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Trans-Gulf of Mexico loop migration of tree swallows revealed by solar geolocation

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Abstract One of the greatest feats of avian migration is the non-stop crossing of extensive areas of inhospitable habitat such as deserts and seas. Differences in spring and autumn migration routes have been reported in species that cross such barriers, and are thought to have evolved in response to seasonal variation in prevailing wind direction. We tested the hypothesis that migration routes vary seasonally with respect to the Gulf of Mexico in the tree swallow *Tachycineta bicolor* using solar geolocators attached and retrieved at 4 breeding sites in central North America. We found that 100 % of birds (n = 10) made a trans-Gulf flight of >850 km from Louisiana south to their wintering grounds in the Yucatan Peninsula in 12–36 hours, achieving minimum ground speeds as high as 32 m/s. Although most days during autumn migration were characterized by unfavorable headwinds blowing to the northwest, migration over the Gulf mostly occurred on days with strong winds blowing to the south. In contrast, in 8 of 9 (88 %) birds on spring migration returned from the wintering grounds towards Louisiana following a clockwise loop pattern flying over land to the west around the Gulf. During this spring period there were few days with prevailing winds from the south to assist northward migration. Results suggest that, despite being up to three times further (ca. 2,700 km), a coastal circum-Gulf spring migration represents the less risky route when wind conditions are not favorable. These findings also help to resolve a long-standing dispute in the literature concerning migration patterns between the US Gulf coast and Mexico, and provide insight into the factors shaping migration strategies of small songbirds migrating across large bodies of water [*Current Zoology* 60(5): 653–659, 2014].

Keywords Ecological Barrier, Geolocation, Gulf of Mexico, Tachycineta bicolor, Tree swallow, Migration

Many bird species perform regular, annual migration movements between breeding and non-breeding areas (Newton, 2010; Rappole, 2013), often doing so across ecological barriers such as water bodies, deserts, mountain ranges and ice fields (Gill et al., 2009). This leads to the concentration of migrants at prominent land features, such as peninsulas and isthmuses, as they attempt to minimize the distance they fly over inhospitable areas devoid of food and/or safe landing areas in which to rest, which may result in physiological constraints. These ecological barriers may vary temporally in their degree of hospitability based on meteorological factors such as wind speed and direction, which may vary seasonally. Therefore, ecological barriers may shape differential migration patterns between seasons (Richardson, 1978; Rappole et al., 1979; Rappole and Ramos, 1994).

The Gulf of Mexico is a major barrier to millions of migratory birds every year as they move twice a year between their North American breeding grounds and non-breeding areas in Central or South America (Able, 1972; Gauthreaux and Belser, 1999; Barrow et al., 2000a, 2000b). Birds must either cross or circumvent the Gulf as they move south in the autumn (Nov –Dec) and north in the spring (Mar –Apr). Movement across this expan-

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sive body of water has been the subject of intense scientific debate, particularly with regard to the routes taken during each migration period. A direct, trans-Gulf route in the spring was first proposed by Cooke (1915), and later supported by others (Lowery, 1945, 1946, 1951, 1955; Gauthreaux, 1971; Gauthreaux et al. 2006). However, Williams (1947) suggested an alternative, coastal, circum-Gulf route, for which other authors found support (Williams, 1950, 1951; Rappole et al., 1979; Rappole and Ramos, 1994). The tendency to adjust migration routes seasonally, termed *route flexibility* (Rappole, 2013), is based on seasonal differences in wind patterns. Over the Gulf of Mexico the winds blow predominantly to the northwest year-round, and large-scale frontal systems delineating air masses of varying densities move from north to south in the autumn. Rappole and Ramos (1994) examined banding and observational data in Texas, Veracruz, and Florida and found support in several songbird species for this proposed westward shift in spring migration route compared to the autumn. However, there has been little direct evidence to evaluate this hypothesis because of the difficultly of directly tracking small songbirds.

