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RESEARCH ARTICLE

Nonbreeding season movements of a migratory songbird are related to declines in resource availability

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ABSTRACT

There have been an increasing number of observations of itinerancy in migratory songbirds, where individuals move among 2 or more widely separated areas during the "stationary" nonbreeding season. Knowledge of such movements and an understanding of what drives them are important for predicting how migratory populations will respond to environmental change. In this study, we investigated nonbreeding movements of the Tree Swallow (*Tachycineta bicolor*), an aerial insectivore that breeds across North America and spends the nonbreeding season around the Gulf of Mexico, Florida, Mexico, Central America, and the Caribbean. With year-round tracking data obtained from 133 light-level geolocators deployed at 12 breeding sites ranging from Alaska to Nova Scotia to North Carolina, we show that 44% of individuals made at least one large-scale movement (range: 301–1,744 km) within the nonbreeding range. The frequency of itinerancy decreased with longitude, such that 75% of individuals made a movement in the western portion of the nonbreeding range compared to only 31% in the east. Using the Normalized Difference Vegetation Index (NDVI) as a proxy for resource availability, we found that when individuals did move, they were more likely to move from sites where resources were deteriorating faster (a more negative change in NDVI prior to departure) than their destination sites. There was also evidence that individuals moved to destination sites with higher NDVI and temperature in the autumn, but not in the winter. Our results suggest movements of Tree Swallows during the nonbreeding season are influenced by resource availability, but because not all individuals used multiple nonbreeding sites, the density of individuals at a site and the level of competition may have also been a factor influencing nonbreeding season movements.

Keywords: aerial insectivore, itinerancy, light-level geolocator, migration, NDVI, *Tachycineta bicolor*, Tree Swallow

Les déplacements d'un oiseau chanteur migrateur au cours de la saison non reproductrice sont reliés au déclin de la disponibilité des ressources

RÉSUMÉ

Un nombre croissant d'observations d'itinérance sont rapportées chez les oiseaux chanteurs migrateurs, où les individus se déplacent entre deux zones éloignées ou plus au cours de la saison non reproductrice "stationnaire." Connaître ces déplacements et comprendre ce qui les cause est important pour prédire comment les populations migratrices réagiront aux changements environnementaux. Dans cette étude, nous avons étudié les déplacements non reproducteurs chez *Tachycineta bicolor*, un insectivore aérien qui se reproduit partout en Amérique du Nord et qui passe la saison non reproductrice dans les environs du golfe du Mexique, en Floride, au Mexique, en Amérique centrale et dans les Caraïbes. Avec des données de suivi obtenues tout au long de l'année à l'aide de 133 géolocateurs mesurant les niveaux de lumière, lesquels ont été déployés à 12 sites de reproduction allant de l'Alaska à la Nouvelle-Écosse et à la Caroline du Nord, nous montrons que 44% des individus ont effectué au moins un déplacement à grande échelle (étendue: 301–1744 km) à l'intérieur de l'aire de répartition non reproductrice. La fréquence de l'itinérance a diminué avec la longitude, de sorte que 75% des individus ont effectué un déplacement dans la portion ouest de l'aire de répartition non reproductrice, comparativement à seulement 31% dans l'est. En utilisant l'indice de végétation par différence normalisée (NDVI) comme indicateur de la disponibilité des ressources, nous avons constaté que lorsque les individus se déplaçaient, ils étaient plus susceptibles de se déplacer à partir de sites où les ressources se détérioraient plus rapidement (une variation plus négative du NDVI avant le départ) qu'aux sites de destination. Des preuves indiquaient que les individus se déplaçaient vers les sites de destination comportant un NDVI plus élevé et des températures plus élevées à l'automne, mais pas en hiver. Nos résultats suggèrent que les déplacements de *T. bicolor* au cours de la saison non reproductrice sont influencés par la disponibilité des ressources, mais qu'en raison du fait que ce ne sont pas tous les individus qui ont utilisé plusieurs sites pendant la saison non reproductrice, la densité des individus à un site et le niveau de compétition peuvent aussi avoir été un facteur qui influence les déplacements durant la saison non reproductrice.

Mots-clés: géolocateur mesurant les niveaux de lumière, insectivore aérien, itinérance, migration, NDVI, *Tachycineta bicolor*

INTRODUCTION

In migratory birds, itinerancy is defined as movements between 2 or more widely separated areas during the "stationary" nonbreeding season (Moreau 1972). Advances in animal tracking technology (e.g., radio telemetry, light-level geolocators, global positioning systems) have facilitated numerous studies on migration in the past decade, particularly in songbirds, and resulted in an increasing number of observations of itinerancy (Heckscher et al. 2011, Delmore et al. 2012, Fraser et al. 2012, Jahn et al. 2013, Renfrew et al. 2013, Liechti et al. 2015, Koleček et al. 2016, Lerche-Jørgensen et al. 2017, Thorup et al. 2017). These large-scale movements challenge previous assumptions that migratory songbirds remain relatively stationary during this period of the annual cycle. Nonbreeding movements may be complete, where all individuals in a given species move between nonbreeding sites (e.g., Heckscher et al. 2011, Jahn et al. 2013, Renfrew et al. 2013). Alternatively, movements may be partial, where only a fraction of the individuals in a given population, or a fraction of the populations of a given species, move between nonbreeding sites (e.g., Delmore et al. 2012, Fraser et al. 2012, Liechti et al. 2015). Knowledge of such movements and an understanding of what drives them are essential for understanding population dynamics in migratory species and, further, how population dynamics may be influenced by environmental change (Thorup et al. 2017).

One hypothesis explaining why individuals move during the nonbreeding season is the resource-availability hypothesis (Stutchbury et al. 2016), which suggests that seasonal and geographic variation in resource availability drives individuals to find higher-quality nonbreeding sites. There is also evidence that it may not be the exact availability of resources that matters, but rather avoiding rapidly declining resource availability that drives movements in some species (Renfrew et al. 2013, Trierweiler et al. 2013). In addition, the competition-avoidance hypothesis (Stutchbury et al. 2016) suggests high density drives poor competitors, who cannot gain access to sufficient resources, to move to another nonbreeding site. Declines in resources will presumably intensify competition, which could force some, but not all, individuals to seek habitats with higher resource availability to avoid competition for limited resources.

