed departure and wind direction bearings into four discreet categories centered on cardinal directions (north: > 315° or < 45°; east: > 45° and < 135°; south: > 135° and < 225°; west: > 225° and < 315°); these directions were informed by departures from other radio-tagged birds departing our study site (Smolinsky et al. 2013, Deppe et al. 2015) and the geography of the coastline (Figure 17). Categories for wind direction were the same as bird departure categories since we expected birds to use wind assistance during migration (Alerstam 1979). We transformed departure time to hours after local sunrise based on Kerlinger and Moore (1989).

We selected two response variables, departure direction and departure time, and used multinomial logistic regression and linear regression, respectively, to create candidate models. We looked for relationships between our response variables and the following predictor variables: fuel load at capture, sex, stopover duration, departure date, density of RTHU at our study site, wind direction, wind speed, temperature, barometric pressure, relative humidity, and precipitation. Departure direction and departure time exchanged roles as response and predictor variables between the two regression models (Table 4). We tested all single variable models, a null model (no variables), global model (all variables) as well as a number of specific additive and interactive models based on previous research and the biology of the species (Tables 5, 6). We interpreted models with a $\Delta AIC_c \leq 2$ to be the best supported model(s) and determined the support of each model based on the calculated weight of each model (Burnham and Anderson 2002).

We used the R statistical language (R Core Team 2015) to perform all statistical analyses. For analysis of circular data, we used package "circular" (Agostinelli and Lund 2013). We used package "nnet" (Venables and Ripley 2002) to perform multinominal logistic regressions. To calculate ΔAIC_c and AIC_c weights we used package "AICcmodavg" (Mazerolle 2015).

Table 4

Description of Predictor Variables Used in Model Selection

Variable	Description	Measure
Fuel load	Grams of mass over lean body mass following methods from Zenzal and Moore (2016)	1.15 ± 0.58 g
Sex	The sex of the bird based on Pyle (1997)	Male = 26 Female = 24
Stopover duration	Number of hours spent on stopover (based on telemetry detections)	32.75 ± 44.15 hr
Departure date	Ordinal date of final detection from telemetry	271 ± 11
Density	Number of hummingbirds banded on the day of departure	10 ± 9.36
Wind direction	Direction from which the wind originated nearest to time of departure	North = 21 South = 6 East = 18 West = 5
Wind Speed	The velocity of the wind in m/s nearest to time of departure	5.49 ± 2.76 m/s
Temperature	Temperature (°C) nearest to time of departure	23.82 ± 3.25 °C
Barometric Pressure	Air pressure (hPa) nearest to time of departure	1015.87 ± 4.70
Relative humidity	Measure of humidity (%) nearest to time of departure	77.64 ± 16.12 %
Precipitation	Amount of precipitation (cm) that occurred over the hour of departure	0.05 ± 0.21

Table 4 (continued).

Departure direction[a]	The cardinal direction of a bird at final telemetry detection	North = 8 South = 5 East = 14 West = 23
Departure time[b]	Number of hours since local sunrise of a bird’s final telemetry detection	3.98 ± 3.49

We provide a measure of each continuous (mean ± standard deviation) and categorical (sample size per group) variable. [a]Predictor variables used for the response variable “departure time”. [b]Predictor variables used for the response variable “departure direction”

Table 5

Model Selection Analysis of Departure times of Ruby-throated Hummingbirds from Fort Morgan, Alabama 2011-2014

