

Constructing and evaluating a continent-wide migratory songbird network across the annual cycle

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Abstract. Determining how migratory animals are spatially connected between breeding and non-breeding periods is essential for predicting the effects of environmental change and for developing optimal conservation strategies. Yet, despite recent advances in tracking technology, we lack comprehensive information on the spatial structure of migratory networks across a species' range, particularly for small-bodied, long-distance migratory animals. We constructed a migratory network for a songbird and used network-based metrics to characterize the spatial structure and prioritize regions for conservation. The network was constructed using year-round movements derived from 133 archival light-level geolocators attached to Tree Swallows (*Tachycineta bicolor*) originating from 12 breeding sites across their North American breeding range. From these breeding sites, we identified 10 autumn stopover nodes (regions) in North America, 13 non-breeding nodes located around the Gulf of Mexico, Mexico, Florida, and the Caribbean, and 136 unique edges (migratory routes) connecting nodes. We found strong migratory connectivity between breeding and autumn stopover sites and moderate migratory connectivity between the breeding and non-breeding sites. We identified three distinct "communities" of nodes that corresponded to western, central, and eastern North American flyways. Several regions were important for maintaining network connectivity, with South Florida and Louisiana as the top ranked non-breeding nodes and the Midwest as the top ranked stopover node. We show that migratory songbird networks can have both a high degree of mixing between seasons yet still show regionally distinct migratory flyways. Such information will be crucial for accurately predicting factors that limit and regulate migratory songbirds throughout the annual cycle. Our study highlights how network-based metrics can be valuable for identifying overall network structure and prioritizing specific regions within a network for conserving a wide variety of migratory animals.

Key words: flyway; geolocator; migration; migratory connectivity; network theory; Tree Swallow.

INTRODUCTION

Each year, billions of animals from across the globe migrate between their breeding and non-breeding grounds (Brower 1996, Holland et al. 2006, Hahn et al. 2009, Harris et al. 2009, Wells 2011, Dingle 2014). Developing effective

conservation strategies for these species, many of which cross international borders, can present enormous challenges (Martin et al. 2007, Wilcove and Wikelski 2008, Runge et al. 2014). One challenge is describing patterns of individual movement between populations in different seasons of the annual cycle (Webster et al. 2002, Norris et al. 2006). Previous studies suggest that understanding such patterns of "migratory connectivity" is critical for predicting how migratory species respond to environmental change (Marra et al. 2006). For example, theoretical (Sutherland and Dolman 1994,

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Taylor and Norris 2010) and experimental laboratory (Betini et al. 2015) studies have shown that events, such as habitat loss, affecting a single population in one season can produce knock-on effects that reverberate throughout both the breeding and non-breeding ranges of a migratory species. Such range-wide effects imply that predicting factors that limit and regulate populations, as well as making decisions about how to allocate limited conservation resources, should incorporate information on how populations are connected between different periods of the annual cycle (Martin et al. 2007).

For small-bodied organisms, such as songbirds (typically <50 g), only recently have individuals been directly followed over the course of an entire year. Developments in the use of archival light-level geolocators (Stutchbury et al. 2009) and, more recently, archival GPS tags (Hallworth and Marra 2015), have created the possibility of describing patterns of range-wide connectivity for small migratory animals (Bridge et al. 2013, McKinnon et al. 2013, Knight and Norris 2016). Geocator-based studies have documented migratory patterns in a variety of songbirds (Ryder et al. 2011, Cormier et al. 2013, Finch et al. 2015, Hallworth et al. 2015, Koleček et al. 2016, Ouweland et al. 2016), as well as highlighted some remarkable journeys (Bairlein et al. 2012, DeLuca et al. 2015). However, few studies have described migratory connectivity across a species' range, or have covered all major regions across a species' range (Fraser et al. 2012, Stanley et al. 2015, Hobson et al. 2015). Furthermore, even fewer have capitalized on this information to make inferences about the relative importance of different regions or populations on the breeding and non-breeding grounds (Rushing et al. 2016, Taylor and Stutchbury 2016).