Itinerancy was initially described in Palearctic–African migrants (Moreau 1972) and it appears to be a common phenomenon in sub-Saharan Africa (e.g., Liechti et al. 2015, Koleček et al. 2016, Thorup et al. 2017) where the decrease in resource availability in the Sahel region following the rainy season (Zwarts et al. 2009) is thought to be the dominant driver of these movements (Lerche-Jørgensen et al. 2017, Thorup et al. 2017, Koleček et al. 2018). Despite what are presumed to be less drastic shifts in resource availability in the Neotropics during the temperate winter, itinerancy has also been documented in some Nearctic–Neotropical migrants (e.g., Heckscher et al. 2011, Delmore et al. 2012, Fraser et al. 2012, reviewed in McKinnon and Love 2018), with evidence supporting the resource-availability hypothesis for some species (Renfrew et al. 2013) but not others (Stutchbury et al. 2016). Given the sheer number of species that migrate to the Neotropics, it is still difficult to draw generalizations about the commonality of itinerancy, how itinerancy varies within a species that originates from spatially diverse breeding locations, and how seasonal changes in resources might drive these movements.

In this study, we investigated nonbreeding movements of Tree Swallows (*Tachycineta bicolor*), a migratory songbird, using data from 133 individuals tracked from 12 breeding sites across North America (Knight et al. 2018a). Tree Swallows are aerial insectivores that also consume bayberries (*Myrica* spp.) and other vegetable matter during the nonbreeding season (Winkler et al. 2011, Piland and Winkler 2015). They begin migrating away from their North American breeding grounds around July, shortly after breeding, and make prolonged stops at short-term residency sites during migration (Knight et al. 2018a, Gow et al. 2019), most likely to molt (Winkler 2006), before reaching their nonbreeding range around Florida, the Gulf of Mexico (e.g., Louisiana), Mexico, Central America, and the Caribbean in autumn. During migration and the nonbreeding season, Tree Swallows roost in large aggregations, which can number hundreds of thousands of individuals at some locations (Winkler 2006); the largest roosts can even be detected by Doppler radar (Laughlin et al. 2013, 2016). Some individuals remain relatively stationary between approximately October and April, while other individuals make large-scale movements within the nonbreeding range (Knight et al. 2018a).

Using range-wide tracking of individuals, our first objective was to quantify the frequency of itinerancy in Tree Swallows. We then compared the frequency of itinerancy and the variation in distance and direction of movement among the 12 breeding sites, and tested for differences in the frequency of itinerancy among 3 distinct migratory flyways that Tree Swallows used for migration (Knight et al. 2018a). Our second objective was to test predictions arising from the resource-availability hypothesis. Specifically, we predicted Tree Swallows that made nonbreeding movements travelled to areas with higher resource availability, as estimated by (1) the Normalized Differential Vegetation Index (NDVI) and (2) temperature (which influences insect availability; Winkler et al. 2013). We also tested for the influence of other factors on nonbreeding movement, including effects of arrival date and latitude of the first (or only) nonbreeding site on whether an individual made a subsequent nonbreeding movement. Following the competition-avoidance hypothesis, we predicted individuals that arrived at nonbreeding regions later would be more likely to move because they had settled in areas with low resource availability to avoid competition with other individuals already occupying areas with high resource availability. We also tested whether itinerancy carried over to affect the date of spring arrival on the breeding grounds. For Tree Swallows, the timing of arrival on the breeding grounds is important because early-arriving individuals lay eggs earlier (Gow et al. 2019) and individuals that lay eggs earlier tend to have larger clutch sizes and fledge more offspring (Shutler et al. 2006, Dunn et al. 2011). If itinerancy had a higher overall energetic cost than remaining stationary, we predicted individuals who made nonbreeding movements would arrive at their breeding grounds later than individuals that remained stationary.

METHODS

Tree Swallows were tracked using archival light-level geolocators (Lotek Wireless models MK6440 and MK6740, as well as geolocators developed by E.S.B.) deployed at 12 sites across their breeding range from 2010 to 2014 ($n = 596$) and retrieved the following year ($n = 152$; Knight et al. 2018a, Gow et al. 2019). Geolocators record light levels in relation to an internal clock and rely on geographic variation in the timing of sunrise and day length to estimate the position (longitude and latitude) of an individual (Hill 1994). In total, 133 geolocators recorded data for the majority of the deployment period without any malfunctions and were used in this analysis. Light data were downloaded using BASTrak software (Biotrack Limited UK 2013), and the BAStag package in R (version 0.1.3; Wotherspoon et al. 2013) was used to visually verify all sunrise and sunset (twilight) transitions. We used the FLightR package in R (version 0.3.6; Rakhimberdiev et al. 2015) to generate a spatial probability distribution for each twilight time, and retained the median location for subsequent analyses. For more detailed methods on geolocator data analysis, see Knight et al. (2018a). The geolocator data used in this study are available from the Movebank Data Repository (Knight et al. 2018b).

Nonbreeding sites were defined as the mean location an individual occupied over the same general area for a period longer than 2 weeks following autumn migration and prior to spring migration (Knight et al. 2018a) and within the Tree Swallow nonbreeding range. They were distinguished from short-term residency sites (also occupied for a period longer than 2 weeks), which Tree Swallows occupy during autumn migration and where they do not remain past autumn (Knight et al. 2018a). Locations occupied for a period shorter than 2 weeks were not considered due to the spatial resolution of geolocators. Tree Swallows visited nonbreeding sites from mid-September to mid-April, and made nonbreeding movements between late October and late March. Nonbreeding movements were defined as a movement of greater than 300 km between nonbreeding sites. This threshold was used to distinguish movements from potential geolocator error, which was estimated to be on average 46 ± 90 (SD) km in latitude and 52 ± 90 km in longitude (Gow et al. 2019). Timing of movements around the spring equinox was determined by a change in longitude indicating movement, rather than latitude, which is difficult to estimate around the equinoxes (Lisovski et al. 2012). An alternative way to determine the timing of movements would have been to identify abrupt changes in the timing of consecutive twilights (e.g., Liechti et al. 2015). Due to the uncertainty around geolocator estimates, a 200-km buffer was drawn around all nonbreeding sites for subsequent analyses.