Model	K	AIC_c	ΔAIC_c	w_i	Log-likelihood
Wind direction	5	255.70	0.00	0.71	-122.17
Wind direction + wind speed	6	258.28	2.59	0.20	-122.17
Wind direction + wind speed + fuel load	7	260.05	4.35	0.08	-121.69
Wind direction * wind speed	9	266.23	10.54	0.00	-121.87
Relative humidity + barometric pressure	4	268.47	12.77	0.00	-129.79
Barometric pressure	3	269.41	13.72	0.00	-131.45
Null model (no variables)	2	270.22	14.53	0.00	-132.98
Relative humidity * barometric pressure	5	270.62	14.92	0.00	-129.63
Wind direction + precipitation + relative humidity + barometric pressure + temperature + wind speed + density + departure date	11	270.77	15.08	0.00	-120.91
Relative humidity + barometric pressure + fuel load	5	270.94	15.25	0.00	-129.79
Wind speed	3	271.65	15.95	0.00	-132.56
Temperature	3	271.95	16.25	0.00	-132.71
Relative Humidity	3	272.03	16.33	0.00	-132.75
Density	3	272.22	16.52	0.00	-132.85
Departure date	3	272.28	16.58	0.00	-132.88

Table 5 (continued).

Precipitation	3	272.38	16.69	0.00	-132.93
Fuel load	3	272.39	16.70	0.00	-132.94
Sex	3	272.44	16.75	0.00	-132.96
Stopover duration	3	272.47	16.77	0.00	-132.97
Relative humidity + fuel load	4	274.38	18.68	0.00	-132.75
Departure direction	5	274.66	18.96	0.00	-131.65
Relative humidity * fuel load	5	276.84	21.14	0.00	-132.74
Density + stopover duration + fuel load	5	277.04	21.34	0.00	-132.84
Departure direction + departure date	6	277.20	21.50	0.00	-131.62
Relative humidity * barometric pressure * fuel load	9	280.09	24.40	0.00	-128.80
Density * stopover duration * fuel load	9	282.50	26.80	0.00	-130.00
Departure direction + stopover duration + fuel load + sex + departure date	8	282.64	26.94	0.00	-131.56
Departure direction * departure date	9	283.89	28.19	0.00	-130.70
Wind direction * wind speed * fuel load	17	283.99	28.29	0.00	-115.43
Wind direction + departure direction + precipitation + relative humidity + barometric pressure + temperature + wind speed + density + stopover duration + fuel load + sex + departure date	17	288.67	32.97	0.00	-117.77

Table 6

Model Selection Analysis of Departure Directions of Ruby-throated Hummingbirds from Fort Morgan, Alabama, 2011-2014

Model	K	AIC_c	ΔAIC_c	w_i	Log-likelihood
Null model (no variables)	3	130.23	0.00	0.40	-61.86
Precipitation	6	130.88	0.65	0.29	-58.46
Sex	6	133.15	2.91	0.09	-59.60
Stopover duration	6	134.53	4.29	0.05	-60.29
Relative humidity	6	135.20	4.97	0.03	-60.62
Departure time	6	135.27	5.04	0.03	-60.66
Table 4 continued					
Temperature	6	136.02	5.79	0.02	-61.03
Departure date	6	136.10	5.87	0.02	-61.08
Fuel load	6	136.26	6.03	0.02	-61.15
Density	6	136.42	6.19	0.02	-61.23
Wind speed	6	136.79	6.56	0.01	-61.42
Barometric pressure	6	137.36	7.13	0.01	-61.70
Departure time and departure date	9	142.34	12.11	0.00	-59.92
Relative humidity + fuel load	9	142.65	12.42	0.00	-60.07
Relative humidity + barometric pressure	9	143.18	12.95	0.00	-60.34

Table 6 (continued).

