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RESEARCH ARTICLE

Stopover biology of Ruby-throated Hummingbirds (*Archilochus colubris*) during autumn migration

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ABSTRACT

Surprisingly little is known about the migration and stopover biology of Ruby-throated Hummingbirds (*Archilochus colubris*), and even less is known about their sex- or age-dependent migration. First, we provide basic information on the migration and stopover biology of this species along the northern coast of the Gulf of Mexico during autumn, including phenology, stopover duration, fuel deposition rate (FDR), arrival mass, and estimated flight ranges. Second, we investigate whether these stopover variables are influenced by age or sex. Age-dependent migration is expected because young, hatch-year birds on their first migration lack the experience of older individuals. Sex-dependent migration is expected because of sexually dimorphic characteristics in wing morphology and body size. We obtained information on arrival mass, phenology, FDR, stopover duration, and estimated flight ranges through banding data, passive integrated transponder tags, radio telemetry, and color marking at a long-term migration station along the northern coast of the Gulf of Mexico. Our data provide strong evidence for age-dependent migration and only weak evidence for sex-dependent migration. Older birds arrived earlier, had larger fuel loads, and had shorter stopover durations than younger birds. In younger birds, we found no effect of sex on FDR, arrival mass, stopover duration, or phenology. Older males arrived with larger fuel loads than females. Finally, we used flight simulation software and our data to estimate that males and older birds were capable of longer potential flight ranges than either females or younger birds.

Keywords: age-dependent, *Archilochus colubris*, intrinsic factors, Ruby-throated Hummingbird, sex-dependent, stopover, migration

Biología en los sitios de parada de *Archilochus colubris* durante la migración de otoño

RESUMEN

Sorprendentemente, se conoce poco sobre la biología de la migración y de los sitios de parada de *Archilochus colubris*, y aún menos sobre la dependencia de la migración en base al sexo y a la edad. Los objetivos de este estudio son dos. Primero, brindamos información básica sobre la biología de la migración y de los sitios de parada de *A. colubris* a lo largo de la costa norte del Golfo de México durante el otoño, incluyendo datos de fenología, duración de la parada, tasa de provisión de combustible (TPC), masa al momento del arribo y rangos estimados de vuelo. Segundo, investigamos si estas variables son influenciadas por la edad y el sexo. Se espera que la migración dependa de la edad ya que las aves jóvenes del primer año que emprenden su primera migración no tienen la experiencia de los individuos más viejos. Se espera que la migración dependa del sexo debido a características de dimorfismo sexual en la morfología del ala y en el tamaño corporal. Obtuvimos información de la masa al momento del arribo, la fenología, la duración de la parada y los rangos estimados de vuelo por medio de datos de anillado, marcadores transpondedores integrados pasivos, radio telemetría y marcado de color en una estación migratoria de largo plazo a lo largo de la costa norte del Golfo de México. Nuestros datos brindan fuerte evidencia de que la migración depende de la edad y soló una evidencia débil de que la migración depende del sexo. Las aves más viejas llegan más temprano, tienen cargas de combustible más grandes y realizan paradas más cortas que las aves más jóvenes. No encontramos un efecto del sexo en las aves más jóvenes en términos de TPC, masa al momento de arribo, duración de la parada o fenología. Los machos más viejos llegaron con cargas de combustible más grandes que las hembras. Finalmente, mediante programas de simulación de vuelo y en base a nuestros datos, estimados que los machos y las aves más viejas eran capaces de realizar vuelos potenciales más largos que las hembras o las aves jóvenes.

Palabras clave: Archilochus colubris, factores intrínsecos, migración, migración dependiente de la edad, migración dependiente del sexo, parada migratoria

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INTRODUCTION

Approximately two-thirds of all birds breeding in eastern North America are Nearctic–Neotropical migrants (Rappole 1995). Although 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 in which to rest and refuel (e.g., Moore et al. 2005). It is estimated that $\geq$70% of time during migration is spent on stopover (Hedenström and Alerstam 1997), when energy expended is thought to be high in relation 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, 1993b, 1993c, 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, thus increasing fuel loads and fueling rates (Carpenter et al. 1991, 1993b, 1993c, Maitav and Izhaki 1994, Yong et al. 1998, Moore et al. 2003, Németh and Moore 2012). However, not all studies have found differences between the sexes during migration (Otahal 1995, Izhaki and Maitav 1998).