The Tree Swallows in this study were classified into 1 of 3 migratory flyways (Knight et al. 2018a). Tree Swallows in British Columbia migrated west of the Rocky Mountains to nonbreeding sites in western Mexico (western flyway), whereas individuals in Alaska and the prairies migrated to nonbreeding sites around the Gulf of Mexico (central flyway), and individuals in the eastern populations migrated to Florida and the Caribbean (eastern flyway; Table 1). These flyways distinguish 3 nonbreeding regions occupied by Tree Swallows, with some mixing among regions (Figure 1). We ran a binomial generalized linear model to determine whether the proportion of individuals that made nonbreeding movements varied by flyway, and tested for the overall effect using a likelihood-ratio test. We report mean proportions ± SD for each flyway.

The NDVI was used as a proxy for resource availability (Figure 2). It is derived from the difference between near-infrared light (reflected by vegetation) and red light (absorbed by vegetation), and is a reliable measure of primary productivity and vegetation quality (Box et al. 1989, Pettorelli et al. 2005). In temperate regions, NDVI is influenced by temperature and precipitation, whereas temperature has little influence on NDVI in tropical regions (Schultz and Halpert 1993). Because insect availability is positively correlated with primary productivity (Siemann 1998, reviewed in Pettorelli et al. 2011), NDVI has been used as a proxy for resource availability in studies of avian insectivores (Balbontín et al. 2009, Thorup et al. 2017, Van Loon et al. 2017). Tree Swallows also feed on bayberries during the nonbreeding season (Winkler et al. 2011), so NDVI may also be a direct measure of vegetative resource availability. NDVI is measured from −1 to 1, where negative values indicate an absence of vegetation (such as over water) and high values indicate high primary productivity (Figure 2).

NDVI data were downloaded from NASA Earthdata (https://earthdata.nasa.gov/), and we used the MOD13C1 V 006 MODIS 16 Day CMG 0.05 Degree (5.6 km) dataset, which provides NDVI measurements in 16-day composites. The mean NDVI value from each nonbreeding location + 200-km radius was extracted for each 16-day composite over which an individual occupied an area. To compare NDVI between departure and arrival sites, we retained the mean NDVI value for both sites from the composite that included the date of departure. We also calculated the change in NDVI from the previous 16-day period prior to departure to the 16-day period at the time of departure (ΔNDVI) at both departure and arrival sites. The change in NDVI estimates whether conditions were improving (positive ΔNDVI) or degrading (negative ΔNDVI) and the magnitude of the change, at both departure and arrival sites, in the 16 days before an individual left a departure site. Conditions throughout the nonbreeding range were, for the most part, declining during the period of these movements (mean ΔNDVI for departure and arrival sites = −0.02 ± 0.03 SD; Figure 2). To test whether Tree Swallows moved from "departure" sites to subsequent "arrival" sites with higher resource availability (as estimated by NDVI and ΔNDVI), we ran 2 general linear mixed effects models using the lme4 package in R (Bates et al. 2015) with NDVI and ΔNDVI as response variables,

TABLE 1. Summary of nonbreeding movements made by individual Tree Swallows from each of the 12 breeding sites and the flyway of each breeding site (Knight et al. 2018a). The proportion of individuals that made a nonbreeding movement from each population was calculated, along with the mean distance those individuals travelled (km) and the percent of movements that were southbound (between 90° and 270°).

Breeding site	Latitude (°N), Longitude (°W)	Flyway	Proportion moved (%)	Mean distance travelled (km) ± SD	Percent of southbound movements
Vancouver, BC	49.21, 123.18	Western	6/7 (86)	775 ± 271	63
Prince George, BC	53.85, 123.02	Western	7/11 (64)	714 ± 295	18
Fairbanks, AK	64.90, 147.70	Central	2/4 (50)	1,472 ± 65	100
Beaverhill, AB	53.40, 112.50	Central	11/23 (48)	1,230 ± 369	67
Saskatoon, SK	52.17, 106.10	Central	11/15 (73)	878 ± 487	65
Ames, IA	42.11, 93.59	Central	2/3 (67)	1,364 ± 155	67
Saukville, WI	43.40, 88.00	Eastern	4/6 (67)	808 ± 323	40
Boone, NC	36.21, 81.67	Eastern	0/6 (0)	NA	NA
Long Point, ON	42.62, 80.46	Eastern	6/23 (26)	689 ± 404	86
Ithaca, NY	42.50, 76.50	Eastern	3/9 (33)	556 ± 71	50
Sherbrooke, QC	45.55, 72.60	Eastern	2/16 (13)	393 ± 59	100
Wolfville, NS	45.10, 64.39	Eastern	5/10 (50)	623 ± 361	43