Wind direction	12	148.08	17.85	0.00	-57.82
Departure time * departure date	12	148.26	18.03	0.00	-57.91
Relative humidity * fuel load	12	149.56	19.33	0.00	-58.56
Relative humidity * barometric pressure	12	150.44	20.20	0.00	-59.00
Density + stopover duration + fuel load	12	151.26	21.02	0.00	-59.41
Relative humidity + barometric pressure + fuel load	12	152.04	21.80	0.00	-59.80
Departure time + stopover duration + fuel load + sex + departure date	15	157.06	26.83	0.00	-56.47
Wind direction + wind speed	15	158.35	28.12	0.00	-57.12
Wind direction + wind speed + fuel load	18	171.09	40.86	0.00	-56.51
Wind direction * wind speed	24	192.78	62.55	0.00	-48.39
Density * stopover duration * fuel load	24	201.67	71.43	0.00	-52.83
Relative humidity * barometric pressure * fuel load	24	211.10	80.87	0.00	-57.55
Wind direction + precipitation + relative humidity + barometric pressure + temperature + wind speed + density + departure date	30	252.83	122.60	0.00	-47.47
Wind direction + departure time + precipitation + relative humidity + barometric pressure + temperature + wind speed + density + stopover duration + fuel load + sex + departure date	42	667.44	537.21	0.00	-33.72
Wind direction * wind speed * fuel load	48	4879.86	4749.63	0.00	-39.93

Results

Departure Time

Most hummingbirds (70%) departed the Fort Morgan Peninsula between sunrise and noon (mean: 10:06, $r = 0.69$, $p < 0.001$; Figure 18), similar to when they were captured and tagged. Out of the 30 candidate models, the top two models included variables associated with surface winds and had a combined weight of 0.91 (Table 5). The model receiving the strongest support ($\Delta AIC_c = 0.00$, AIC_c weight = 0.71) was a single variable model with wind direction as the predictor. The second best model, which received weak support ($\Delta AIC_c = 2.59$, AIC_c weight = 0.20), included wind direction and wind speed as predictor variables. Most birds (89%) that departed in the morning (n=36) did so with winds out of the north or east. Birds departing after noon (n = 14) did so under a variety of wind conditions; however, a large number of afternoon departures (43%) occurred when winds were out of the south whereas morning departing birds never left in south winds. Winds were generally light (70% of departures; < 6 $m \cdot s^{-1}$) to moderate (25%; 6 – 10 $meters \cdot second^{-1}$) when birds departed the study area in the morning. Birds departing after noon did so in weak (58% of departures) to moderate winds (29%). Regardless of departure time, very few birds (n = 4) departed in strong winds (> 10 $meters \cdot second^{-1}$), which were predominantly (75%) from the north.

