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INTEGRATING INFORMATION FROM GEOLOCATORS, WEATHER RADAR, AND CITIZEN SCIENCE TO UNCOVER A KEY STOPOVER AREA OF AN AERIAL INSECTIVORE

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Abstract.—Determining the distribution of stopover and overwintering areas of migratory animals is essential for understanding population dynamics and building predictive models. Tree Swallows (*Tachycineta bicolor*) are small songbirds that breed across North America. Data from Doppler weather radar and eBird indicate that Tree Swallow numbers increase throughout October and November in southeastern Louisiana, but then decrease during December. We thus hypothesized that southeastern Louisiana is a stopover area used by Tree Swallows during fall migration before they move to farther overwintering areas. We tested this hypothesis by attaching light-logging geolocators to Tree Swallows at five breeding sites spanning the species' breeding range from British Columbia to Nova Scotia, and then tracking their fall migration routes, stopover sites, and wintering locations. Of 38 individuals that returned in the following breeding season, 11 birds from three breeding sites (Saskatchewan, Wisconsin, and Ontario) used southeastern Louisiana as a stopover site. Arrival date and duration of stay closely matched observations from both eBird and radar data. From Louisiana, most Tree Swallows continued their migration to one of three wintering sites: peninsular Florida, the Bahamas, or the Yucatán Peninsula, whereas two birds remained until spring within 200 km of the stopover area. Our results (1) suggest that southeastern Louisiana is an extended stopover site for Tree Swallows that originate from a wide geographic range on the breeding grounds; and (2) demonstrate how geolocators, combined with other sources of movement information, reveal habitat use throughout the annual cycle. *Received 5 December 2012, accepted 20 February 2013.*

Key words: annual cycle, habitat use, migration, stopover sites, *Tachycineta bicolor*, Tree Swallow.

Integración de Información de Geolocalizadores, Radares de Clima y Ciencia Ciudadana para Descubrir un Área de Parada Migratoria Clave de un Insectívoro Aéreo

Resumen.—Determinar la distribución de áreas de parada e invernada de los animales migratorios es esencial para comprender su dinámica poblaciona y para la construcción de modelos predictivos. *Tachycineta bicolor* es un ave canora pequeña que se reproduce a través de Norte América. Los datos de radares climáticos Doppler y de eBird indican que los números de *T. bicolor* aumentan durante octubre y noviembre en el sureste de Luisiana, pero luego disminuyen durante diciembre. Planteamos la hipótesis de que el sureste de Luisiana es un área de parada usada por *T. bicolor* durante la migración de otoño, antes de moverse hacia sitios de invernada más lejanos. Evaluamos esta hipótesis por medio de geolocalizadores livianos acoplados a individuos de *T. bicolor* en

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cinco áreas de reproducción que comprenden toda el área de distribución reproductiva de la especie, desde Columbia Británica hasta Nueva Escocia, y rastreamos su ruta migratoria, sitios de parada y localidades de invernada. De 38 individuos que regresaron en la siguiente temporada reproductiva, 11 aves de tres sitios de reproducción (Saskatchewan, Wisconsin y Ontario) usaron el sureste de Luisiana como sitio de parada. La fecha de llegada y la duración de su estadía correspondieron de cerca con las observaciones de eBird y de los radares. Desde Luisiana, la mayoría de individuos continuó su migración hacia uno de tres sitios de invernada: la península de Florida, las Bahamas o la península de Yucatán, mientras que dos aves permanecieron a menos de 200 km del área de parada hasta la primavera. Nuestros resultados sugieren que el sureste de Luisiana es un sitio de parada extendida para individuos de *T. bicolor* provenientes de un área geográfica amplia de la distribución reproductiva de la especie, y demuestran cómo los geolocalizadores, combinados con otras fuentes de información sobre el movimiento, permiten conocer el uso del hábitat a través del ciclo anual.

Understanding factors that influence population dynamics of migratory organisms requires knowledge of habitat use and movements throughout the annual cycle (Sherry and Holmes 1995, Norris and Marra 2007, Faaborg et al. 2010). Most studies describing migratory connectivity have focused on connecting breeding areas with primary overwintering sites (e.g., Chamberlain et al. 1997, Hobson and Wassenaar 1997, Kelly et al. 2005, Boulet et al. 2006, Norris et al. 2006). However, many migrant birds move between two or more stopover sites during their autumn and spring migrations (Moore 2000), and determining locations of stopover sites is a critical step for both conservation (Mehlman et al. 2005) and building population models to predict how migratory animals will respond to environmental change (Warnock et al. 2004, Sheehy et al. 2011).

For most small-bodied birds, we have information on use of stopover sites from only a limited number of long-term banding sites (e.g., Fransson et al. 2005, Priestley et al. 2010, D. F. DeSante et al. unpubl. data). Identifying stopover sites can be challenging because of the difficulty of directly tracking individuals during migration. Furthermore, determining whether stopover sites are used by multiple breeding or nonbreeding populations requires information on movements across a species' range. Recent advances in light-logging geolocators make it possible to follow daily movements of individuals throughout the annual cycle (e.g., Stutchbury et al. 2009, Bairlein et al. 2012, Fraser et al. 2012), providing opportunities for identifying stopover sites and estimating how many breeding or nonbreeding populations use these sites during migration.