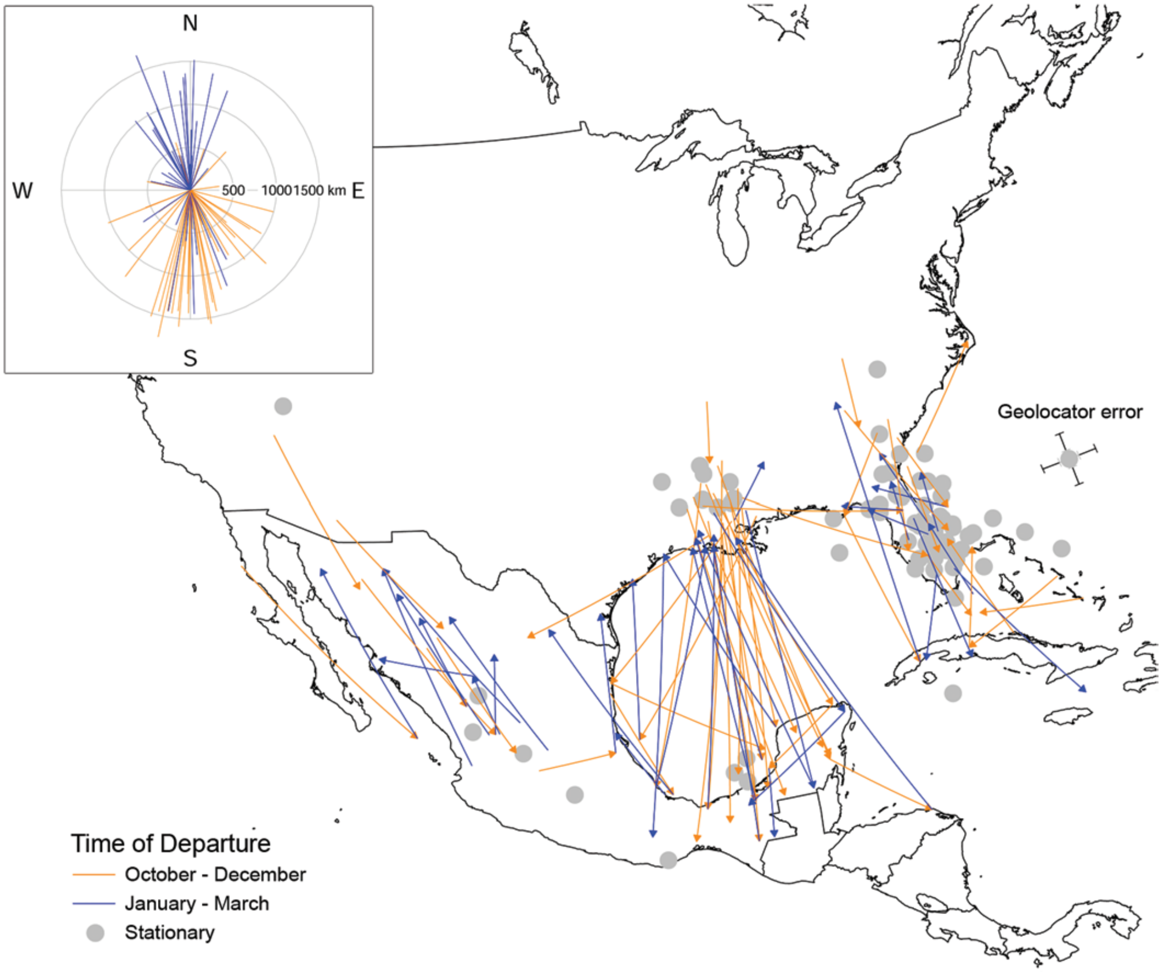

FIGURE 1. Stationary locations (gray dots) and nonbreeding movements of Tree Swallows (84 movements made by 59 individuals; 49 southbound and 35 northbound movements). Orange lines indicate movements that occurred between October and December and blue lines indicate movements that occurred between January and March. Inset compass shows the direction (degrees) and distance (km) of movements (lines are not to same scale as lines on map). Migration distance varied from 301 km to 1,744 km. Shown on the right, geolocator error was on average 46 km (gray bars) ± 90 km (SD; black bars) in latitude and 52 km (gray bars) ± 90 km (SD; black bars) in longitude.

respectively. Fixed effects included in both models were site (whether the response variable was measured at a "departure" or "arrival" site), season (autumn: Oct–Dec or winter: Jan–Mar), individual sex, year (2011–2014), and an interaction between site and season. Individual identity was included as a random effect. Results are reported as parameter estimates ± SE and 95% confidence intervals that do not overlap zero were used to determine parameter significance.

Given that temperature influences resource (insect) availability for aerial insectivores (Taylor 1963, McCarty and Winkler 1999, Winkler et al. 2013), we also compared minimum, mean, and maximum temperatures between departure and arrival sites. North American Regional Reanalysis (NARR) temperature data were obtained from the NOAA Earth System Research Laboratory (https://www.esrl.noaa.gov/psd/data/). These data had a grid resolution of approximately 0.3° (32 km) and were based off air temperature measurements taken every 3 hr at 2 m from the surface of the ground. Minimum, mean, and maximum temperatures were extracted for each nonbreeding area (location + 200-km radius). We ran 3 general linear mixed effects models (Bates et al. 2015) with minimum, mean, and maximum temperature the week prior to departure as the response variables, respectively, and the same fixed and random effects as the NDVI models outlined above. Results are reported as parameter estimates ± SE and 95% confidence intervals that do not overlap zero were used to determine parameter significance.

We also tested several determinants and consequences of itinerancy. First, we used a binomial generalized linear model to test the effect of the date of arrival and latitude

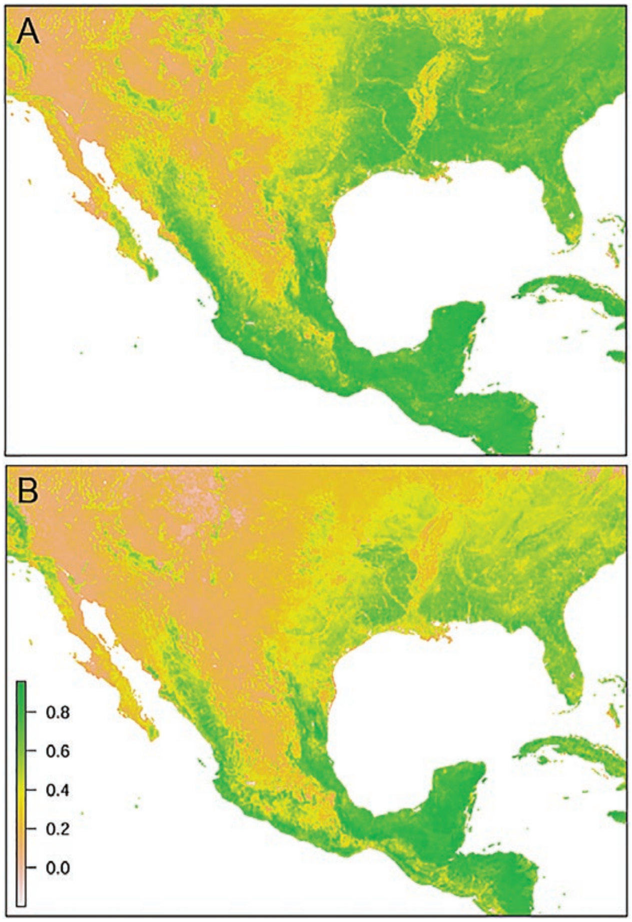

FIGURE 2. NDVI values from (**A**) October 2014 and (**B**) January 2015 in southern North America, where Tree Swallows are located in the nonbreeding season. NDVI values ranging from 0 to 1 indicate increasing primary productivity. Values below zero indicate ice or water.

at the first (or only) nonbreeding site on the probability of making a nonbreeding movement. The response variable was whether an individual made a subsequent nonbreeding movement or not and the predictor variables were nonbreeding arrival date, latitude, and longitude of the arrival site. To determine if there was a potential cost to making a nonbreeding movement, we used a general linear model with spring arrival date as the response variable. The predictor variables were whether an individual made a nonbreeding movement or not (binary) and breeding latitude. All results are presented as parameter estimates ± SE.