Age-related asymmetries may also influence migration because younger, hatch-year birds tend to be less efficient foragers and are often subordinate to older, after-hatch-year birds (Gauthreaux 1978, Burger 1988, Wunderle 1991, Woodrey 2000). Banding records during migration are consistent with that expectation, in that 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 its 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, owing to their aggressive nature, small size, reverse sexual size dimorphism (Ridgway 1911, Weidensaul et al. 2013), high metabolism (0.022 mL O_2 min^{-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 than most migrants, given that smaller birds can generally carry more fuel reserves in relation to their fat-free mass (Hedenström and Alerstam 1992) and have larger fuel deposition rates (FDR; 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 may influence 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 the present study was to provide basic information on the stopover biology of Ruby-throated Hummingbirds, including phenology, stopover duration, FDR, arrival condition, and estimated flight ranges of individuals that had stopped along the northern coast of the Gulf of Mexico 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

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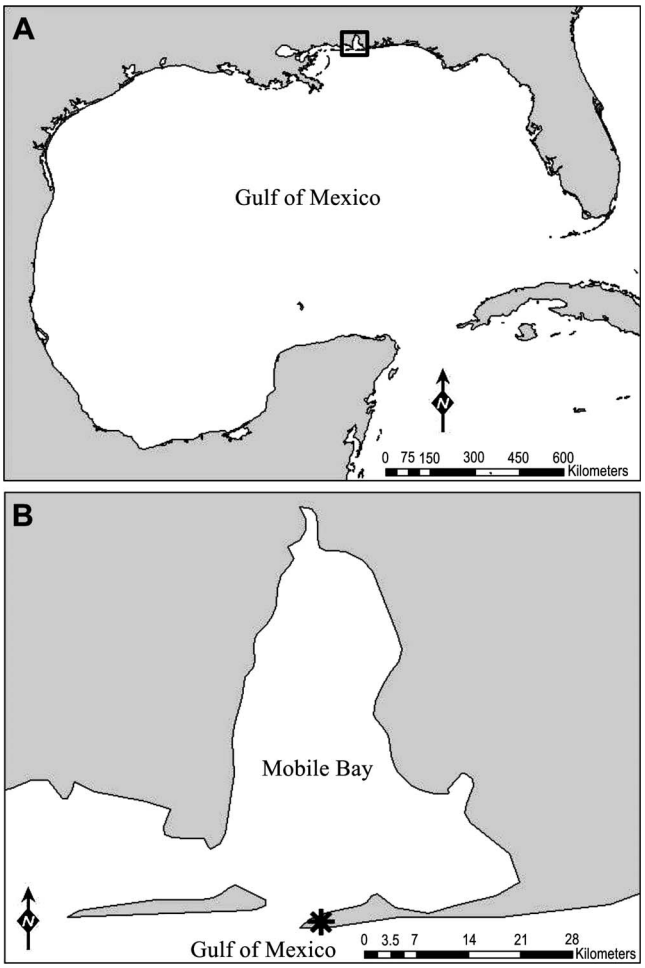


FIGURE 1. (**A**) Gulf of Mexico region, with Mobile Bay area enclosed by a square. (**B**) Fort Morgan peninsula in coastal Alabama, USA. Asterisk indicates study site.

(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 birds of the 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 FDR than females; (3) stopover duration would be shorter in adults and males; and (4) females (with their more energetically efficient wing design) and adults would have longer flight ranges than males and young birds (cf. Pennycuick 2008).

METHODS

Field Site and Data Collection

We captured Ruby-throated Hummingbirds using 29–32 nylon mist nets (12.0 × 2.6 m or 6.0 × 2.6 m with 30 mm mesh) at the Bon Secour National Wildlife Refuge, Fort Morgan, Alabama, USA (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 km from the end of the Fort Morgan Peninsula and was dominated by slash pine (*Pinus elliottii*), sand live oak (*Quercus geminata*), myrtle oak (*Q. 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 were not always associated with nets. While the placement of feeders at nets was intended to increase sample sizes, we recognize that this subsequently influenced other factors, such as FDR.