Recent studies using light sensing devices known as solar geolocators (Stutchbury et al., 2009) have shed light on the migratory behavior of some passerine bird species when crossing ecological barriers. Bächler et al. (2010) used geolocators to determine that four hoopoes *Upupa epops* from the same breeding site followed three different autumn migration routes across the Mediterranean Sea. Tøttrup et al. (2012) showed seasonal differences in migration routes in red-backed shrikes *Lanius collurio*, revealing a loop migration pattern around the Red Sea. Seasonal difference in migration routes with respect to the Gulf of Mexico has also been shown. Delmore et al. (2012) tracked four Swainson's thushes *Catharus ustulatus* that crossed the Gulf directly in the autumn and returned in the spring via a westward, coastal route, while Callo et al. (2013) found that ten red-eyed vireos *Vireo olivaceus* crossed the Gulf directly in both seasons. Seasonal variation in migration routes has even been demonstrated within species. Stanley et al. (2012) reported that, while the autumn migration routes of ten wood thrushes *Hylocichla mustelina* were always to the east of those in the spring, spring routes varied among individuals, and sometimes within individuals between years encompassing both trans-Gulf and circum-Gulf trajectories. These complicated patterns, even within a single species, suggest a flexible response to environmental conditions during each migratory period and they highlight the need for further research on additional species.

In our study, we examine the *route flexibility hypothesis* by tracking autumn and spring migration routes across the Gulf of Mexico by tree swallows *Tachycineta bicolor* equipped with geolocators. Tree swallows are small insectivorous birds that breed throughout most of temperate North America and winter in the southeastern U.S., Mexico and Central America (Winkler et al., 2011). Specifically, we predicted differential migration patterns based on the speed and direction of wind patterns over the Gulf, with trans-Gulf movement only occurring when favorable tailwind conditions exist during autumn migration but not spring migration.

1 Materials and Methods

During the 2011 and 2012 breeding seasons (May–July), we deployed geolocators (Lotek Wireless model MK6440, 2011; MK6740, 2012; with 10 mm light stalk) on adult tree swallows (males ≥ 1 year old, females ≥ 2 years old) over 2 breeding seasons (2011, n = 108; 2012, n = 45) at four sites in North America: St. Denis, Saskatchewan (SK; 52.2°N, 106.1°W; 2011, n = 40; 2012, n = 20), Saukville, Wisconsin (WI; 43.4°N, 88.0°W; 2011, n = 35), Long Point, Ontario (ON; 42.5°N, 80.1°W; 2011, n = 33; 2012, n = 10), and Ames, Iowa (IA; 42.1°N, 93.6°W; 2012, n = 15). We attached geolocators with a modified leg-loop backpack harness (Rappole and Tipton, 1991; Stutchbury et al., 2009; Laughlin et al., 2013; Gómez et al., 2014), which had a combined mass of ≤1.0 g (<5% of body mass).

During the subsequent breeding season, we trapped all returning birds at nest boxes at each site and removed the geolocator. We calculated each geolocator's specific calibration value using BASTRACK software (British Antarctic Survey [BAS], Cambridge, United Kingdom) as in Laughlin et al. (2013). In summary, we used the BASTRACK program Locator Aid to perform a dynamic on-bird calibration procedure for each bird during the period after nesting yet before migration. This was possible as birds were still at or near their known breeding location during this period, which allowed comparison of the breeding location to derived location estimates using various sun-angles. The average sun-angle value over this period for each bird was then used to derive location estimates throughout the migration period using the BASTRACK program BirdTracker. During the interval over which birds were moving between either side of the Gulf, we plotted locations determined at both midday (midpoint between sunrise and sunset of day$_i$) and midnight (midpoint between sunset and sunrise of day$_{i+1}$) to better estimate departure and arrival times. These locations are on the finest scale of temporal resolution possible with the geolocator models we used. Midnight position estimates that were located over water at a distance from land less than the margin of error (± 81.7 km; Laughlin et al., 2013) were assumed to be roosting on the coast. This is realistic given that tree swallows do not typically migrate at night (Winkler, 2006). During the spring migration period, which mostly occurred within 2 weeks of the spring equinox, it was difficult to distinguish shifts away from the wintering site using longitude alone. This was particularly true for one bird (geolocator number 474) that remained at or near the same longitude along the western Gulf coast; this bird was, therefore, excluded from the spring migration analysis. For the remaining birds, it was possible to estimate east/west movements in the spring by plotting longitude values. For autumn migration, we estimated ground speeds by dividing the known minimum distance between successive geolocator-derived locations by the duration of the flight. These estimates therefore represent minimum ground speeds, as individuals may have travelled a greater distance in less time.