RESULTS

Of the individuals tracked, 44% (59/133) made at least 1 nonbreeding season movement, 17% (22/133) made at least 2 nonbreeding season movements, and 2% (3/133) made 3 movements. Overall, movements ranged from 301 to 1,744 km between nonbreeding sites (mean = 886 km, SD = 430 km). Between mid-October and mid-March, there were 49 southbound movements (between 90° and 270°) and 35 northbound movements (0–90° and 270–360°; Figure 1). The majority of southbound movements were between October and December (41/49; 84%), whereas the majority of northbound movements were between January and March (30/35; 86%), resulting in a significant difference in the direction of movement between seasons compared to a null expectation of 50:50 ratio (chi-square test: $\chi^2 = 39.68$, df = 1, $P < 0.001$). Among individuals where the sex was known ($n = 129$), there was no evidence that movements to another nonbreeding site were sex-biased (28/70 females moved, 29/59 males moved; chi-square test: $\chi^2 = 1.09$, df = 1, $P = 0.30$) or that the direction of movement differed between sexes (16/41 movements by females were northbound, 17/43 movements by males were northbound; chi-square test: $\chi^2 = 0.002$, df = 1, $P = 0.96$).

The proportion of individuals that made a nonbreeding movement, mean distance travelled, and the percent of southbound movements are summarized by breeding population (Table 1). The proportion of individuals that made a nonbreeding movement was significantly different among flyways (LRT, df = 2, $\chi^2 = 16.36$, $P < 0.001$). The highest proportion of individuals that made a nonbreeding movement was from the western flyway (mean = 0.75 ± 0.16), followed by individuals in the central flyway (mean = 0.59 ± 0.13) and individuals in the eastern flyway (mean = 0.31 ± 0.24).

When individuals moved among nonbreeding sites, they generally went from lower- to higher-quality sites (Figures 3, 4). NDVI (Table 2), ΔNDVI (Table 3), minimum temperature (Table 4), mean temperature (Table 5), and maximum temperature (Table 6) were all significantly higher at arrival sites than departure sites. However, the interaction between site and season in the NDVI, minimum temperature, mean temperature, and maximum temperature models suggested that these results were primarily driven by effects of these environmental variables on autumn movements, not winter movements. In contrast, for ΔNDVI, there was no significant interaction between site and season, suggesting that the higher ΔNDVI at arrival sites was consistent between seasons. There was no significant difference in any of the environmental variables measured between sexes. Year had a significant effect on NDVI, minimum temperature, and mean temperature.

Arrival date at the nonbreeding grounds and latitude were not significant predictors of whether an individual made a subsequent nonbreeding movement (Table 7). However, there was a significant negative effect of longitude on the frequency of nonbreeding movements, meaning that there was a higher frequency of movements in the western portion of the nonbreeding range compared to the east. There was no significant effect of whether an

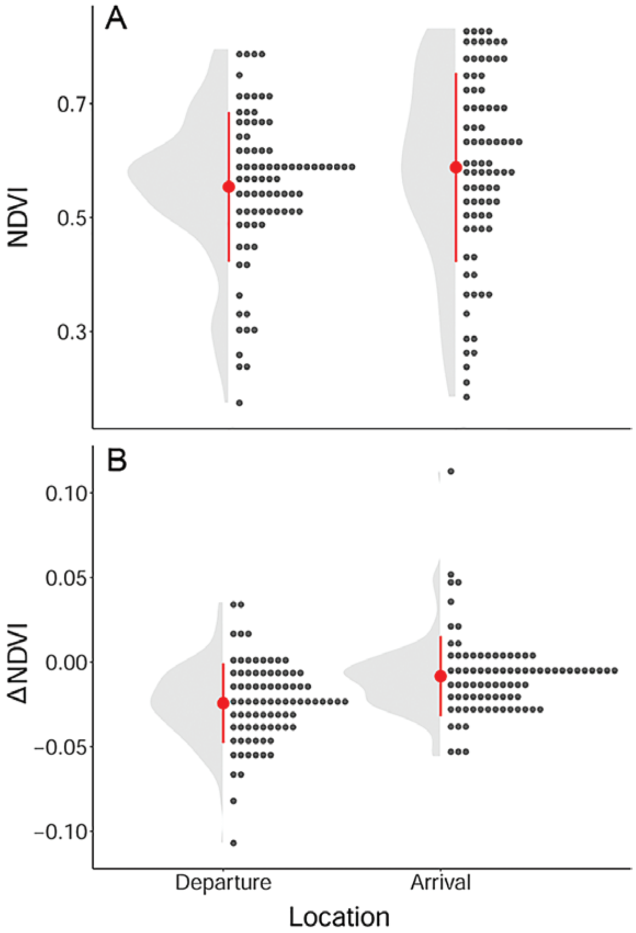

FIGURE 3. Split violin and dot plots (displaying individual observations) with mean ± SD showing (**A**) the difference in NDVI between departure and arrival sites, (**B**) the difference in ΔNDVI (from the previous NDVI value to the NDVI value at the time of departure) between departure and arrival sites of Tree Swallows.

individual made a nonbreeding movement on spring arrival date, when accounting for breeding latitude (Table 8).