TABLE 1. Year of study, capture effort, and capture rate per 100 net-hours (1 net-hour = 12 m of net open for 1 hr) of Ruby-throated Hummingbirds during autumn migration in coastal Alabama, USA.

Year	Dates of operation	Net-hours	Capture rate
2010	August 31–October 28	8,427	8.72
2011	August 30–October 30	7,778	11.61
2012	September 2–October 30	9,910	2.76
2013	August 26–October 31 [a]	8,575	3.69
2014	August 25–November 1	9,493	5.31

[a] We were unable to access our study site because of the U.S. Government shutdown during October 1–13, 2013.

We banded Ruby-throated Hummingbirds ($n = 2{,}729$) with a USGS aluminum leg band, aged them as hatch-year (HY; "young") or after-hatch-year (AHY; "old"), sexed them according to Pyle (1997), estimated fat (Helms and Drury 1960), measured natural wing chord and mass (to nearest 0.01 g 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 in the form of either a radio-tag (~300 mg; $n = 55$; JDJC Corp., Fisher, Illinois, USA) or a passive integrated transponder (PIT) tag (~100 mg; $n = 549$; Cyntag, Cynthiana, Kentucky, USA). During 2012–2014, a subset of birds were auxiliary-marked with back color tags (~30 mg; $n = 446$) as described by Kapoor (2012); these birds received only one type of auxiliary marker in addition to an aluminum leg band. All auxiliary-marked birds were included in subsequent analyses because radio-tags, the marker type most likely to have effects on individuals due to weight and

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size, did not affect Ruby-throated 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 included only 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 a 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 on the basis of regressions of mass and wing length of Ruby-throated Hummingbirds captured at our site between 2010 and 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 g; females: 3.12 ± 0.10 g; these and all other results are presented as median ± SD unless otherwise indicated). Estimated fat-free mass was then subtracted from the mass of each bird at initial capture; the difference should provide the fuel load carried by the individual upon capture.

We estimated minimum stopover duration 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 that using the most precise data provides an accurate portrayal of stopover biology. Birds captured only 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 the sexes was limited to HY birds because of low sample sizes of AHY birds captured each year.

We estimated FDR (g day^{-1}) using the method described by Cherry (1982), which provides a way to standardize the amount of time between initial capture and final capture, given that 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 g; mean ± SD) using birds recaptured on the same day, ≥3 hr after the initial capture (transient birds, $n = 37$; mean [± SD] time between captures = 5.85 ± 2.17 hr). We chose a 3 hr time lapse because birds may continue to show a stress response to handling up to 1 hr after capture (Holberton et al. 1996). Individuals should have acclimated to handling and resumed refueling after 3 hr. We corrected the mass of all individuals used in this analysis to noon using the mean hourly FDR. We determined FDR by subtracting the corrected mass at initial capture from the corrected mass at final capture and dividing that value by the number of days elapsed between captures. We were able to compare only HY males and females that stopped over (nontransient 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, given that 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 rather than 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, given that 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 m (air density = 1.17 kg m^{-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. Because all other data were not normally distributed even after attempting standard transformations (log and square root), all 2-way comparisons used Mann-Whitney *U*-tests (Mann and Whitney 1947). For each phenology and arrival condition,

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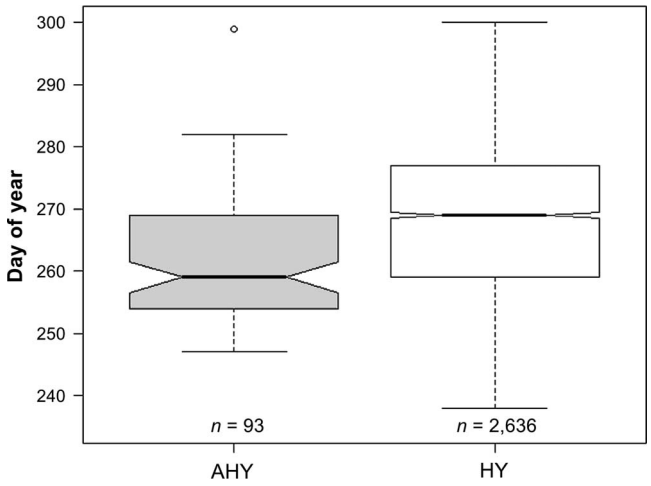