Tree Swallows are small (~20 g) migratory birds that breed throughout much of North America (Winkler et al. 2011). Shortly after breeding, individuals aggregate in large nocturnal roosts that form near breeding grounds (Burney 2002, D. R. Norris et al. unpubl. data). After 1 to 2 months, individuals migrate south to their wintering grounds, located along the Atlantic and Gulf coasts of southeastern North America, Mexico, Central America, and the Caribbean (Winkler et al. 2011), where they also form roosts, some of which contain well over 1 million birds (Burney 2002). However, direct linkages among specific breeding, stopover, and wintering areas, as well as details of migration phenology, are unknown in Tree Swallows and most other songbird species.

Here, we use citizen science (eBird) records and weather radar to show that Tree Swallows arrive in the lower Mississippi Valley in southeastern Louisiana en masse in October and November, use abundant sugarcane fields as roosting habitat, and then appear to significantly decrease in number after the sugarcane harvest, migrating out of the area toward their main overwintering sites. On the basis of these observations, we examine the hypothesis that southeastern Louisiana is used primarily as a stopover site by Tree Swallows before individuals continue toward overwintering sites. An alternative explanation is that Tree Swallows do not actually leave southeastern Louisiana, but that the sugarcane harvest forces Tree Swallows to disperse to smaller roosts that are not readily visible on radar. To examine these hypotheses, we attached light-level geolocators to birds at five breeding sites across North America to track their fall migration routes, stopover sites, and wintering locations.

Methods

Locating Tree Swallow roosts using NEXRAD Doppler weather radar.—Our study area in southeastern Louisiana for both radar and eBird data is a circle with a radius of 175 km centered near Slidell, Louisiana, at the KLIX Doppler weather radar station (30°20′N, 89°49′W). This circle covers all of southeastern Louisiana and much of southern Mississippi (Fig. 1A). We chose 175 km radius as the cutoff because large swallow roosts are less easily detectable on radar beyond that distance. The United States has 159 WSR-88D radar stations throughout the country, continuously scanning the aerosphere for precipitation patterns. Birds, bats, and insects are often also detected in radar data (Kunz et al. 2008, Chilson et al. 2012a). The WSR-88D program was introduced in the early 1990s, and these data are archived and freely available online from the National Climatic Data Center (see Acknowledgments). In the nonbreeding season, many swallow species ascend at dawn from their nocturnal roosts in large numbers into the aerosphere. Large swallow and martin roosts appear on morning Doppler weather radar as "ring-echoes," an annulus (or semi-annulus) of pixels that expands with each successive sweep of the radar beam (Fig. 1A–C; Russell and Gauthreaux 1998, Winkler 2007). Roost-rings expand until either birds descend below the altitude detected by radar or the density of birds becomes too low for detection by the radar beam.

We downloaded WSR-88D Doppler weather data from the National Climatic Data Center for station KLIX in Slidell, Louisiana, from October 2011 through April 2012. We scanned radar data visually each morning during the hour following local sunrise and noted suspected Tree Swallow roosts within the study area. Locations, habitat, and species composition for most of these roosts were verified by visiting the roosts. Although we did not visit each roost in person, roosts that were not visited displayed the roost-ring structure on radar that is diagnostic of Tree Swallows (i.e., speed of departure and shape of roost-ring) and were located in typical roosting habitat (*Phragmites* reed beds) known on the basis of eBird data to attract numerous Tree Swallows. For