One approach that can be used to describe and evaluate patterns of network connectivity and regions connected by migratory routes is network theory (Taylor and Norris 2010). A network is described as a graph, which is composed of *nodes* that are connected by *edges* (Urban and Keitt 2001). Network theory has been applied in a wide variety of contexts, including studies on social networks (Scott 2012), metabolic networks (Guimera and Amaral 2005), transportation networks (Guimera et al. 2005), and electrical circuits (Ferrer i Cancho et al. 2001). Recently, there has also been an increase in the use of network theory in landscape ecology, most commonly for modelling metapopulations (Urban et al. 2009). One of the primary advantages of using network theory in landscape ecology is it can be used to identify the relative importance of habitat patches, represented by nodes, for maintaining habitat connectivity (Urban and Keitt 2001, Estrada and Bodin 2008). More advanced approaches have also combined elements of network theory with habitat or resource selection models (Dancose et al. 2011) to identify preferred corridors between habitat patches, particularly within fragmented landscapes (Decout et al. 2012, Proctor et al. 2015). Results using both basic network and more advanced approaches are valuable for predicting how populations will respond to landscape disturbance and for making better conservation decisions.

A recent application of network theory involves evaluating the importance of different areas used by migratory animals throughout the annual cycle. In a migratory network, nodes are the regions or populations within each season, and edges represent the migratory movements connecting nodes. Three

basic sets of nodes are represented in a migratory network: breeding nodes, non-breeding nodes (areas typically used during the non-breeding period for extended periods of time, excluding migration), and stopover nodes (temporary sites used during migration; Taylor and Norris 2010). A more complex approach involves developing population models within migratory networks that predict how migratory populations and connections within the network will respond to environmental change (Taylor and Stutchbury 2016, Taylor et al. 2016), and identifying the most important habitats and routes in a migratory network (Wiederholt et al. 2013). However, such models are data intensive because they require demographic information for each node and edge, which are usually unavailable for all nodes and, therefore, rely on several key assumptions (e.g., density dependence operating in the breeding and non-breeding season). Habitat suitability modeling has also been combined with a network approach in migratory populations (Poor et al. 2012), but this also requires additional information on habitat characteristics. In contrast, network-based metrics rely solely on the spatial structure of the network, although connections can be weighted to reflect differences in the use of nodes and edges (Calabrese and Fagan 2004, Minor and Urban 2007, Nicol et al. 2016). Thus, similar to metapopulation networks, there is potential for network theory to provide key insights into the dynamics and conservation of migratory animals. Despite this, to our knowledge, basic network metrics have only been applied once to migratory waterfowl (Buhnerkempe et al. 2016) and once to shorebirds (Iwamura et al. 2013), but never to songbirds: one of the most diverse and abundant migratory taxa in the world.

In this study, we describe a migratory network for a songbird, the Tree Swallow (*Tachycineta bicolor*), and use network metrics to describe the overall structure and evaluate the importance of regions for maintaining network connectivity. In doing so, we also provide insight into the stopover and non-breeding ecology of this species. By tracking individuals originating from 12 different breeding populations using archival light-level geolocators, our first goals were to describe how breeding populations were connected to non-breeding nodes and stopover nodes, and then quantify the overall strength of migratory connectivity in the network. Our next goal was to use network metrics to identify structure in the network in the form of migratory flyways. Butler (1988) proposed four likely migratory routes for Tree Swallows: the Atlantic coast, the Mississippi River drainage, the eastern slope of the Rocky Mountains, and the Pacific coast. Because of the spatial coverage of our geocator deployment, we predicted that we would identify the flyways along the Atlantic and Pacific coasts, and along the Mississippi River. Our final goal was to use network-based metrics to evaluate the relative importance of non-breeding and stopover nodes in the network, in terms of maintaining overall network connectivity.

METHODS

Study species

Tree Swallows are small (~20 g) songbirds that occupy open habitats, often near bodies of water (Winkler et al.

2011), where they forage for flying insects (Quinney and Ankney 1985, McCarty and Winkler 1999a). They have an extensive breeding distribution across northern and central North America where they nest in natural or previously excavated tree cavities (Dobkin et al. 1995) and nest boxes (Holt and Martin 1997, Lawler and Edwards Jr. 2002). Tree Swallows migrate in July or August shortly after the breeding season and roost in large flocks during migration, usually in cane and reed beds over water (Winkler 2006, Laughlin et al. 2013). They spend the non-breeding season primarily in Florida, along the Gulf of Mexico, Mexico, Central America, and the Caribbean, where they consume insects, as well as berries from bayberry trees (*Myrica* spp.).