FIGURE 2. Passage dates of after-hatch-year (AHY) and hatch-year (HY) Ruby-throated Hummingbirds during autumn migration (*y*-axis indicates ordinal date; ordinal day 240 = August 28). Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicate interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

we compared sexes of only HY birds for each year of the study (except 2013 for the phenology analysis), because 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 stopover duration 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 stopover duration for male and female HY birds that were recaptured on a subsequent day after initial capture. All statistical analyses were performed using R 3.1.3 (R Development Core Team 2015).

RESULTS

Phenology

The overall passage (2010–2014) of Ruby-throated Hummingbirds through coastal Alabama spanned some 62 days, occurring between day 238 (August 26) and day 300 (October 27), with a mean passage date of 268 ± 11 (September 25), capturing 0.12 birds net-hour^{-1}. When examining individual age and sex classes, we found differences in arrival timing between age groups, but not between the sexes.

Older birds arrived earlier than younger birds when all years were pooled ($W = 79{,}156$, $P < 0.001$, Cohen's $d = 0.60$; Figure 2). The phenology of older birds was more constrained, with all but one 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).

In 2010, HY females arrived earlier than males by 4 days ($W = 53{,}916$, $P < 0.001$, adjusted alpha = 0.01; Figure 4), but we found no difference in arrival timing during any of

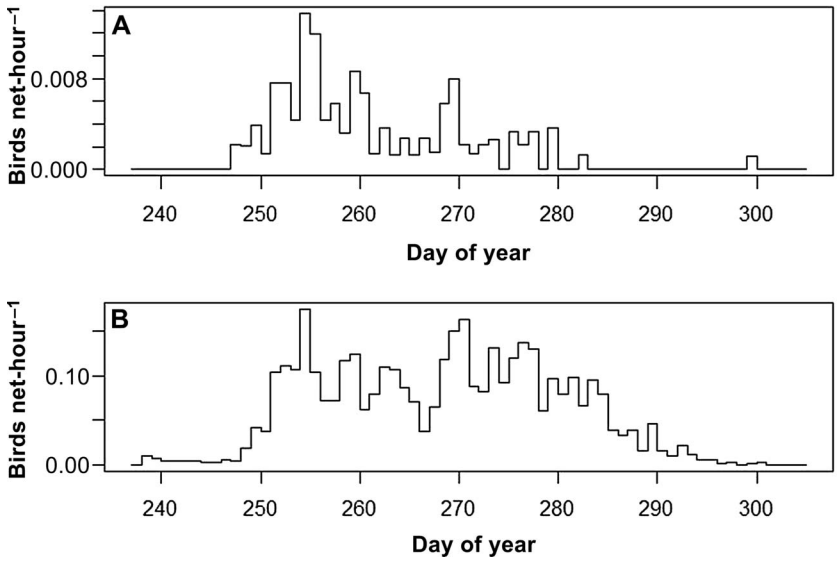


FIGURE 3. Phenology of (**A**) after-hatch-year and (**B**) hatch-year Ruby-throated Hummingbirds captured from 2010 to 2014 (*x*-axis indicates ordinal date; ordinal day 240 = August 28).