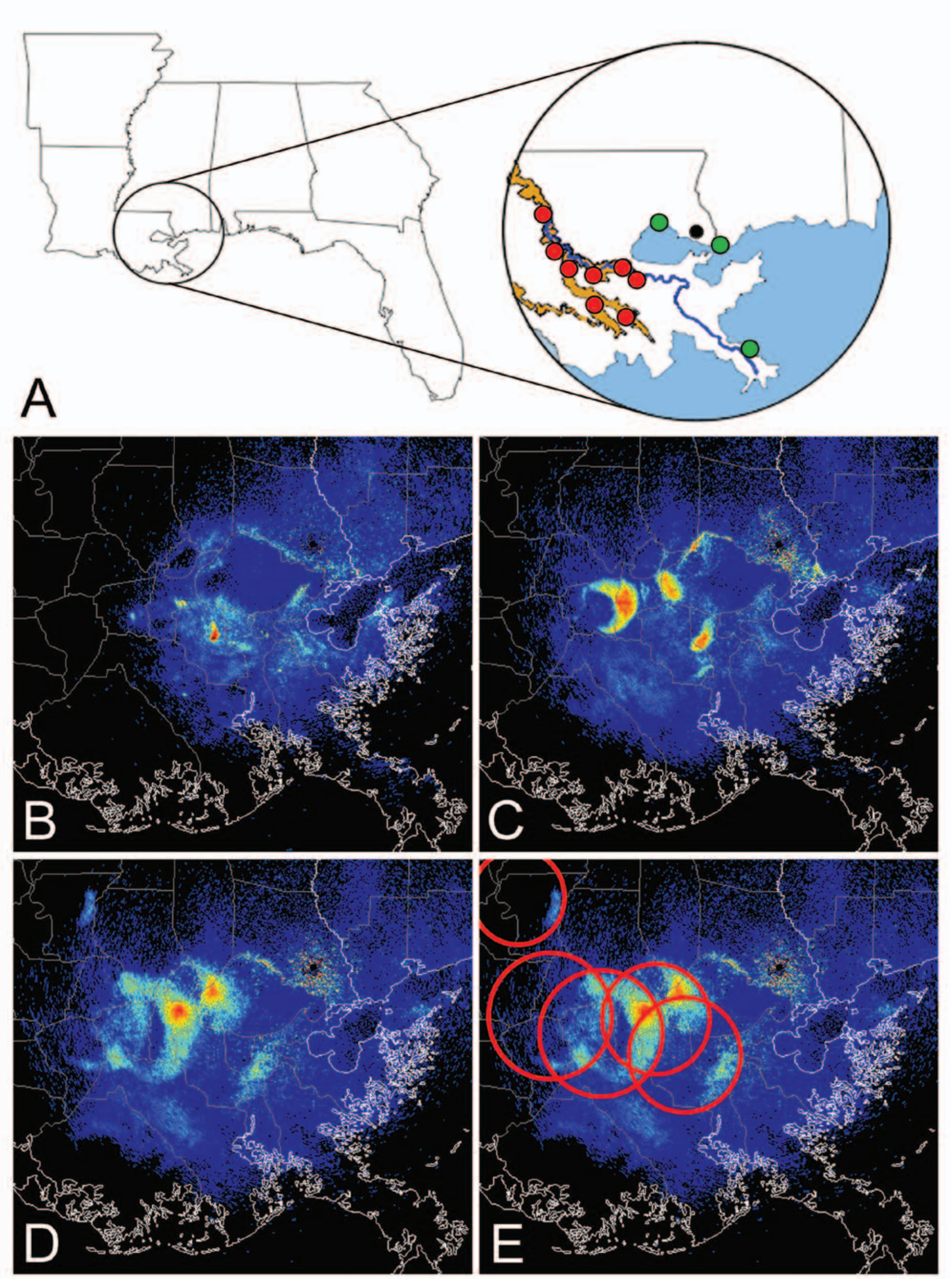

FIG. 1. (A) Map showing study area in Louisiana. Black circle is study area for radar and eBird data: a circle of radius 175 km centered at KLIX radar station near Slidell, Louisiana (black dot at center of circle). Red dots are sugarcane roosts, green dots are wetland roosts, blue line is Mississippi River, and brown area is approximate extent of sugarcane production in study area. (B–E) Example of successive Doppler radar images from station KLIX on 1 November 2010 in the hour following local sunrise. (B–D) Emergence and subsequent expansion of five Tree Swallow roosts (successive panels are ~20 min apart). (E) The same scan as panel D, but showing the manually added circles over roosts from which we calculated roost radii. Roosts are (from west to east) Baton Rouge, Plattenville, Vacherie, Edgard, and Luling.

each radar scan in which a roost-ring appeared, we drew a circle around the roost annulus (or semicircle) using a Web-based application (developed by D.R.S.). The application automatically calculates the radius, latitude, and longitude of the center of each roost-ring. Although estimating numbers of birds within Doppler weather-radar scans remains problematic (Russell and Gauthreaux 1998; but see Chilson et al. 2012b), we used the maximum detectable radius of the expanding roost rings as an index that is positively related to roost size. However, we do not yet understand the precise relationship between roost size and maximum radius, which may be nonlinear. For each roost, we calculated the maximum detectable radius, and for each day that roosts appeared, we summed the maximum detectable radii of all roosts.

Estimating bird distribution using eBird records.—eBird is a citizen-science-based program run jointly by the National Audubon Society and the Cornell Lab of Ornithology that collects bird observations. eBird is a repository of tens of millions of bird sightings submitted by birders around the world (Wood et al. 2011), and millions of new observations are submitted every month. Thus, this resource reflects spatial and temporal patterns of the distribution and abundance of birds. We downloaded eBird data from the Avian Knowledge Network (see Acknowledgments) from 2006–2011 for the same study area from which we analyzed radar data. We calculated the proportion of eBird reports submitted each day that included Tree Swallows, a value we refer to as "frequency." Following Hurlbert and Liang (2012), we used frequency of Tree Swallow reports rather than abundance of Tree Swallows to reduce bias that may be introduced by the sighting of extremely large roosts. For example, an observer visiting a large roost site in the morning or evening may submit an observation of 1 million Tree Swallows, whereas an observer in the same area of more dispersed foraging birds during the day may report much smaller numbers. A linear regression of frequency of Tree Swallow reports versus total number of reports ($r^2 < 0.01$, $F = 1.1$, df = 1 and 211, $P = 0.30$) verified that the total number of reports submitted to eBird does not influence the frequency of Tree Swallow observations within those reports.