Meteorological data were accessed from the National Data Buoy Center (www.ndbc.noaa.gov) for offshore weather station numbers MRSL1 (29.44°N, 92.06°W) and 42055 (22.20°N, 94.00°W). Station MRSL1 (anemometer height = 23.4 m a.s.l.) is located 17 km southwest of Shell Keys, Louisiana, and lies directly in the migration path of any birds passing directly over the Gulf in the autumn. Station 42055 (anemometer height = 5 m a.s.l.) lies in the southwest Gulf, 400 km east of Tampico, Mexico. Although swallows are thought to migrate above the height of the anemometers (Winkler, 2006), these instruments provide the most relevant wind data available for the spring and autumn migration periods, respectively, and are visually similar to predictive wind models at greater heights. We analyzed wind data using the circular statistics program Oriana (version 4.02, Kovach Computing Services). We calculated the tail wind component of average daily wind direction using the formula $V_w \cos(\varphi_t - \varphi_w)$, where V_w is the wind velocity, φ_t is the track direction of the bird between departure and arrival locations, and φ_w is the mean daily wind direction (Åkesson and Hedenström, 2000). All reported values are means ± *SE*.

2 Results

In the breeding seasons following deployment, we recovered 44 geolocators: 31 from 2011 (SK: 11 of 40, 27.5 %; WI: 6 of 35, 17.1 %; ON: 14 of 33, 42.4 %) and 13 from 2012 (SK: 5 of 20, 25.0%; IA: 4 of 15, 26.7%; ON: 4 of 10, 40.0%). Ten (22.7 %) of these birds over-wintered in Mexico (4 males, 6 females; Table 1), while the remainder went to Florida, Cuba, or remained in the Mississippi Valley (D.R.N. et al., unpublished data). Those ten birds were confronted with the decision to cross or circumvent the Gulf of Mexico. In the autumn, they all took a direct over-water route (Fig. 1) traveling a minimum distance of 1,280 (± 68 km) in as few as 12 (n = 2 birds), 24 (n = 6 birds) or 36 (n = 2 birds) hrs and flew at an average minimum ground speed of 17 m/s (range = 11–32; Table 1). Mean day time (0600–1800 h) wind speed and direction during the autumn migration period (01 Nov–01 Dec) at station MRSL1 off the Louisiana coast was 6.5 m/s to the WNW (298 ± 15°) in 2011 and 4.7 m/s to the WNW (290 ± 16°) in 2012 (Fig. 2A, B), suggesting that most days have unfavorable wind directions for crossing the Gulf from N to S. Nevertheless, all but one of the birds flew over the Gulf in the autumn with tailwind assistance (Fig. 2A, B, Table 1).

In the spring, the majority of birds (88%; 8 of 9) appeared to follow a coastal circum-Gulf route (Fig. 3). One bird (geolocator number 474) remained close to the western Gulf coast for the late winter and so determining spring migration route was not possible from longitude estimates alone. Mean day time wind speed and

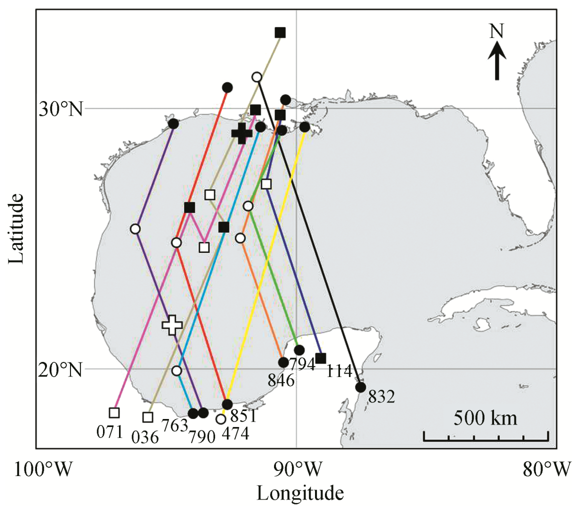

Fig. 1 Migratory movements of 10 tree swallows depicting autumn (Nov) trans-Gulf routes between the US Gulf Coast and Mexico