Geolocator deployment and retrieval

Light-level geolocators are small archival devices that estimate the latitude and longitude of an animal by recording light levels periodically (every 2 or 10 min) in relation to an internal clock (Afanasyev 2004). Estimates of geographic location rely on geographic variation in the timing of sunrise and sunset (Hill 1994). Latitude is determined from day length and longitude from the time of the solar noon or midnight in relation to a standard clock. During the spring and autumn equinoxes, night and day length are approximately equal across latitudes, which increases the degree of uncertainty in estimates of latitude, but not in longitude. The archival nature of geolocators means the device must be retrieved to collect these data. The batteries typically last one year, but the batteries in some become completely discharged partway through the year, making those tracks incomplete.

Geolocators weighing 0.7–1.0 g were deployed at 12 breeding sites across the Tree Swallow breeding range (Fig. 1). Geolocators were attached to individuals weighing >20 g (representing <5% of their body mass) using a leg-loop harness (Rappole and Tipton 1991, Stutchbury et al. 2009) made of 1 mm diameter ethylenepropylene-diene rubber O-rings (O-Rings West, Seattle, Washington, USA). In total, 140 of the 561 geolocators (25%) deployed from 2010 to 2014 were retrieved the following year (Lotek Wireless model MK6440 in 2010 and 2011, MK6740 from 2012 to 2014, with a 10 mm stalk in all years; Table 1). An additional 35 geolocators developed by E. S. Bridge were deployed in Ithaca, New York, and 12 of these geolocators were recovered. Of the 152 total geolocators that were retrieved, 133 (83%) recorded light levels for the majority of deployment periods without any malfunctions and were used in this analysis. The data used in this study are available from the Movebank Data Repository (Knight et al. 2018).

Geolocator analysis

Light data downloaded from geolocators were converted to .lig files. Clock drift (where the geolocator's internal clock can shift away from the reference time throughout the deployment) was adjusted for using the Decompressor program in the BASTrak software package (Biotrack Limited, Wareham, UK 2013). Geolocator data were then analyzed using the BASTag package version 0.1.3 (Wotherspoon et al. 2013) and FLIGHTR package version 0.3.6 (Rakhimberdiev et al. 2015) in R version 3.2.3 (R Core Development Team

2015). The BASTag package was used to detect, delete, and edit twilight times by importing and visualizing the light data using the preprocessLight function. Light levels for M-series geolocators were recorded on a scale from 0 to 64, with zero being complete darkness and 64 being anything above a low level of sunlight (a truncated maximum), whereas the geolocators developed by E. S. Bridge recorded light levels on a scale from 0 to 127. Twilight times (sunrise and sunset) were defined as the time when the light level passed through a threshold of 2.5 for the M-series geolocators and 4.5 for the geolocators developed by E. S. Bridge. False twilight detections, such as light in the middle of the night or darkness in the middle of the day, were removed or the twilight time was adjusted to the appropriate time of sunrise/sunset based on the previous or following days. Twilight times that were unclear due to shading were also removed. Shading is characterized by light levels that fall and rise around the threshold as an individual moves in and out of shade (rather than a steady increase at sunrise and a steady decrease at sunset), as well as a twilight time that is not close to the twilight times of the previous and following days. Tree swallows are open area birds, thus there were very few instances of shading. We then used the FLIGHTR package, which uses a state-space hidden Markov model, to estimate locations from the geolocator data. Data were first calibrated to the known location (the breeding site) when the tag was on the bird at the beginning and end of deployment. Calibration was used to find the relationship between the measured and expected light levels at a given location, and the calibration parameters were then used to estimate the twice-daily locations. Discoloration of the clear casing around the light sensor over the course of deployment can bias the light measurements and was accounted for by assuming the change in the calibration slope from the beginning to the end of deployment was linear. Up to 15% of outliers in twilight times were then removed by FLIGHTR. Finally, using the particle filter algorithm (with 10^6 particles) in FLIGHTR, a spatial probability distribution was generated for each twilight time and used to compute the most probable track of each individual. We used the median location from the spatial probability distribution of each twilight in subsequent analyses.