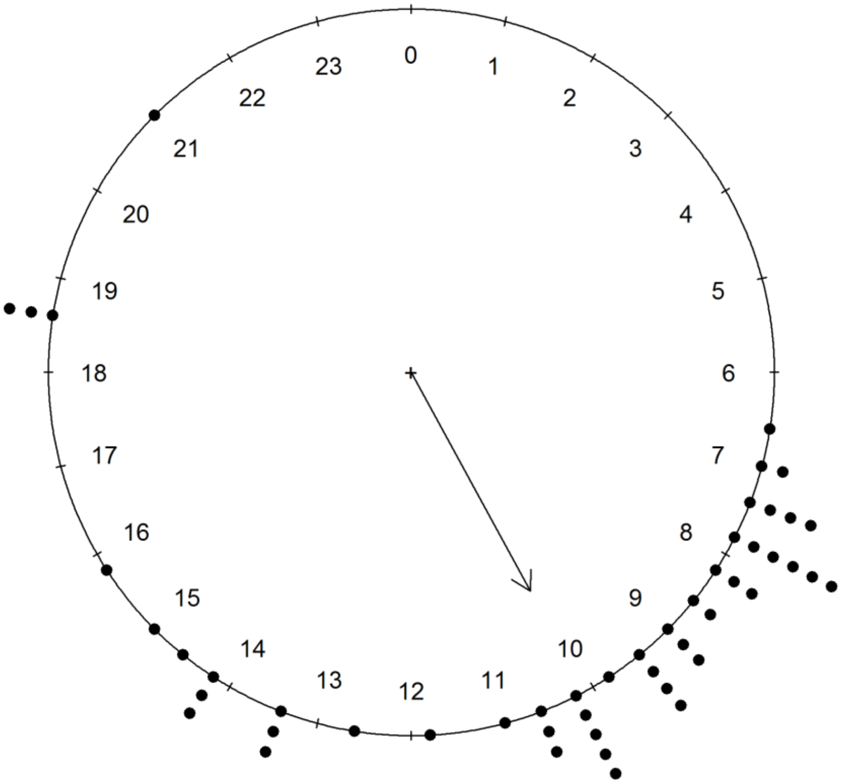


Figure 18. Departure Times of Ruby-throated Hummingbirds

Departure times of Ruby-throated Hummingbirds (n = 50) from coastal Alabama. Individual birds are represented by black dots, the arrow represents the mean departure time (10:06), and the length of the arrow indicates the vector length (0.69).

Departure Direction

Although departure directions of RTHU leaving the Fort Morgan Peninsula were uniformly distributed and quite variable (mean: 240°, r = 0.18, p = 0.22), most birds (74%) departed in either a westerly or easterly direction (Figure 19). Of the 30 candidate models, the top two models were the null model and the precipitation only model, and both had a combined weight of 0.69 (Table 6). The null model was the best supported model ($\Delta AIC_c = 0.00$, AIC_c weight = 0.40), which suggests that the variables (Table 4) included in the models are not influencing the departure direction of RTHU during autumn migration. The second model, which also received strong support ($\Delta AIC_c = 0.65$, AIC_c weight = 0.29), included the amount of precipitation at departure. The majority of birds (92%) departed when there was no precipitation, regardless of direction. During instances of high precipitation (~1 centimeter; n = 2) birds departed east and in instances of low precipitation (~0.25 centimeters; n = 2) departures were east and west.