Symbols (2011, circles; 2012, squares) represent midday (hollow) or midnight (filled) location estimates. Lines connect 12-hour successive locations for each individual (3-digit geolocator number). Crosses represent weather stations at MRSL1 (filled) and 42055 (hollow).

Table 1 Flight and wind characteristics during autumn trans-Gulf of Mexico migration in tree swallows

Geolocator number	Sun-angle value[a]	Sex	Year	Departure date[b]		Arrival date[b]		Distance (km)	Flight duration (h)	Min. ground speed (m/s)	Tail wind (m/s)
832	-5.12	F	2011	midday	10-Nov	midnight	11-Nov	1393	12	32	7.2
846	-4.67	M	2011	midnight	10-Nov	midnight	11-Nov	1122	24	13	8.9
851	-4.42	F	2011	midnight	10-Nov	midnight	11-Nov	1359	24	16	8.9
474	-4.50	F	2011	midnight	17-Nov	midday	17-Nov	1294	12	30	9.1
794	-4.73	M	2011	midnight	17-Nov	midnight	18-Nov	973	24	11	8.5
790	-4.25	M	2011	midnight	18-Nov	midnight	19-Nov	1246	24	14	0.5
763	-5.38	F	2011	midnight	24-Dec	midnight	25-Dec	1254	24	15	6.0
114	-4.50	F	2012	midnight	6-Nov	midnight	7-Nov	1035	24	12	-4.2
071	-5.51	F	2012	midnight	18-Nov	midday	19-Nov	1410	36	11	3.7
036	-4.33	M	2012	midnight	28-Nov	midday	29-Nov	1724	36	13	4.9

[a] Values calculated after deployment yet before migration; [b] Dates represent the last location before, or first location after crossing the Gulf; [c] Average tail wind on the day of departure