There are two “behavioral states” in the FLIGHTR model that are defined by the distance of displacement of an individual between twilights. Individuals are considered in a “migrating state” when they move more than 45 km between twilights, whereas they are considered in a “sedentary state” when they move <45 km, as per the defaults of the FLIGHTR program. This behavioral model better accounts for migrating birds that stop for prolonged periods, punctuated by rapid migratory movements (Rakhimberdiev et al. 2015). We combined this behavioral model with a mask that allowed individuals to fly over water (any movement between twilights > 45 km), but not enter a sedentary state over water (any movement between twilights < 45 km). The spatial object used for the water mask did not perfectly outline the coast, so some location estimates were slightly offshore.

Network terminology

We constructed and analyzed the migratory network by adopting terminology from graph theory (Urban and Keitt

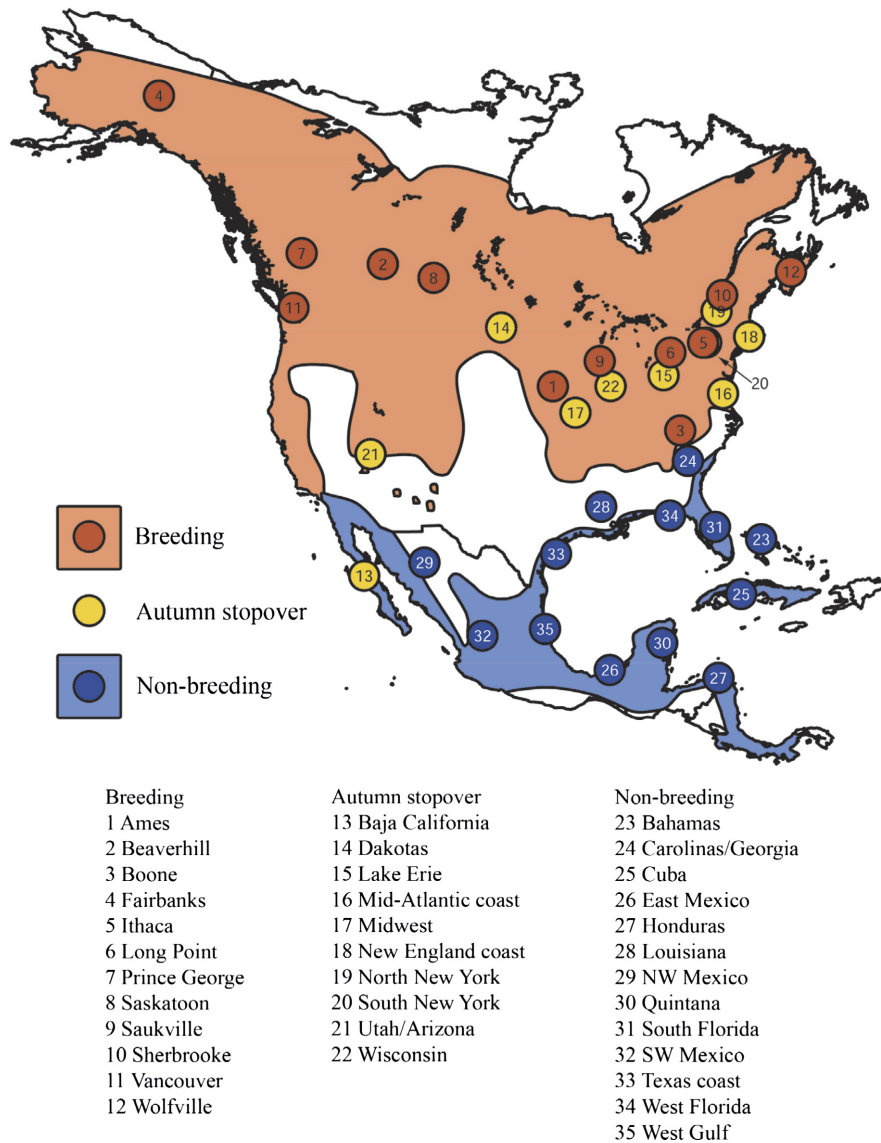


FIG. 1. Breeding (dark orange), autumn stopover (yellow), and non-breeding (dark blue) nodes, superimposed on a map showing the breeding (orange) and non-breeding (blue) ranges of Tree Swallows (BirdLife International and NatureServe 2015). Breeding nodes represent the 12 sites where geolocators were deployed, while the autumn stopover and non-breeding nodes represent locations determined through geolocator tracking and network analyses. The map is a World2Hires map (Becker and Wilks 1993) with an Albers Equal-Area projection. Breeding locations are listed in Table 1.