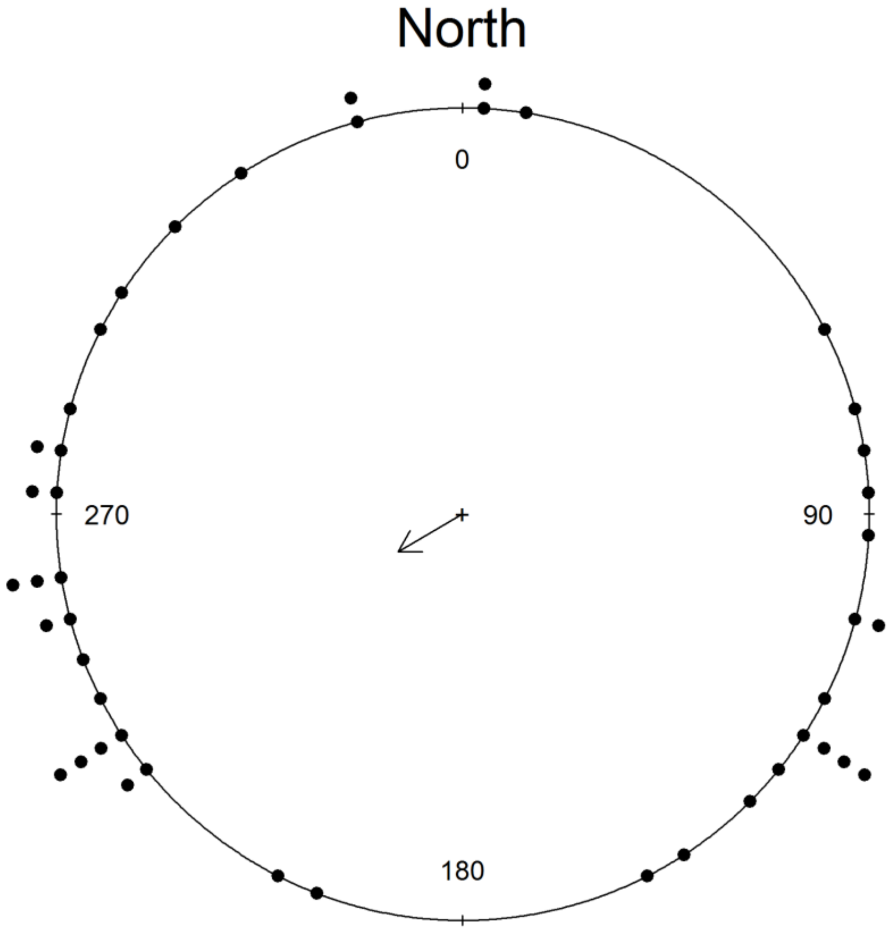


Figure 19. Departure Directions of Ruby-throated Hummingbirds

Departure directions of Ruby-throated Hummingbirds (n = 45) from coastal Alabama. Individual birds are represented by black dots, the arrow represents the mean departure angle (240°), and the length of the arrow indicates the vector length (0.18).

En Route Detections

While most radio-tagged RTHU departed the day they were captured (n = 29; 5.03 ± 6.27 hours on stopover), those that did stay (n = 21) tended to stopover for several days (71.01 ± 45.49 hours). After RTHU departed the Fort Morgan Peninsula we detected individuals on the Spanish Fort tower (north shore of Mobile Bay) as well as the Dauphin Island tower (Figure 17A). Three individuals made reverse movements from the Fort Morgan peninsula. One individual detected by the Spanish Fort tower was redetected on Fort Morgan one day later before departing to the southwest; the two other individuals detected by the Spanish Fort tower were never redetected on Fort Morgan, possibly taking an overland route around Mobile Bay. Birds flying west over Dauphin Island tended to fly more slowly compared to individuals departing overwater off the coast of the island. We never detected radio-tagged RTHU in Saraland, AL nor on the Yucatan Peninsula or Texas coasts, despite detecting other radio tagged songbird migrants on these towers (Deppe et al. 2015; Deppe et al. unpublished data). We acknowledge that the probability to detect RTHU outside of Alabama was lower than other tagged migrants due to the transmitter itself; the lower power output and signal strength of the transmitter would have reduced the range of the tracking towers. Since the lifespan of the transmitter was also lower, the battery could have died if the bird made an especially long stopover or depending on the speed of migration in the case of circum-Gulf flight. As an example, in 2013 one radio-tagged Hummingbird was observed in Corpus

Christi, Texas at a resident’s hummingbird feeder two weeks after departing the Fort Morgan Peninsula (USGS Bird Banding Lab, Personal Communication), beyond a transmitter’s expected lifespan.

Discussion

Departure Time

Foraging ecology and weather are likely the primary selective forces on the diel schedule of migrants (Kerlinger and Moore 1989). In our study, RTHU generally departed the Fort Morgan Peninsula in the morning, which is consistent with the behavior of other diurnal landbird migrants (Kerlinger and Moore 1989; Strandberg and Alerstam 2007; Ward and Raim 2011). Diurnal migrants also tend to exhibit a fly and forage migration strategy (e.g. Strandberg and Alerstam 2007; Ward and Raim 2011). RTHU, while theoretically capable of making a trans-Gulf flight, may make short stopovers at food patches throughout the day as they migrate to meet energetic demands rather than allocating time to fueling periods before or after bouts of flight as is the case for most nocturnal migrants since their primary food source, nectar, may be sporadically distributed. As evidence, we noted that several birds detected flying over Dauphin Island took longer to reach the western side of the island compared to birds flying off the Dauphin Island coast, suggesting that overland birds were using the habitat they encountered.