Geolocators.—In summer 2011, we deployed geolocators (Lotek Wireless model MK12-S, with 10-mm light stalk) on adult Tree Swallows ($n = 177$) at five breeding sites across North America: Wolfville, Nova Scotia (45°6′N, 64°21′W; $n = 30$); Long Point, Ontario (42°39′N, 80°26′W; $n = 33$); Saukville, Wisconsin (43°23′N, 88°01′W; $n = 35$); Saskatoon, Saskatchewan (52°13′N, 106°04′W; $n = 40$); and Prince George, British Columbia (53°50′N, 122°57′W; $n = 39$). We attached geolocators with a modified leg-loop backpack harness (Stutchbury et al. 2009), which had a combined mass of ≤1.0 g (<5% of body mass). Prior to deployment, we calibrated each geolocator in two distinct phases. Static (off-bird) calibration was used to identify changes in light sensitivity between the two periods before deployment and after retrieval the following year. For these calibration periods, we placed geolocators on the roof of a building near the deployment site at Long Point, Ontario, and away from artificial light for 7 days in early June 2011 and again in July 2012. Using a light threshold value of 5 on the arbitrary scale of 0 to 64 used in BASTRACK software (British Antarctic Survey [BAS], Cambridge, United Kingdom), we determined that there were similar average sun elevation angles for the two periods (–5.38° pre-deployment, –5.34° post-retrieval). After geolocators were deployed on birds, we performed dynamic on-bird calibration for each bird for the period after nesting and before migration when birds were still at or near their known breeding location but no longer using nest boxes (mean duration ± SD = 17 ± 6 days). The start of migration is defined here as a pronounced movement of ≥100 km from the breeding site that resulted in another location in the same direction the next day. Sun angle values determined in this way more accurately reflected conditions during deployment by accounting for potential shading effects caused by a bird's behavior (Fudickar et al. 2012, Lisovski et al. 2012). We considered calibration on the breeding grounds (shortly after breeding) to be sufficient for the entire annual cycle because Tree Swallows generally roost in *Typha* marshes in both the breeding (Dunn and Whittingham 2005; but for western populations, see Hayes and Cohen 1987) and nonbreeding season (present study). We used each geolocator-specific sun angle determined during dynamic calibration to plot estimated locations using BIRD TRACKER (BAS). On-bird sun angles ranged from –4.05° to –5.34° and resulted in a mismatch with true breeding locations by an average 50.6 ± 22 km in latitude (range: 11–98 km) and 55.2 ± 29 km in longitude (range: 24–99 km). Geolocator positions during this period were accurate to within an average distance of 81.7 ± 24 km.

Following visual inspection of twilight transitions in TRANSEDIT (BAS) to remove obvious outliers caused by unusual shading events or behavior, we used live-calibration sun angles calculated for each geolocator to estimate birds' latitude and longitude using midnight locations. Because estimating latitude is problematic during the equinox periods, when day length is equal at all latitudes, we excluded 15 days on either side of the equinoxes (as in Fraser et al. 2012). To determine location probabilities (e.g., Bächler et al. 2010) during the main stopover and overwintering locations, we used the KDE and Isopleth commands in the Geospatial Modeling Environment (Beyer 2012) to produce 50% and 95% kernel density estimates.

Results

Radar and eBird.—The summed daily radii of all Tree Swallow roosts located on Doppler radar from October 2011 to April 2012 increased throughout October, peaked in mid-November, began to decrease in December, and remained low throughout the rest of the study period. October through December 2011 is the period in which eight roosts were located in sugarcane fields along the lower Mississippi Valley (Table 1 and Figs. 2 and 3). By the end of December, sugarcane had been completely removed. Figure 2

Table 1. Location and duration of all Tree Swallow roosts as seen on Doppler weather radar station KLIX, Slidell, Louisiana, October 2011–April 2012.

Roost name	Location (latitude, longitude)	Habitat	Start date	End date	Duration (days)
Edgard	30.03, –90.53	Sugarcane field	11-Oct	20-Dec	70
Vacherie	29.97, –90.80	Sugarcane field	12-Oct	9-Dec	58
Luling	29.94, –90.39	Sugarcane field	12-Oct	20-Dec	69
Lockport	29.62, –90.49	Sugarcane field	14-Oct	9-Dec	56
Thibodeaux	29.73, –90.80	Sugarcane field	17-Oct	11-Nov	25
Plattenville	30.02, –91.02	Sugarcane field	17-Oct	30-Nov	44
Iberville	30.17, –91.16	Sugarcane field	17-Oct	18-Nov	32
Baton Rouge	30.48, –91.27	Sugarcane field	17-Oct	5-Nov	19
Pearl River S.	30.22, –89.59	Wetland	5-Nov, 29-Feb [a]	20-Nov, 16-Mar [a]	15, 17 [a]
N. Pontchartrain	30.39, –90.17	Wetland	28-Dec	21-Feb	56
Miss. Delta	29.36, –89.30	Wetland	9-Jan	20-Apr	101

[a] Roost appeared in November 2011, dissolved, and formed again in February 2012.