DISCUSSION

Itinerancy of Tree Swallows was partial, with nearly half (44%) of the Tree Swallows tracked in this study having made at least one large-scale nonbreeding movement. Most of the southern movements were in the autumn and the northern movements in the winter, although all movements were among nonbreeding areas where other individuals stayed throughout the nonbreeding season (Figure 1). Following movement, individuals remained at these sites for 2 weeks to several months. The proportion of individuals that moved from each flyway varied, with populations in the western flyway having the highest proportion of individuals moving around western Mexico, followed by an intermediate proportion of individuals from the central flyway making nonbreeding movements around the Gulf of Mexico, and the fewest movements made by populations in the eastern flyway around Florida and the Caribbean. This was consistent with the frequency

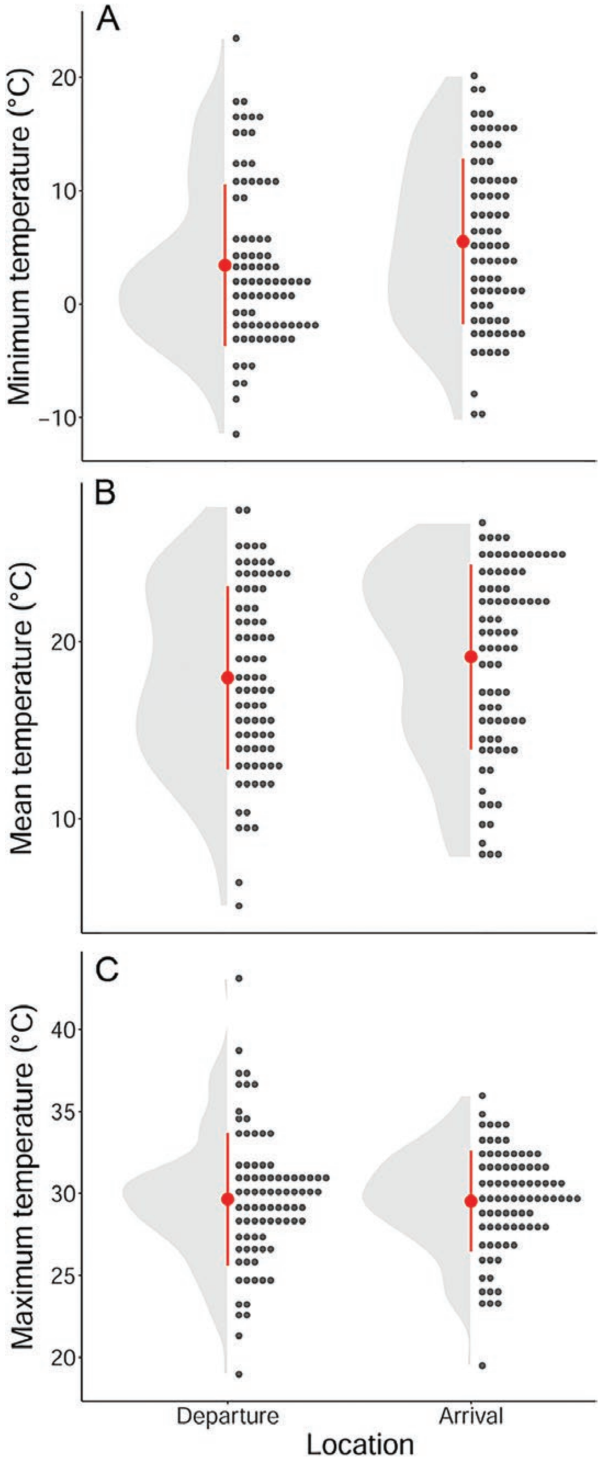

FIGURE 4. Split violin and dot plots (displaying individual observations) with mean ± SD showing (**A**) the difference in minimum temperature between departure and arrival sites, (**B**) the difference in mean temperature between departure and arrival sites, and (**C**) the difference in maximum temperature between departure and arrival sites of Tree Swallows.

TABLE 2. Model summary of parameter estimates from a general linear mixed effects model explaining NDVI based on whether the location of Tree Swallows was a departure or arrival site, season (Autumn: Oct–Dec or Winter: Jan–Mar), individual sex, year, and individual identity (random effect). The intercept represents the NDVI predicted at departure sites during the autumn of 2011.

Parameter	Estimate ± SE	*t* value	95% CI	SD
Random effect				
Individual ID				0.08
Fixed effects				
Intercept*	0.59 ± 0.03	20.85	0.54, 0.65	
Site (Arrival)*	0.11 ± 0.02	5.58	0.07, 0.15	
Season (Winter)	−0.01 ± 0.02	−0.39	−0.06, 0.04	
Sex (Male)	−0.02 ± 0.03	−0.91	−0.07, 0.03	
Start year (2012)*	−0.09 ± 0.03	−2.71	−0.15, −0.03	
Start year (2013)*	0.08 ± 0.04	1.97	0.003, 0.15	
Start year (2014)*	−0.12 ± 0.04	−3.05	−0.19, −0.04	
Site (Arrival): Season(Winter)*	−0.16 ± 0.03	−5.44	−0.22, −0.10	

*Represents parameters with 95% CIs that do not overlap zero.

TABLE 3. Model summary of parameter estimates from a general linear mixed effects model explaining the difference in ΔNDVI (from the previous NDVI value to the NDVI value at the time of departure) based on whether the location of Tree Swallows was a departure or arrival site, season (Autumn: Oct–Dec or Winter: Jan–Mar), individual sex, year, and individual identity (random effect). The intercept represents the NDVI predicted at departure sites during the autumn of 2011.

Parameter	Estimate ± SE	*t* value	95% CI	SD
Random effect				
Individual ID				1.10×10^{-09}
Fixed effects				
Intercept*	−0.03 ± 0.004	−6.64	−0.04, −0.02	
Site (Arrival)*	0.02 ± 0.005	3.98	0.01, 0.03	
Season (Winter)*	0.02 ± 0.005	3.90	0.01, 0.03	
Sex (Male)	−0.001 ± 0.003	−0.36	−0.008, 0.005	
Start year (2012)	−0.006 ± 0.004	−1.46	−0.01, 0.002	
Start year (2013)	−0.005 ± 0.005	−1.00	−0.02, 0.005	
Start year (2014)	−0.007 ± 0.005	−1.38	−0.02, 0.003	
Site (Arrival): Season(Winter)	−0.004 ± 0.006	−0.74	−0.02, 0.008	

*Represents parameters with 95% CIs that do not overlap zero.

of itinerancy decreasing with increasing nonbreeding longitude, although there was no effect of nonbreeding latitude. The highest frequency of itinerancy occurring in western Mexico suggests that resource availability likely plays a major role in driving nonbreeding movements of Tree Swallows because primary productivity was relatively low in this region compared to the rest of the nonbreeding range (Figure 2). Similar results of itinerant movements away from dry areas with low productivity have been observed in Great Reed Warblers (*Acrocephalus arundinaceus*; Koleček et al. 2018).