The fly-and-forage strategy may be beneficial in some ways, but it also incurs costs and risks to migrants. The disadvantages of fly-and-forage fueling include: 1) longer migration distance taking a circum-Gulf route, and 2) increased predation risk (Aborn 1994). However, these disadvantages are likely minimal for RTHU during autumn migration. A longer migration distance increases time cost; however, detours around ecological barriers may reduce transport cost of fuel or may result in higher fueling rates (Alerstam 2001; Lindström et al. 2011), which may explain why fuel load was not included in the top selected model. The time cost of this strategy is likely not great because arrival on the wintering grounds may not be urgent given their generalist foraging strategy allowing for adaptations to changes in resource density (Lara 2006). In terms of predation risk, hummingbirds are not thought to be under significant risk (Miller and Gass 1985; but see Zenzal et al. 2013), discounting the role predation plays on their migration strategy. *En route* fueling is advantageous because it reduces flight costs in two ways: 1) fly-and-forage migrants replenish energy stores while making progress toward their migratory destination (Alerstam 2001, 2009), and 2) flight costs are reduced because fly-and-forage migrants require less fat reserves for each bout of flight compared to nocturnal migrants, which typically do not forage during flight. Previous research suggests that RTHU maximize these benefits given that their migration appears to be correlated with flowering phenology (Bertin 1982). Further, RTHU typically arrive on the Alabama coast with some fat stores (Zenzal and Moore 2016), allowing RTHU a margin of safety to meet the high energetic demands when resources may not be available given the distribution of floral resources may be patchy.

Weather also plays an important role in the diel patterns of migrants (Kerlinger and Moore 1989). Departure time was associated with wind direction and to a lesser extent wind speed, which is consistent with atmospheric conditions more conductive to migratory flight (Kerlinger and Moore 1989). RTHU mainly departed with winds out of the north and east, these conditions seemed to be less variable in the morning compared to the afternoon. North winds are typically indicative of cold fronts, which are often associated with migrant passage (Hassler et al. 1963; Richardson 1978). Most Hummingbird departures (89%) occurred in east winds, which were either following winds for 44% of individuals departing west or weak headwinds for 29% of individuals departing east. Although birds generally departed in weak winds, wind speeds were more variable for birds departing later in the day compared to birds departing in the morning. There are several non-mutually exclusive explanations for why some RTHU departed later in the day: (1) they may have had inadequate fuel stores to depart earlier in the day, (2) they may have been selecting the best available conditions for departure (cf. Dänhardt and Lindström 2001), or (3) they were unable to acquire resources at our study site and moved to find better stopover habitat. Our results support the hypothesis that diurnal migrants should resume migration in the morning in order to take advantage of less turbulent atmospheric conditions (Kerlinger and Moore 1989).

Departure Direction

RTHU tended to take an eastern or western heading when leaving the Fort Morgan Peninsula, which coincides with the East-West orientation of the coastline. When RTHU encounter the GOM during fall passage, they must make a decision about what direction to continue migration – move along the gulf coast consistent with circum-gulf movement or move out over the GOM consistent with trans-gulf flight. The RTHU tracked in this study may be using the coast as a leading line (*sensu* Mueller and Berger 1967), which parallels the direction of travel and separates suitable and unsuitable habitat. If RTHU are using a fly-and-forage strategy, then circum-gulf movement would be expected to utilize this strategy. In contrast to RTHU, radio-tagged songbirds departed the coast in autumn heading south out over the GOM (Smolinsky et al. 2013; Deppe et al. 2015), behavior consistent with trans-Gulf migration.

The movement of RTHU parallel with the northern coast of the GOM was not associated with any variables included in the models (Table 4). This result is in direct opposition to radio-telemetry data on songbirds, which found that weather and fuel were important predictors of departure decisions (Deppe et al. 2015); however, if RTHU use a circum-gulf fly-and-forage strategy we would not expect weather or fuel load to be important when using this risk averse strategy. Age and foraging strategy are two factors not included in our models that might influence departure direction. Young inexperienced birds, the subjects of this study, may inherit a “program” to migrate in a particular direction (e.g. Helbig 1991) and arrive with lower fat stores compared to adults (Zenzal and Moore 2016). However, further study is needed on the stopover biology and migration strategies of adult RTHU. Another non-exclusive possibility is that young birds may be disoriented when they encounter the coast (e.g. Ralph 1978).