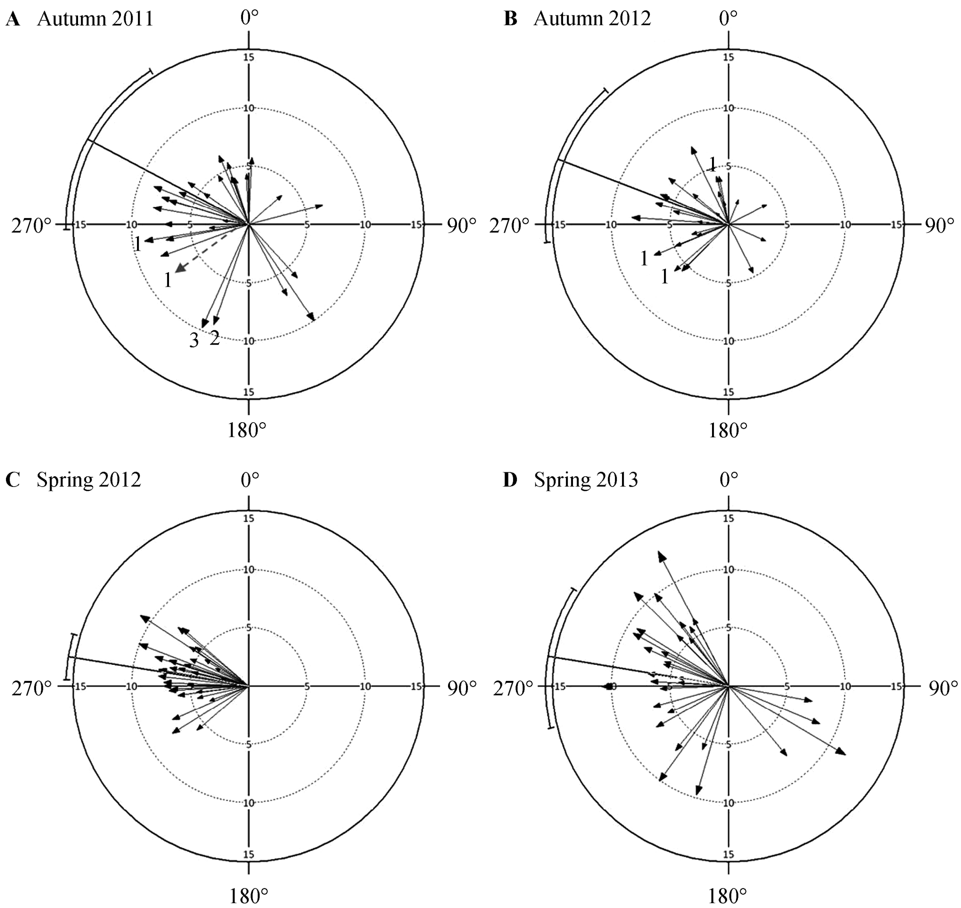

Fig. 2 Arrow plots representing mean daytime (0600–1800 h) direction and speed of winds at station MRSL1 (see Fig. 1 for locations of MRSL1 and 42055) for the autumn migration period (01 Nov–01 Dec) in A) 2011 and B) 2012, and station 42055 for the spring migration period (10 Mar–10 Apr) in C) 2012 and D) 2013

Each arrow represents mean daytime wind direction, where the direction in which the arrow points is where the wind is blowing to; longer arrow length denotes higher mean wind speed; concentric circles demarcate 5, 10, and 15 m/s wind speed. Mean ± 95% C.I. wind direction is indicated with anchors emanating from the compass centers in the direction the wind is blowing. Numbers represent the number of individuals that crossed the Gulf on the day with that wind direction and speed. In (A), one bird that crossed in late December outside the time period of all other birds is indicated with a dashed grey arrow and a grey number.