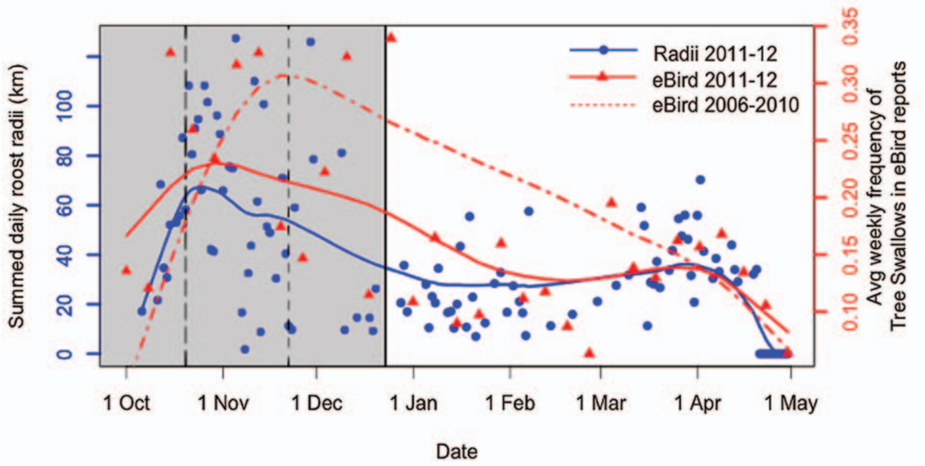

FIG. 2. Daily summed roost-ring maximum radii (left *y*-axis, blue circles) and averaged weekly frequency of eBird reports that contain Tree Swallows (right *y*-axis, red triangles), and their associated smoothing curves, October 2011–April 2012. Dashed red curve represents averaged daily eBird frequency of Tree Swallow reports for October–April, 2006–2010, on the same right *y*-axis scale. Shaded area represents duration of sugarcane roosts; roosts in the nonshaded area are in wetlands. Long-dashed vertical line represents mean arrival date for Tree Swallows with geolocators (20 October), and short-dashed vertical line is mean departure date for Tree Swallows with geolocators (22 November).

shows a vertical bar at 23 December, after which no sugarcane roosts appeared on radar, and both roost radii and eBird frequencies decreased.

To correlate the arrival and departure of geolocator-bearing birds with changes in the aggregate number of Tree Swallow roosts detected on radar, we fitted logistic curves to changes in the numbers of Tree Swallow roosts as seen on Doppler radar from October through December. The curves were fitted using the glm function in the stats-package of the R programming language by specifying a binomial distribution and a logit link (R Development Core Team 2011). From these curves, calculated separately for increase and decrease in roost numbers, we calculated the 90th percentiles of curves as arrival and departure windows, respectively. We calculated inflection points of arrival and departure curves to estimate mean arrival and departure dates from radar data and compared these to mean dates from geolocator birds. Mean arrival and departure dates from radar were 17 October and 29 November, respectively. Arrival and departure windows were 6–28 October and 31 October–29 December, respectively.

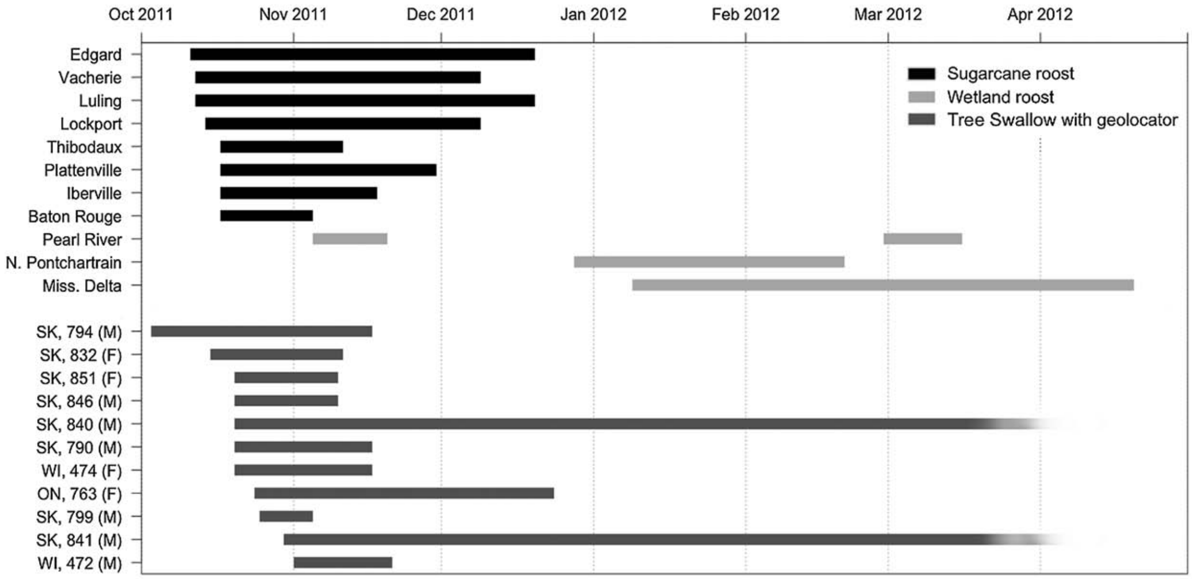

FIG. 3. Timeline showing the location and duration of Tree Swallow roosts that appeared on NEXRAD radar station KLIX in Slidell, Louisiana, October 2011–April 2012 (black bars are sugarcane roosts, light gray bars are wetland roosts), and the breeding-ground origin (SK = Saskatoon, Saskatchewan; WI = Saukville, Wisconsin; ON = Long Point, Ontario), geolocator number, sex, and approximate arrival, duration, and departure date of Tree Swallows fitted with geolocators that stopped over in southeastern Louisiana in 2011. The spring departure dates of two birds were masked by the equinox and are here faded to reflect this uncertainty.

Table 2. Timing and onward migration distances of Tree Swallows using southeastern Louisiana as a late-fall stopover site in fall 2011 (SK = Saskatoon, Saskatchewan; WI = Saukville, Wisconsin; ON = Long Point, Ontario).