Regardless of how individuals end up on the GOM coast during migration, they must decide how to negotiate the GOM. Our data suggest that young RTHU passing through Fort Morgan, AL are circumventing the GOM to take advantage of suitable habitat along the coast, consistent with a fly-and-forage migration strategy. Once a naïve young bird encounters the coastline, they may simply turn either east or west and counter turn when geography permits (e.g. Jander 1975; Alerstam 1978a, 1978b; Moore 1982) to move around the GOM. If RTHU are counter turning *en route*, then circum-navigating individuals will turn south as soon as feasible which would be in east Texas or peninsular Florida. Citizen science data (eBird) provides evidence for this hypothesis: Hummingbird passage is moderate in south Florida during autumn migration and heavy along the Texas coast (Sullivan et al. 2009). That pattern is consistent with the behavior of our radio-tagged birds departing east and west from the Fort Morgan Peninsula, decreasing the likelihood that radio-tagged birds are behaving in response to the radio-tag (see Zenzal et al. 2014 for information on tagging effects).

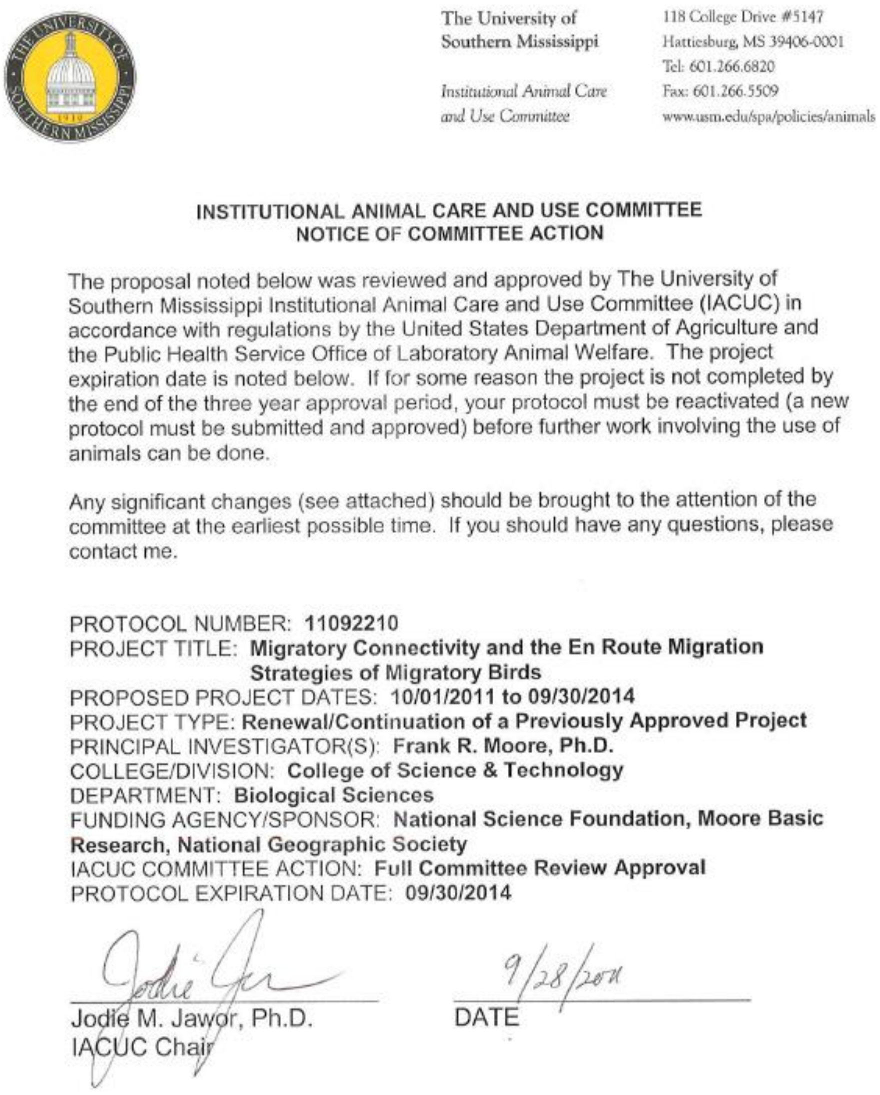
While recent attempts have been made to discern the migratory routes of RTHU (e.g. Supp et al. 2015), our work is the first to track individual RTHU to examine how they respond to the GOM during autumn migration. Most RTHU depart the Alabama coast moving approximately parallel with the coastline, which is indicative of circum-Gulf flight. Moreover even though the probability was low due to battery life and signal strength, we never detected a signal from our automated radio tower network along the Yucatan Peninsula that might suggest a trans-gulf movement but more study is needed using more refined technology when available (see Deppe et al. 2015). Finally, banding data reveals that the mean passage date of RTHU on the Yucatan Peninsula, the majority of which are HY birds (82%), is more than a month later than mean passage date along the Alabama coast (Deppe and Rotenberry 2005; Zenzal and Moore 2016). Moreover, banding records from south Florida, Cuba, and Isla Contoy affirmed few RTHU during autumn migration (M. Davis, personal communication; Deppe et al., unpublished data), discounting the possibility of a Caribbean migration route. The disconnect in passage timing, lack of telemetry detections along the Yucatan coast, anecdotal observation of a radio-tagged hummingbird along the Texas coast, and citizen-based observations during autumn (Sullivan et al. 2009), and modelled flight ranges of birds carrying a radio-tag (Zenzal et al. 2014)—all support the argument that young, hatch-year RTHU departing coastal Alabama follow a circum-Gulf route westward during autumn migration; although the route taken by birds caught in Yucatan is unclear (e.g., Deppe and Rotenberry 2005).