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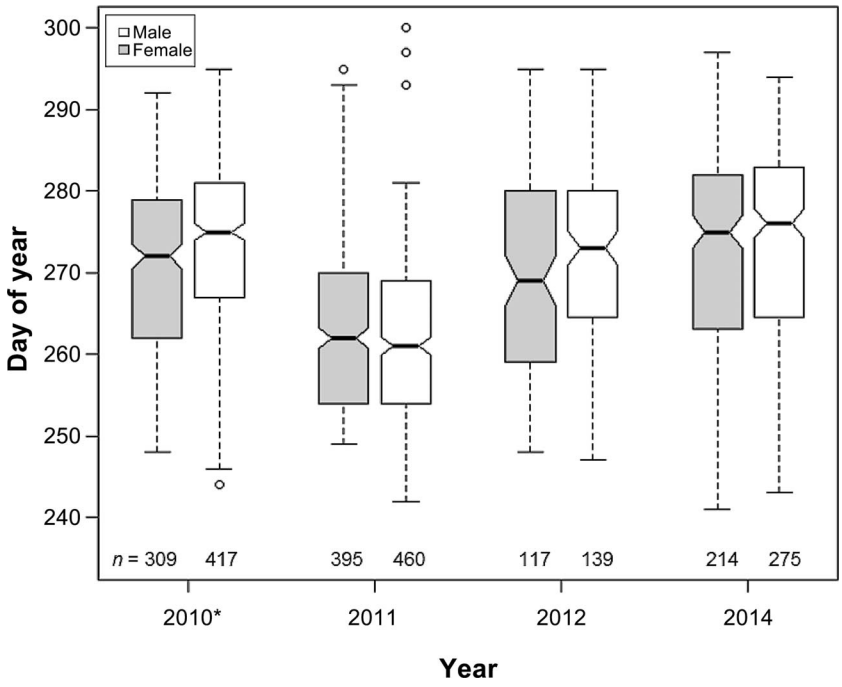


FIGURE 4. Passage dates of hatch-year Ruby-throated Hummingbirds by male and female for 2010–2012 and 2014 (*y*-axis indicates ordinal date; ordinal day 240 = August 28). Asterisk indicates significant difference between sexes. Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicate interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

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 ($W = 1{,}148.5$, $P = 0.55$). Given the overall trend that supported our null hypothesis, evidence suggests that Ruby-throated Hummingbirds do not exhibit differential migration timing by sex in autumn.

Arrival Condition

Overall, birds arrived with substantial fuel loads, carrying an estimated 0.92 ± 0.53 g (above lean body mass [LBM]: 33% males, 29% females) of fat upon initial capture (Figure 5). Arrival condition ranged from 0.53 g (below LBM: 19% males, 17% females) below fat-free body mass to 2.80 g (above LBM: 99% males, 90% females) above fat-free body mass (Figure 5).

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 the sexes in 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 than older females ($W = 762$, $P = 0.04$; Figure 5). Our results suggest stronger differences between the sexes in older birds, but these differences are not reflected in younger birds.

Stopover Duration

The majority of birds captured (~89%) were transients, never detected again. Among nontransient birds, the overall length of stopover for birds recaptured ≥1 day after initial capture was 2 ± 2 days. Stopover duration 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 ≤3 days from initial capture. We found no difference between the sexes (HY only, $P > 0.02$, adjusted alpha = 0.01; Figure 8), but we found an effect of age ($W = 213$, $P = 0.05$, Cohen's $d = 0.80$; Figure 7) on stopover duration. All AHY birds ($n = 3$) were only redetected 1 day after initial capture, whereas 62% of HY birds ($n = 376$) were redetected ≥2 days after 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.

Fuel Deposition Rate

The overall FDR of nontransient individuals was 0.10 ± 0.24 g day^{-1} (increase to LBM: 4% males, 3% females),

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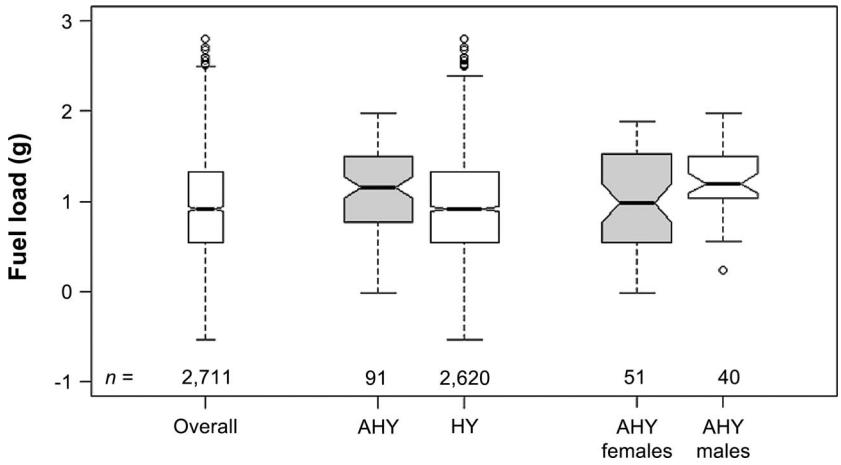