				Southeast Louisiana				
Band number	British Antarctic Survey geolocator number	Sex	Breeding site	Arrival date	Departure date	Stopover duration (days)	Wintering region	Distance from Louisiana to main wintering site (km)
2321-10994	794	M	SK	4-Oct [a]	18-Nov	45a	Yucatan	1202
2321-10851	832	F	SK	16-Oct	12-Nov	27	Yucatan	974
1851-75491	474	F	WI	21-Oct	18-Nov	28	Eastern Mexico	1359 [b]
2351-32559	790	M	SK	21-Oct	18-Nov	28	Yucatan	1342
1671-55771	840	M	SK	21-Oct [a]	15-Apr [a]	177 [a]	Southern USA	125
2321-11763	846	M	SK	21-Oct	11-Nov	21	Eastern Mexico	1386
2321-11377	851	F	SK	21-Oct	11-Nov	21	Eastern Mexico	1360
2311-93640	763	F	ON	25-Oct	25-Dec	61	Eastern Mexico	1255
2321-10896	799	M	SK	26-Oct	6-Nov	11	Bahamas	1226
2351-32201	841	M	SK	31-Oct [a]	15-Apr [a]	167 [a]	Southern USA	204
1831-01663	472	M	WI	2-Nov	22-Nov	20	Florida	930

[a] Date influenced by effect of latitude estimates close to equinox (see text for further details).

[b] Winter location shifted north by sensor shading. See text for further explanation.

The proportion of total eBird reports that include Tree Swallows (Tree Swallow frequency) also increased sharply during October 2011, peaked in early November 2011, and began to steadily decrease throughout the rest of the winter and into spring (mean [± SD] number of reports submitted per week = 206 ± 72; Fig. 2). Averaged weekly frequency of Tree Swallow reports for 5 years (2006–2010; mean number of reports submitted per week = 348 ± 91) also shows a similar pattern of a peak in late October and early November and a gradual decline throughout the rest of winter (Fig. 2, dashed red line), which suggests that 2011–2012 was not an atypical year for eBird reports. Radar and eBird data were positively correlated (Pearson's $r = 0.43$, $t = 5.0$, df = 114, $P < 0.001$).

Geolocators.—We retrieved 38 geolocators (21%) in 2012 from the five deployment sites (Table 2): 2 of 39 from British Columbia; 11 of 40 from Saskatchewan; 6 of 35 from Wisconsin; 13 of 33 from Ontario; and 6 of 30 from Nova Scotia. Of the 38 Tree Swallows that returned with geolocators (Fig. 4), 11 (29%) spent some time in southeastern Louisiana during early winter before moving to their main overwintering site. These birds originated from three breeding sites: 8 of 11 (73%) from Saskatchewan, 2 of 6 (33%) from Wisconsin, and 1 of 13 (8%) from Ontario. Excluding one bird whose arrival date was masked by the equinox, mean (± SD) arrival date to Louisiana was 20 October ± 5 days, and mean departure date was 22 November ± 18 days (Fig. 3). Eight of the 11 birds that used southeastern Louisiana arrived within the 6–28 October arrival window as calculated from the radar data, and the mean arrival date for birds with geolocators was 3 days earlier than the mean arrival date estimated from radar.

Nine of 11 birds departed Louisiana during the sugarcane roost departure window, and the mean departure date of birds with geolocators was 7 days earlier than the departure date estimated from radar. These nine birds left Louisiana destined for three distinct overwintering regions in the Yucatán Peninsula, Mexico ($n = 7$), peninsular Florida ($n = 1$), and the Bahamas ($n = 1$; Fig. 5). For four birds whose mean estimated winter position was over water, we chose the nearest location on land (mean difference ± SD = 79 ± 47 km). For one bird whose mean winter location was located >200 km over the Gulf of Mexico, we chose the nearest point on land to the south. We made this decision even though the Texas coast was closer because unusual sensor shading between the autumn and spring equinoxes is known to artificially increase latitude estimates in the Northern Hemisphere (Lisovski et al. 2012). Mean distance traveled to wintering locations after stopping over in Louisiana was 1,225 ± 168 km.

Two male birds (geolocator nos. 840 and 841; Fig. 5) remained within 230 km of the stopover area for the rest of the winter. We did not include these birds in the calculation of mean departure date from the geolocator data. One bird moved slightly northeast

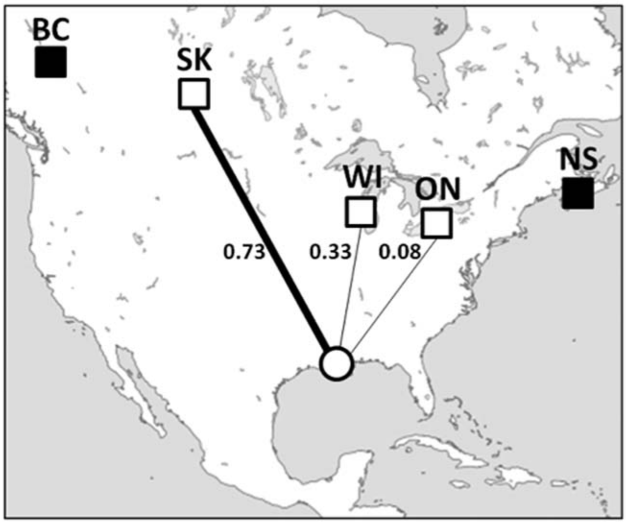

Fig. 4. Map showing the breeding sites (SK = Saskatoon, Saskatchewan; WI = Saukville, Wisconsin; ON = Long Point, Ontario; hollow squares) of Tree Swallows fitted with geolocators that staged in southeastern Louisiana (hollow circle). For two of the breeding sites (BC = Prince George, British Columbia; NS = Wolfville, Nova Scotia; black squares), none of the individuals traveled through Louisiana during fall migration. Numbers represent the proportion of individuals from each breeding site that staged in southeastern Louisiana, and the thickness of the connecting lines is proportional to the percentage of all geolocator-fitted birds that staged in southeastern Louisiana.