Individuals that moved appeared to be tracking resources, as suggested by their movement to nonbreeding sites with higher indices of resource availability. First, at the time of departure, NDVI was higher at arrival sites than at departure sites, although this trend was only driven by movements in the autumn. In contrast, the change in resource availability (ΔNDVI) was higher at arrival sites than at departure sites in both the autumn and the winter. In late autumn and winter, when movements occurred, habitat quality was generally deteriorating throughout the nonbreeding range (Figure 2), and our results suggest that Tree Swallows moved to areas with conditions that were declining less rapidly or even improving. A similar pattern of avoiding declining conditions has been observed in other species, such as the Bobolink (*Dolichonyx oryzivorus*; Renfrew et al. 2013) and Montagu's Harrier (*Circus pygargus*; Trierweiler et al. 2013). For Tree Swallows, an extreme example of avoiding declining conditions occurred with individuals ($n = 8$) that left southern Mexico and Central America in late winter for Louisiana and Texas. These individuals arrived at areas with lower absolute resource availability (as measured by NDVI), but generally improving conditions (positive ΔNDVI), unlike

TABLE 4. Model summary of parameter estimates from a general linear mixed effects model explaining minimum temperature based on whether the location of Tree Swallows was a departure or arrival site, season (Autumn: Oct–Dec or Winter: Jan–Mar), individual sex, year, and individual identity (random effect). The intercept represents the NDVI predicted at departure sites during the autumn of 2011.

Parameter	Estimate ± SE	*t* value	95% CI	SD
Random effect				
Individual ID				2.38
Fixed effects				
Intercept*	2.66 ± 1.36	1.95	0.08, 5.28	
Site (Arrival)*	6.97 ± 1.28	5.46	4.48, 9.46	
Season (Winter)*	3.71 ± 1.40	2.66	0.98, 6.39	
Sex (Male)	−1.86 ± 1.15	−1.62	−4.02, 0.31	
Start year (2012)	−1.59 ± 1.44	−1.10	−4.32, 1.13	
Start year (2013)	−0.78 ± 1.72	0.45	−2.48, 4.03	
Start year (2014)*	−2.51 ± 1.65	−1.52	−5.63, −0.62	
Site (Arrival): Season(Winter)*	−9.90 ± 1.86	−5.31	−13.53, −6.26	

*Represents parameters with 95% CIs that do not overlap zero.

TABLE 5. Model summary of parameter estimates from a general linear mixed effects model explaining mean temperature based on whether the location was a departure or arrival site of Tree Swallows, season (Autumn: Oct–Dec or Winter: Jan–Mar), individual sex, year, and individual identity (random effect). The intercept represents the NDVI predicted at departure sites during the autumn of 2011.

Parameter	Estimate ± SE	*t* value	95% CI	SD
Random effect				
Individual ID				2.56
Fixed effects				
Intercept*	17.75 ± 1.02	17.39	15.82, 19.71	
Site (Arrival)*	4.95 ± 0.81	6.08	3.36, 6.54	
Season (Winter)*	2.87 ± 0.93	3.07	1.01, 4.65	
Sex (Male)	−0.91 ± 0.92	−0.99	−2.66, 0.83	
Start year (2012)	−1.81 ± 1.15	−1.56	−3.99, 0.38	
Start year (2013)	−0.003 ± 1.38	−0.002	−2.62, 2.61	
Start year (2014)*	−3.66 ± 1.31	−2.79	−6.15, −1.17	
Site (Arrival): Season(Winter)*	−7.85 ± 1.19	−6.61	−10.17, −5.53	

*Represents parameters with 95% CIs that do not overlap zero.

the deteriorating conditions in eastern Mexico at the time of departure (negative ΔNDVI). More commonly, however, individuals moved to sites with conditions that were still declining (negative ΔNDVI), but less rapidly than at departure sites.

Although declining resource availability (ΔNDVI) appears to be the environmental variable that best explains movement throughout the nonbreeding season, we did also detect temperature differences between arrival and departure sites. Temperature (by all measures) tended to be higher at arrival sites (min: 8.4°C, mean: 21.6°C, max: 30.5°C) than departure sites (min: 2.2°C, mean: 17.0°C, max: 29.0°C) in autumn, but not in winter. This suggests that the differences in temperature were largely driven by southern movements to warmer areas, which were more frequent in autumn, while northern movements often coincided with decreasing temperatures. This finding provides some additional support for the resource-availability hypothesis in autumn because aerial insects, the main food source for Tree Swallows, are typically grounded at low temperatures (Taylor 1963, McCarty and Winkler 1999, Winkler et al. 2013), lowering resource availability.

While our results suggest Tree Swallows move to track resources throughout the nonbreeding range, competition avoidance may also play a role in driving these movements. There was no significant difference in the arrival date at the nonbreeding grounds between individuals that moved and individuals that remained stationary, suggesting that better competitors do not arrive earlier and force later-arriving individuals to move. There was also no bias toward either sex in the proportion of individuals that made a movement. However, less than half of the individuals tracked made large-scale movements and several individuals remained in the same areas from which others had departed, withstanding presumably less favorable conditions than individuals that moved. Tree Swallows

TABLE 6. Model summary of parameter estimates from a general linear mixed effects model explaining maximum temperature based on whether the location was a departure or arrival site of Tree Swallows, season (Autumn: Oct–Dec or Winter: Jan–Mar), year, and individual identity (random effect). The intercept represents the NDVI predicted at departure sites during the autumn of 2011.