Conclusions

Our analysis provides insight into how RTHU negotiate the GOM and reveals to what extent we can generalize what we know about songbird migration to RTHU. The miniaturization of radio transmitters allowed us to collect movement ecology data on one of North America’s smallest migratory birds. We provide direct evidence on the movement ecology of RTHU in relation to the Gulf of Mexico and show that Hummingbird migration differs from the migration of songbirds. Departure time of RTHU is influenced by weather variables as predicted, specifically wind direction and to a lesser extent wind speed.

Departure direction was not influenced by intrinsic or extrinsic factors included in our models, consistent with a fly-and-forage, circum-Gulf migration strategy. A circum-Gulf strategy is further supported by our automated radio telemetry network as well as banding and citizen science data. Diurnal migration allows RTHU to forage while they migrate and may allow them to identify stopover locations with available resources. Furthermore, a circum-Gulf route necessitates the availability of high quality stopover sites along the coast, which is especially critical in relation to encroaching development (Hutto 2000; Abdollahi et al. 2005; Buler and Moore 2011).

APPENDIX A – IACUC Approval Letter



The University of
Southern Mississippi

*Institutional Animal Care
and Use Committee*

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INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER: **11092210**
PROJECT TITLE: **Migratory Connectivity and the En Route Migration Strategies of Migratory Birds**
PROPOSED PROJECT DATES: **10/01/2011 to 09/30/2014**
PROJECT TYPE: **Renewal/Continuation of a Previously Approved Project**
PRINCIPAL INVESTIGATOR(S): **Frank R. Moore, Ph.D.**
COLLEGE/DIVISION: **College of Science & Technology**
DEPARTMENT: **Biological Sciences**
FUNDING AGENCY/SPONSOR: **National Science Foundation, Moore Basic Research, National Geographic Society**
IACUC COMMITTEE ACTION: **Full Committee Review Approval**
PROTOCOL EXPIRATION DATE: **09/30/2014**

Jodie Jawor
Jodie M. Jawor, Ph.D.
IACUC Chair

9/28/2011
DATE

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