FIGURE 5. Fuel load of Ruby-throated Hummingbirds at initial capture. Shown are overall pattern, comparison between age groups (HY = hatch-year, AHY = after-hatch-year), and comparison between AHY males and females for all years pooled. Fat load = amount of fuel over fat-free body mass. Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicate interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

ranging from a negative rate of 0.94 g day^{-1} (decrease to LBM: 33% males, 30% females) to a maximum of 1.04 g 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, $P = 0.76$, $r = –0.009$, $n = 1,158$), or 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.

Flight Models

The overall estimated flight range was 2,261.63 ± 1,152.94 km, with a minimum of 16 km and a maximum of 4,960 km. 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 farther than younger birds and females, respectively (Figure 10). We found no interaction between age and sex ($F_{1,117} = 1.30$, $P = 0.26$). A visual sensitivity analysis of the models found that fuel load was the most influential factor of these flight range calculations.

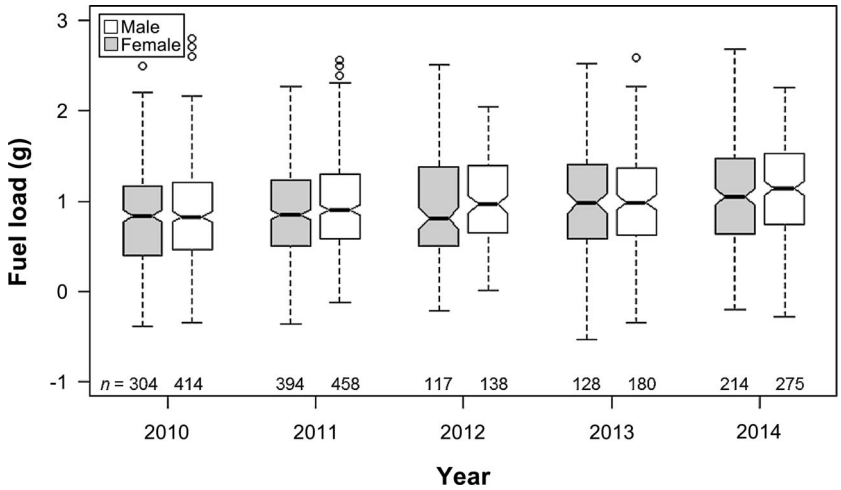


FIGURE 6. Fuel loads of hatch-year Ruby-throated Hummingbirds by male and female for 2010–2014. Fat load = amount of fuel over fat-free body mass. Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicate interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

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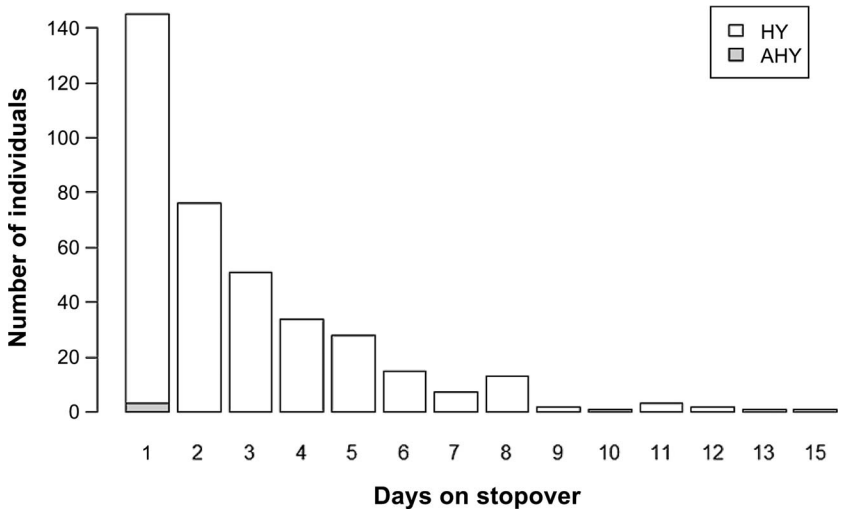


FIGURE 7. Distribution of Ruby-throated Hummingbird stopover durations between age groups when all years are pooled (HY = hatch-year, AHY = after-hatch-year; *x*-axis shows minimum stopover durations).