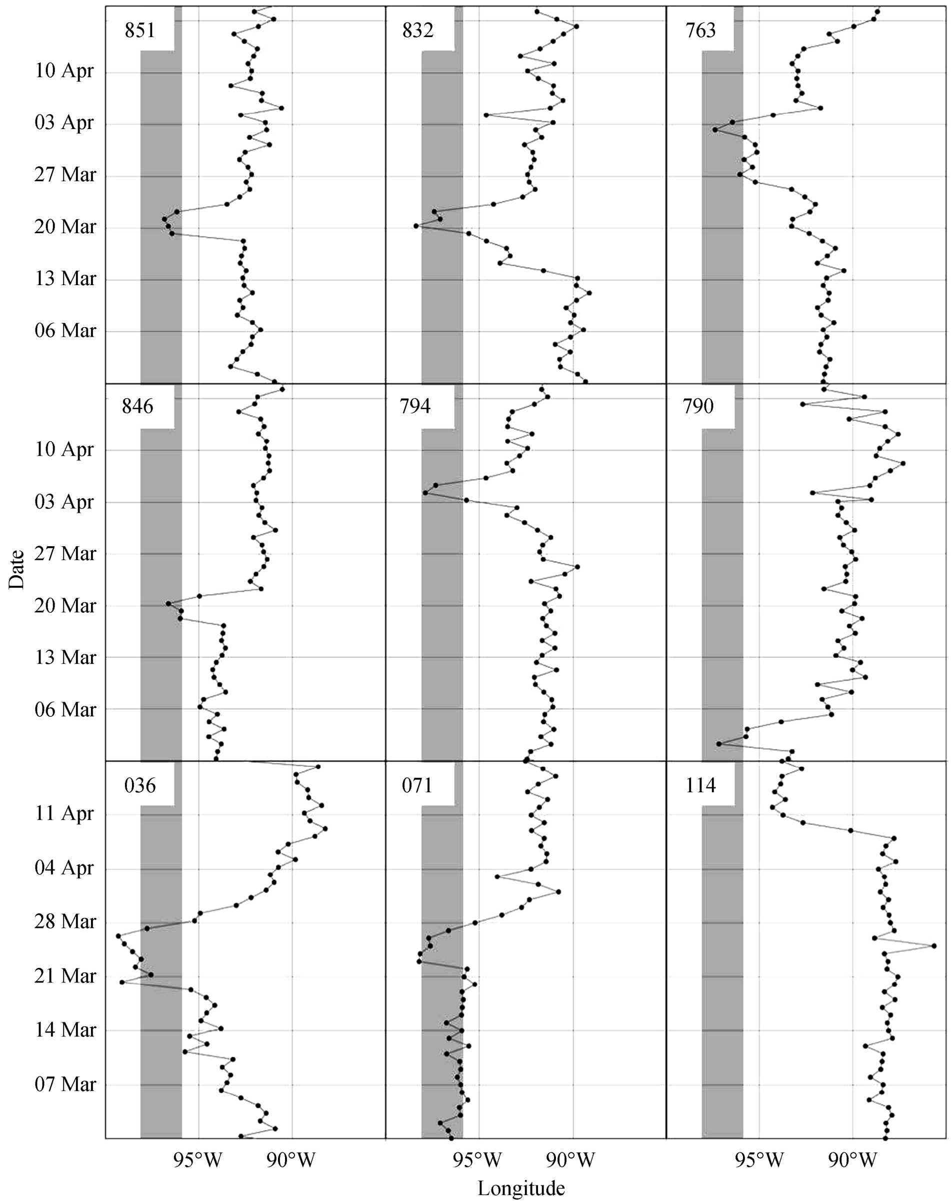

Fig. 3 Longitudinal changes during spring migration showing the east-west-east circum-Gulf movements of 8 birds crossing longitudes 96°W–98°W (i.e. the approximate longitude of the western Gulf coast, indicated with a vertical bar shaded in light grey)
The direct trans-Gulf crossing by 1 bird (geolocator number 114) is depicted in the bottom right panel. Note that one bird (geolocator number 474) remained close to the western Gulf coast throughout the late-winter period, making departure difficult to determine by longitude alone; this bird has been excluded from the analysis and is not depicted here.

direction during the spring (10 Mar–10 Apr) at station 42055 was 6.4 m/s to the W (279 ± 3°) in 2012 and was 7.7 m/s to the W (279 ± 12°) in 2013 (Fig. 2C,D), which meant that most days birds would not be assisted by tailwinds if they chose to fly over the Gulf. The only individual (geolocator number 114; Fig. 1) to fly a direct trans-Gulf route in the spring did so in 24 hrs or less.

3 Discussion

In this study, we show that tree swallows that winter in Mexico, as predicted by the *route flexibility hypothesis*, use different strategies with respect to autumn and spring migration routes, taking a direct over-water trans-Gulf route in the autumn from the US coast to Mexico versus an indirect, circum-Gulf coastal return route in the spring. These results from geolocators on ten birds are consistent with field observations of the distributions of tree swallows in the autumn (Winkler, 2006): despite their occurrence in winter in Yucatan and further south in Central America, tree swallows are virtually unheard of amid the millions of swallows passing along the coast of Veracruz, to the north and west, in the autumn. These observations also do a great deal to help interpret migrant swallows seen mid-Gulf from boats or oil platforms (Winkler, 2006). Swallows can be very flexible in their migration strategies. Even tree swallows, which have the shortest migrations of any of the North American swallow species and appear to do most of their migration in short hops between successive nocturnal roost sites (Winkler, 2006), are clearly regularly capable of long over-water flights.