2001, Urban et al. 2009, Taylor and Norris 2010). Networks (or graphs) are composed of *nodes* that are connected by *edges*. In a migratory network, nodes can be considered regions or populations that are connected by migration (edges). Three sets of nodes are represented in this migratory network: breeding nodes, non-breeding nodes, and stopover nodes. A network is considered *directed* if movement along the edges (migration) is in one direction, such as the network we developed. Otherwise it is considered *undirected* if individuals migrate in both directions between a set of nodes. A *weighted* network has varying edge weight. For example, edges could be weighted by the number or proportion of individuals moving between nodes (as was done in this network), or the distance between nodes. A network is considered *connected* if every node in the network is, whether

biologically practical or not, reachable, either directly or indirectly, from another node. Therefore, a network may be made up of one or more *components*, depending on whether the entire network is connected or if some components are disconnected from the rest of the network. Nodes may also contain attributes. In our case, they contained geographic coordinates, but nodes may also contain information on demographics or habitat quality.

Defining elements of the network

To identify nodes in the network, we first defined individual stopover and non-breeding sites as the median location an individual occupied over the same general area for greater than two weeks. This cut-off was chosen because short

TABLE 1. Summary of 561 M-series geolocators deployed between 2010 and 2014 across 12 breeding sites and 35 E. S. Bridge geolocators deployed in 2011 in Ithaca, New York, USA.

Location	Province/State	Latitude (°N), longitude (°W)	Years geolocators deployed	Number of geolocators deployed	Number of geolocators retrieved
Fairbanks	Alaska	64.90, 147.70	2013	12	4
Vancouver	British Columbia	49.21, 123.18	2014	28	8
Prince George	British Columbia	53.85, 123.02	2011, 2012	64	12
Beaverhill	Alberta	53.40, 112.50	2013, 2014	70	24
Saskatoon	Saskatchewan	52.17, 106.10	2011, 2012	60	16
Ames	Iowa	42.11, 93.59	2012	15	4
Saukville	Wisconsin	43.40, 88.00	2011, 2012	55	6
Boone	North Carolina	36.21, 81.67	2014	30	6
Long Point	Ontario	42.62, 80.46	2010–2013	91	25
Ithaca	New York	42.50, 76.50	2011, 2012	60	17
Sherbrooke	Québec	45.55, 72.60	2012, 2014	51	18
Wolfville	Nova Scotia	45.10, 64.39	2011, 2012	60	12

Note: In total, 140 M-series and 12 E. S. Bridge geolocators were recovered.

stopovers are difficult to identify with the spatial resolution of geolocators. The points in these general areas were within a few degrees of longitude and latitude, depending on the quality of the track, but within up to several degrees of latitude around the equinox due to error in latitude estimates during that period. Non-breeding sites were defined as locations where at least one individual remained for greater than two weeks until initiating spring migration. However, many individuals occupied more than one non-breeding site during the non-breeding period and all non-breeding sites an individual occupied were included in the network. Autumn stopover sites were defined as locations between the breeding and non-breeding sites in which no individuals remained past the autumn (no later than November), meaning that spring migration to breeding sites was not initiated from these sites. Only one-half of the swallows (51%) made spring stopovers that were greater than two weeks (all individuals were likely stopping during spring migration but our resolution could not detect these short stopovers), so spring stopovers were not included in the network. Clusters of autumn stopover and non-breeding sites were grouped into nodes that represent larger geographic areas for network analysis (Appendix S1: Fig. S1). In some cases, nodes were used as both autumn stopovers by some individuals and non-breeding nodes by others and in these circumstances, we classified the node based on its dominant use (Appendix S1). Edges were defined as connections between pairs of nodes, through migration. To determine whether there were differences in the number of autumn stopover nodes and non-breeding nodes visited between breeding populations, these count data were analyzed using generalized linear models with a Poisson distribution (GLM, family Poisson), and there was no overdispersion in these data.