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, arrival condition, stopover biology (FDR and stopover duration), and departure (flight range), 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 1993b, and references therein). While we expected similarities between species, each experiences 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 (i.e. the Gulf of Mexico), and otherwise have access to largely contiguous hospitable areas during passage (La Sorte et al. 2014). Moreover, the 2 species experience different competitive interactions: Ruby-throated Hummingbirds face interspecific competition on the wintering grounds (Weidensaul et al. 2013), whereas Rufous Hummingbirds

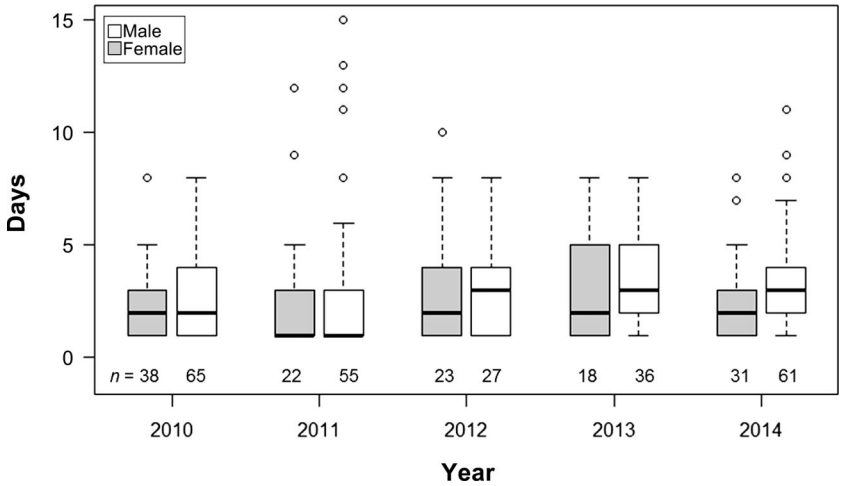


FIGURE 8. Stopover duration of hatch-year Ruby-throated Hummingbirds by male and female for 2010–2014 (*y*-axis indicates minimum stopover duration). Central black line indicates median, top and bottom of box indicate interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

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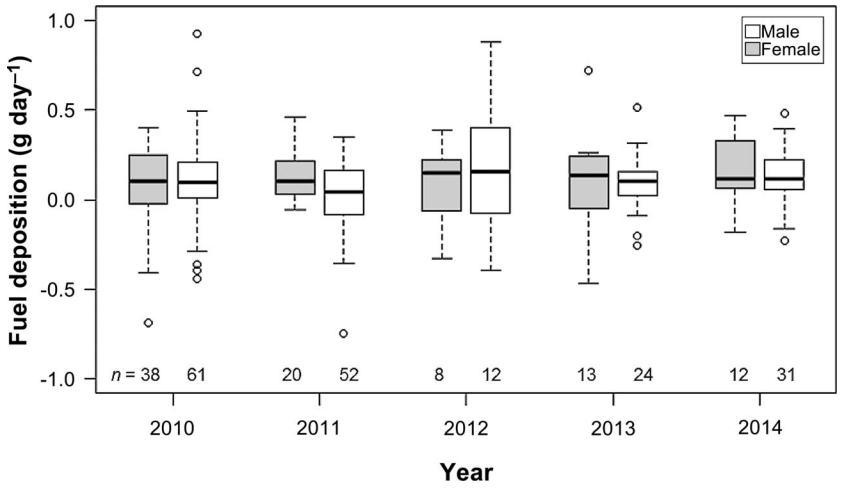


FIGURE 9. Fuel deposition rates of hatch-year Ruby-throated Hummingbirds by male and female for 2010–2014. Central black line indicates median, top and bottom of box indicate interquartile range, and whiskers indicate total range. Circles above and below whiskers indicate location of outliers.