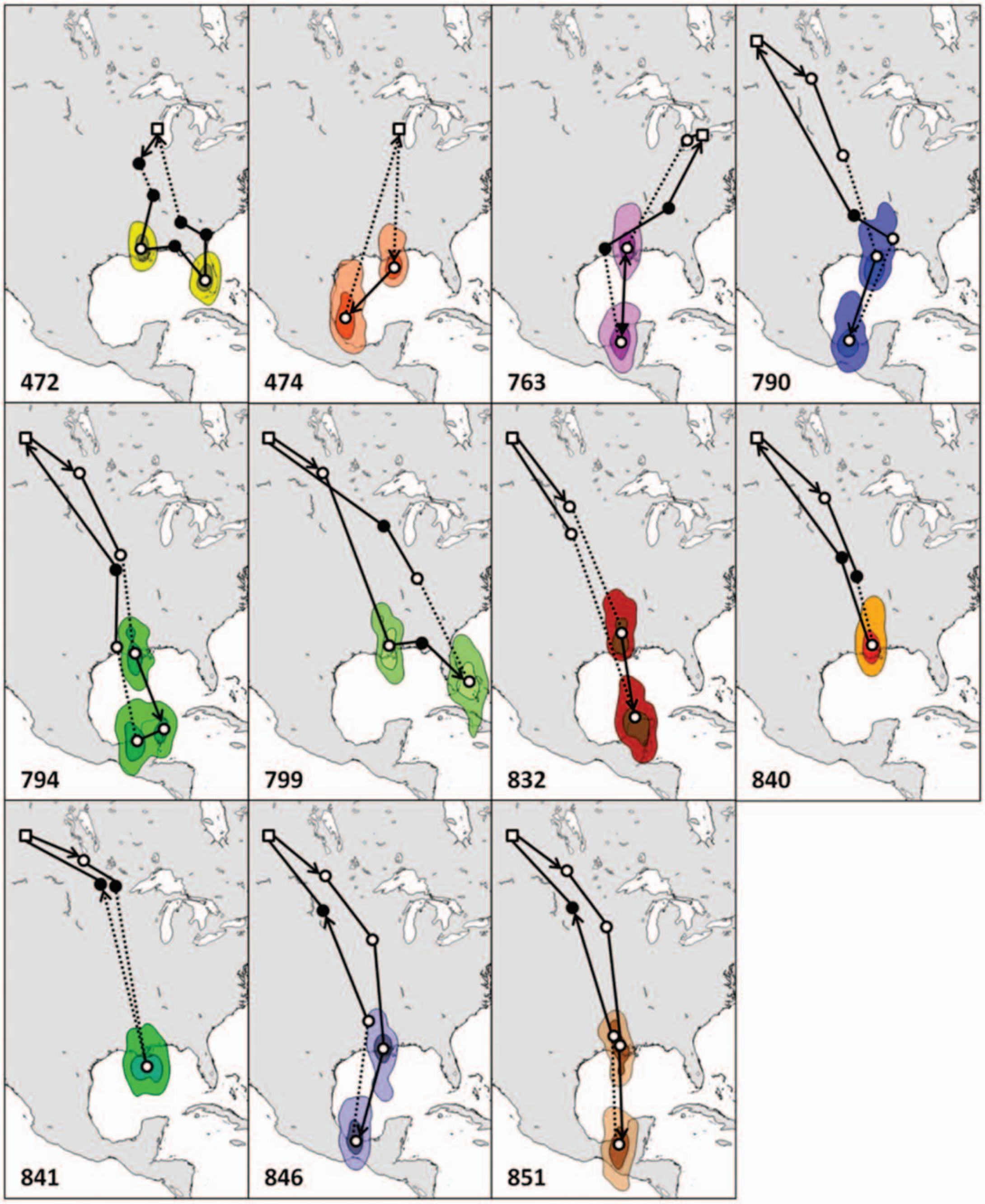

FIG. 5. Maps showing migration routes and kernel density polygons of stopover and overwintering locations for all 11 Tree Swallows that used southeastern Louisiana as a stopover area during fall migration in 2011. Each panel represents a single individual with 95% kernel density polygons located within 50% kernel density polygons in each stopover and wintering period. Migration routes are presented as solid lines, with dotted lines representing gaps in location estimates due to equinox periods. Hollow dots represent mean locations where birds remained for >7 days, solid dots represent single locations to illustrate the route taken, hollow squares represent breeding sites (as in Fig. 4), and numbers refer to geolocator numbers (as in Table 2).

from the study area, and the departure date of the other bird was difficult to estimate. This was due to consistency in longitude estimates combined with latitude-masking caused by the equinox. The other 27 of 38 Tree Swallows did not travel to southeastern Louisiana as a stopover site, and instead used other stopover sites closer to their breeding origin before migrating to their overwintering areas (D. R. Norris et al. unpubl. data).