Undoubtedly, wind patterns in the Gulf contribute to the observed migration routes, as has been noted by others (Alerstam, 1979; Kemp et al., 2010). Prevailing wind directions were remarkably similar between years in both the autumn and spring periods, predominantly blowing from the southeast, which suggests that migrating swallows may encounter similar wind conditions each year. As suggested by Rappole and Ramos (1994), this consistent selection pressure may have created the divergent migration patterns we observed in this study. Importantly, strong autumn winds (i.e. >5 m/s) occasionally blew from the north, as seen on 8 days in 2011 (Fig. 2A), and 5 days in 2012 (Fig. 2B), facilitating a direct over-water migration for 6 birds in 2011 (1 bird crossed on 24 December with a mean wind speed of 7.8 m/s from 57.3°) (Fig. 2A), and 2 of 3 birds in 2012 (Fig. 2B) although 1 bird (geolocator number 114; Table 1) crossed into a light headwind (<5 m/s). Interestingly, while the spring wind pattern suggests a lack of strong southerly winds to assist northward passage in 2012 (Fig. 2C), there were several days in 2013 that exhibited these wind characteristics (Fig. 2D), although only one bird chose to cross the Gulf directly in the spring (geolocator number 114; Fig. 3). This suggests that birds may be somewhat flexible in their specific migration route depending on wind conditions at departure.

Movement in the spring is typically considered to be more rapid than in the autumn (Newton, 2008). This pattern is thought to be driven by evolutionary pressure, particularly in males, to arrive early at breeding areas, establish a high-quality breeding territory and advertise for mates (Kokko, 1999). In our study, however, we show that autumn migration across the Gulf is very rapid, most likely due to the necessity to complete a trans-Gulf flight in one flight, and lengths of each route differ; a direct trans-Gulf route to Yucatan ~850 km while a coastal circum-Gulf route is ~2,700 km. Such rapid autumn migration movements would undoubtedly necessitate rapid flights. In *Hirundinidae* species migratory ground speeds have been estimated at 11–22 m/s (Lyuleeva, 1973). We found the minimum ground speed of most birds when crossing the Gulf in our study to be higher, particularly for two birds that flew at a minimum of 30 m/s and 32 m/s respectively (Table 1). One potential criticism of the ground speed estimates concerns the influence of positional error in location estimates derived from geolocators. The magnitude of error when using geolocators is known to be influenced by a number of factors, including species-specific roosting behaviors, and shading effects during twilight hours caused by clouds (Fudickar et al., 2012). Laughlin et al. (2013) estimated positional error of 81.7 km for tree swallows during periods when the birds were carrying geolocators. Accounting for this positional error in departure and arrival locations, the minimum ground speed remains as high as 28 m/s. This ground speed is similar to, or even higher than, other well-documented species. For example, the bar-tailed godwit *Limosa lapponica*, is known to perform a non-stop flight of 8,100–11,600 km over 6–9 days, which corresponds to a mean ground speed of ~17 m/s (Gill et al., 2009). Klaassen et al. (2011) found that great snipe *Gallinago media* make a non-stop flight of 4,300–6,800 km in 48–96 h, which corresponds to a ground speed of 15–27 m/s. Of course, it is unlikely that tree swallows would maintain such high speeds for sustained periods, as, once the Gulf is crossed, they can resume simultaneous movement and feeding as is their wont. The high ground speeds observed for these birds are much higher than those observed (ca. 8 m/s) during flight trials in still air in the breeding season (Bowlin and Winkler, 2004), and it is likely that these high ground speeds are not paralleled by equally high air speeds and that they are only attainable with the assistance of tail winds. Nevertheless, it is remarkable that they travel over such a large body of water in a relatively short time period.

In a recent study examining a major stopover site of tree swallows in southwest Louisiana, Laughlin et al. (2013) showed that seven of the ten of the birds that were also used in this study utilized sugarcane roosts near the Gulf Coast for 33 ± 6 d in autumn. This protracted staging period would provide adequate time to accumulate fat stores in preparation for a non-stop over-water flight across the Gulf of Mexico. This fact, when combined with tail winds experienced on departure days, helps explain how tree swallows were capable of traveling this distance non-stop. Further spatiotemporal data derived from devices such as geolocators that are deployed on additional Nearctic-Neotropical migratory songbirds will expand our knowledge of selective pressures shaping the migration routes in these diverse taxa and strengthen our general understanding of avian migration.

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