encounter interspecific competition throughout their annual cycle (e.g., Wolf and Hainsworth 1971, Powers and McKee 1994, McCaffrey and Wethington 2008). The 2 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 having 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 stopover duration than birds that arrived with larger stores. This suggests 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 Gulf of Mexico, the average bird captured at our study site could make the

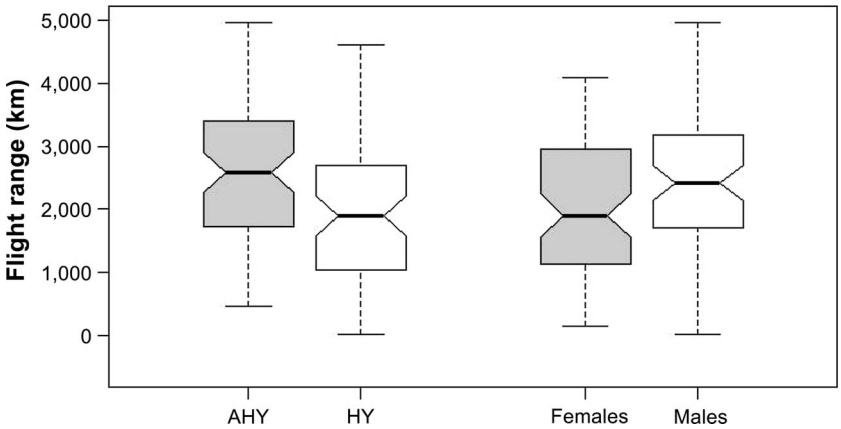


FIGURE 10. Potential flight ranges of Ruby-throated Hummingbirds by age (HY = hatch-year, AHY = after-hatch-year) and sex groups. Central black line indicates median, notch shows 95% confidence interval, top and bottom of box indicate interquartile range, and whiskers indicate total range.

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~1,000 km flight across the Gulf of Mexico 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 Gulf of Mexico, 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 those of 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, given that hummingbirds have higher metabolic rates than other migrants that were 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 passerine species (e.g., Woodrey and Chandler 1997, Woodrey and Moore 1997, Jakubas and Wojczulanis-Jakubas 2010). Adult Ruby-throated Hummingbirds leave more northerly 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 more slowly than adults (e.g., spend longer at each stopover site, make additional stops en route, or take a less direct migratory route), which would increase travel time and might explain the disparity we observed between the numbers of old and young birds at our study site.

Older birds arrived with larger fuel loads and tended to stay a shorter time at our site than younger birds, both of which may be due to younger birds having less efficient foraging, social subordinacy, or disorientation than 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). Although 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 one would expect (1:1 to 1:3) assuming 2 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 Gulf of Mexico. Young birds on their first migration may not recognize the Gulf of Mexico 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), whereas adults depart from locations farther inland. Some young migrants arriving at our site may be disoriented (Ralph 1978) or follow a migratory route different from that of adults (Hake et al. 2003, Agostini 2004); perhaps older birds depart inland sites and make trans-Gulf flights, whereas younger birds follow the coast around the Gulf of Mexico.

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 this species 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, the 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 stopover duration, 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

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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 those found in older individuals (Stiles et al. 2005), which might lessen any differences in aerodynamic performance.

Although there was no difference between sexes in young birds, older males arrived with larger fuel loads than older females. The strong differences in wing morphology and WDL (Stiles et al. 2005) could affect 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 adult male Ruby-throated Hummingbirds are socially dominant over females as in other hummingbird species (e.g., Feinsinger and Colwell 1978, Kodric-Brown and Brown 1978, Carpenter et al. 1993b). 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 results describe the autumn migration of Ruby-throated Hummingbirds along the northern coast of the Gulf of Mexico. 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 HY birds did not differ in their stopover biology, but older males had larger fuel loads upon arrival than 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 in 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 that species 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.

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Author contributions: T.J.Z. and F.R.M. conceived the study and developed the methods. T.J.Z. conducted the research and analyzed the data. T.J.Z. and F.R.M. wrote the paper. T.J.Z. and F.R.M. contributed substantial materials, resources, and funding.

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