DISCUSSION

Our study demonstrates how data from geolocators can be used to examine hypotheses about habitat use in a period of the annual cycle that is extremely challenging to study. From citizen-science and radar observations, we generated the hypothesis that southeastern Louisiana is used as stopover site by Tree Swallows during fall migration. Our geolocator data largely supported this hypothesis: most of the Tree Swallows with geolocators that went through Louisiana arrived by the beginning of November, and most left by the middle of November and into early December (Fig. 3). Our results also suggest that southeastern Louisiana is used as a stopover area by several breeding populations of Tree Swallows across North America, and as an overwintering site by some individuals, before the birds continue on to a variety of primary overwintering areas.

This area of the northern Gulf coast, which is the southern end of the Mississippi Flyway, is used by many species of migratory birds as an autumn stopover, most notably Neotropical migrants that are preparing for a trans-Gulf flight to Central America (Able 1972, Moore 2000). The large number of Tree Swallows that use southeastern Louisiana each autumn suggests that this area is an important stopover site during fall migration of this species, but the significance of this region for annual-cycle processes is not yet fully understood. As more tracking data are becoming available for migratory birds, it is clear that migration strategies can be complex, composed of previously unknown major stopover sites (present study) and even multiple wintering areas (e.g., Stach et al. 2012).

Stopover sites can be used for many reasons, including molt or refueling for the migration itself (Warnock 2010). Most adult Tree Swallows captured in the study area in late October and November have already completed molt (A. J. Laughlin et al. unpubl. data), supporting previous claims that Tree Swallows complete prebasic molt prior to, and in some cases during, their journey southward (Stutchbury and Rohwer 1990). Therefore, this area is not used as a molting area before heading toward the final wintering areas. It is possible that southeastern Louisiana is a stopover area to accumulate fat reserves for crossing the Gulf of Mexico, as is the case for many other Neotropical migrant species. However, these stopover bouts typically last <1 week (Woodrey and Moore 1997). Tree Swallows with geolocators stayed, on average, 32 days in southeastern Louisiana. Birds that crossed the Gulf to the Yucatan appeared to have done so in <1 day, whereas birds that migrated on toward Florida appeared to have done so over land. It does not seem likely, therefore, that Tree Swallows would require a month to gain fat reserves before these flights.

Another, not mutually exclusive, possibility is that sugarcane fields provide a high-quality roosting habitat in an area that has lost >5,000 km^2 of wetlands over the past century (Couvillion et al. 2011). It is perhaps not coincidental that the departure of Tree Swallows with geolocators is concurrent with gradual harvest of sugarcane fields that cover >1,600 km^2 statewide and mature around the time when southbound Tree Swallows arrive. When Tree Swallows arrive each fall, the sugarcane crop is at its full height (~4 m) and covers an almost continuous area along the banks of the lower Mississippi River. Sugarcane harvest usually begins in early November, in many places at once, and lasts for nearly 2 months, creating a checkerboard pattern of available roosting habitat that gradually disappears until the crop is completely removed. Numbers of Tree Swallows in sugarcane roosts appear to decrease as harvest continues, and, although it is difficult to quantify, roosts of well over 1 million birds decrease to the tens of thousands near the end of harvest (A. J. Laughlin et al. unpubl. data). From a stopover perspective, it appears that the sugarcane fields are used as stopover habitat for Tree Swallows from October through December, and wetland areas are used as overwintering habitat for birds that remain. In spring, radar and eBird data suggest another influx of Tree Swallows on their northward migration (Fig. 2). Only wetland roosts are used during this period because the sugarcane has not yet grown to sufficient height for roosting by Tree Swallows.

Does the sugarcane harvest drive most Tree Swallows out of southeastern Louisiana, or could it be that a gradual decrease in winter temperatures also suppresses the local food supply of flying insects? A complex combination of factors is most likely. Anecdotal evidence for this question comes from the New Orleans journal of John James Audubon, who in October of 1822 wrote extensively of the "white-bellied" swallows that were abundant during October, but seen throughout the winter months only in warmer winters (Audubon 1929). This suggests that the pattern of a large number of Tree Swallows funneling through the southern end of the Mississippi Flyway each autumn may not be a recent phenomenon. It is important to note, however, that some Tree Swallows remain in the area and use southeastern Louisiana as their main overwintering site after the sugarcane harvest, as two of the birds with geolocators did (Fig. 3). It is difficult to quantify how many Tree Swallows remain in the area, but Tree Swallow roosts form in wetland areas after harvest (and are large enough to show up on the stationary NEXRAD radar stations), and Tree Swallows remain an important part of the area's avifauna throughout the winter.

We combined three independent sources of data to discover a key autumn stopover area for several widely separated populations of Tree Swallows. To our knowledge, ours is the first study to combine citizen-science data (eBird) with Doppler radar data to discover a potential spatiotemporal pattern in the abundance of birds. We then used an individual tracking device that tested and provided strong evidence for our hypothesis about the southeastern Louisiana stopover area. Combining multiple sources of data enables us to test hypotheses about habitat-use patterns throughout the annual cycle. Our results suggest that southeastern Louisiana is likely a key stopover site for migratory Tree Swallows from central North America. Removal or degradation of this site would, therefore, likely influence multiple breeding and nonbreeding populations (Sheehy et al. 2011), which could have knock-on effects for the entire migratory network of this species (Taylor and Norris 2010).

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