Parameter	Estimate ± SE	*t* value	95% CI	SD
Random effect				
Individual ID				1.62
Fixed effects				
Intercept*	28.89 ± 0.78	37.13	27.42, 30.39	
Site (Arrival)*	1.60 ± 0.69	2.32	0.25, 2.94	
Season (Winter)*	1.63 ± 0.77	2.13	0.09, 3.09	
Sex (Male)	0.06 ± 0.67	0.08	−1.22, 1.34	
Start year (2012)	−0.32 ± 0.85	−0.37	−1.92, 1.29	
Start year (2013)	0.85 ± 1.01	0.84	−1.06, 2.76	
Start year (2014)	−1.10 ± 0.97	−1.14	−2.94, 0.73	
Site (Arrival): Season(Winter)*	−3.71 ± 1.00	−3.70	−5.67, −1.75	

*Represents parameters with 95% CIs that do not overlap zero.

TABLE 7. Model summary of parameter estimates from a binomial generalized linear model explaining whether an individual Tree Swallow moved or not based on the arrival date at the first (or only) nonbreeding site, latitude, and longitude at that nonbreeding site.

Parameter	Estimate ± SE	*z* value	*P*
Intercept	−3.77 ± 5.70	−0.66	0.51
Nonbreeding arrival date	−0.02 ± 0.01	−1.67	0.10
Nonbreeding latitude	−0.08 ± 0.05	1.39	0.16
Nonbreeding longitude	−0.09 ± 0.03	−3.58	<0.001

gather in large roosts during the nonbreeding season (Winkler 2006, Laughlin et al. 2013) and it may be the case that these habitats cannot support such high densities of swallows, even if they are able to persist on bayberries when insects are scarce (Piland and Winkler 2015). Either poor competitors are forced out regardless of their arrival date or some individuals choose to risk the energetic and mortality costs of moving to another nonbreeding site for the benefit of higher resource availability. Given that nonbreeding movements did not carry over to influence breeding arrival date, which would likely alter egg laying dates (Gow et al. 2019) and subsequent reproductive success (Shutler et al. 2006, Dunn et al. 2011), there does not appear to be a disadvantage to either strategy in terms of reproductive success. However, because we did not compare body condition between individuals that moved and those that were stationary, we cannot speak to how either strategy influenced physical condition upon arrival at the breeding grounds.

Results from this study are in contrast to previous studies on Nearctic–Neotropical migrants, where species that are known to track resources in the nonbreeding season have demonstrated complete itinerancy. For example, Bobolinks originating from 3 different breeding populations all made synchronized nonbreeding movements as they tracked resources in South America (Renfrew et al. 2013). In other species where itinerancy is complete, it is also suspected that changes in resource availability play an important role (Jahn et al. 2013, Heckscher et al. 2015). These species are predominantly frugivorous and granivorous, foraging on resources that are patchy in distribution across both time and space (Jahn et al. 2013, Renfrew et al. 2013). In contrast, Purple Martins (*Progne subis*) are aerial insectivores that roost in large aggregations similar to those of Tree Swallows and have demonstrated partial itinerancy (Stutchbury et al. 2016). They do not appear to track resources, but rather are more likely cued by increasing roost density (Stutchbury et al. 2016). Tree Swallows feed on both aerial insects and bayberries during the nonbreeding season, in addition to wintering farther north where more dramatic seasonal shifts in resources occur. This may explain why Tree Swallows that moved appeared to be tracking resources as do other frugivores, but also how roosting behavior could have facilitated competition avoidance and may have been a factor in the decision to move. Unfortunately, we can only speculate, because we could not directly measure roost density.

There were several additional limitations to our study. First, we did not measure NDVI or temperature at nonbreeding sites where individuals were stationary, so we cannot say how resource availability influenced the decision to move. We could only make inferences about individuals that had already made the decision to move. Second, while geolocators provide an opportunity to advance our

TABLE 8. Model summary of parameter estimates from a general linear model explaining spring arrival date of Tree Swallows based on whether the individual made a nonbreeding movement and breeding latitude.

Parameter	Estimate ± SE	*t* value	*P*
Intercept	72.01 ± 8.47	5.50	<0.001
Nonbreeding movement (Yes)	3.38 ± 2.08	1.63	0.11
Breeding latitude	0.89 ± 0.18	4.92	<0.001

understanding of bird migration (reviewed in Knight and Norris 2016, McKinnon and Love 2018), the spatial resolution limits our ability to detect smaller-scale itinerant movements (e.g., Smith et al. 2011). In addition, due to the archival nature of geolocators, we only studied individuals that survived the nonbreeding season, missing important information about whether nonbreeding movements influence survival. We also had insufficient data to make comparisons of body condition between individuals that moved and those that remained stationary. Future research will be important for determining whether survival or body condition are influenced by different nonbreeding strategies.

Implications for Conservation of Migrants

Effective conservation of declining migratory species requires information about how populations are connected between seasons. Such information is essential for building predictive models to understand how habitat loss in a given region in one season will influence populations across their range (Taylor and Norris 2010, Taylor and Stutchbury 2016). Nonbreeding movements further complicate migratory networks, particularly when movements are partial and asynchronous. As itinerancy is increasingly documented in songbirds, it is evident that many species may have more complex movement dynamics than previously thought, and yet we lack this information for most migratory species.

Over the past few decades, environmental change has influenced the timing of events during the annual cycle in birds (Dunn and Winkler 1999, Jenni and Kéry 2003, Jonzén et al. 2006) and current migration schedules may be poorly timed with future seasonal resource availability under various climate change scenarios (Thorup et al. 2017). It remains to be determined how well individuals will be able to adjust their behavior to match these environmental changes, as well as how subsequent changes in the frequency of itinerancy could influence body condition and survival. For Tree Swallows that appear to use changing environmental conditions as a cue to seek sites with higher resource availability, it is possible that changes in temperature or rainfall, along with expected increases of extreme weather events (Cai et al. 2014), could alter the timing and frequency of nonbreeding movements. In addition, habitat loss occurring throughout the nonbreeding range of Tree Swallows may result in more nonbreeding movements to compensate for increasing density of Tree Swallows in remaining habitat patches. It appears Tree Swallows may already be adjusting to changes in habitat, because many individuals departed Louisiana around the time that their sugar cane roosting habitat was being harvested (Laughlin et al. 2013). Further, because these nonbreeding movements were not complete and appear to be driven by shifting environmental conditions, Tree Swallows may be well suited to adapt the timing and frequency of their movements in response to environmental change (Dodge et al. 2014).

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†This author is deceased.

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