Describing the strength of migratory connectivity in the network

The most common method for quantifying the strength of migratory connectivity between seasons in songbirds is the Mantel test (Ambrosini et al. 2009, Cormier et al. 2013, Stanley et al. 2015, Finch et al. 2015, Hallworth and Marra 2015, Koleček et al. 2016), which measures the correlation

(r_M) between two matrices, each containing pairwise distances between all individuals in the network at two different periods of the annual cycle. However, this method does not account for uncertainty in geocator estimates. Cohen et al. (2017) recently developed a new metric, MC, which not only accounts for uncertainty in geocator estimates, but also accounts for sampling that is not proportional to abundance. MC uses transition probabilities between discrete regions rather than distance matrices between individuals to estimate a correlation coefficient. To estimate the strength of connectivity, we calculated both r_M and MC, which allowed us to directly compare these estimates while putting our estimates in the context of previous studies.

We calculated the Mantel correlation coefficient (r_M) between the breeding sites and autumn stopover sites, as well as between the breeding and non-breeding sites, using the location of both the first and final non-breeding sites that an individual visited during the non-breeding season (two non-breeding calculations). This was done because, based on our definitions, 59% of individuals visited multiple non-breeding sites. We also ran Mantel tests on “communities” defined by the network analysis (see definition and estimation of communities in *Network metrics* section) to determine how analyzing a subset of the species’ range influenced estimates of the strength of migratory connectivity. Using the *ade4* package in R (Dray and Dufour 2007), the r_M value was estimated and the P value was based on 10,000 random permutations between the two sets of sites. The randomization procedure was used because the distances between individuals in each matrix are not statistically independent. When the Mantel correlation coefficient, r_M , approaches one, there is a strong positive correlation between the two matrices, meaning that individuals that breed close together also tend to spend the other portion of the annual cycle close together (strong migratory connectivity). Conversely, a Mantel correlation coefficient of zero indicates that individuals that breed close together disperse during subsequent periods of the annual cycle, resulting in extensive mixing between breeding and non-breeding populations (weak migratory connectivity). A negative Mantel correlation coefficient indicates that individuals that breed close together spend the other portion of the annual cycle farther apart.

The MC metric was calculated to estimate the strength of migratory connectivity between the same periods of the annual cycle as the Mantel test, using the *estMC* function (1,000 resamples) from the *MigConnectivity* package in R (Cohen et al. 2017). Geolocator uncertainty was incorporated into the analysis by measuring the error in geolocator estimates when Tree Swallows were at known deployment locations on the breeding grounds. We also incorporated indices of relative abundance from breeding regions that were originally defined for the network analysis (see *Weighting the network based on migratory strategy and relative abundance*) to account for differences in sampling effort in relation to Tree Swallow abundance. As with r_M , an MC value approaching one indicates that individuals that are close in one season are close to one another in the other season (strong migratory connectivity), an MC value of zero indicates no relationship in the distance between individuals between seasons (weak migratory connectivity), and a negative MC value indicates individuals that are close in one season are farther apart in the other.

Network metrics

We used a variety of metrics to evaluate the network. *Community structure* identifies whether there are groups of nodes within the network that are connected to each other more densely than to the rest of the network (Newman 2003, Urban et al. 2009). The community structure in our study was based on a propagating labels algorithm, where each node in the network is assigned an initial unique label and then these labels iteratively change to adopt the label that each node shares with the majority of its neighbors (Raghavan et al. 2007). At the completion of the algorithm, connected nodes with the same label form a community. In the community structure analysis, there was no rule that nodes had to be grouped into communities, so there was at least one from each set (breeding, stopover, and non-breeding). However, given the nature of the directed movements, it is highly likely that, if distinct communities are identified, they will have at least one node from each set. These communities, therefore, may represent migratory flyways that Tree Swallows use to migrate between their breeding and non-breeding grounds.

Related to the community structure analysis, we also calculated a metric that measures a node's level of interaction with other communities. The *participation coefficient* measures how many of the edges connected to a particular node are connected to other nodes within its community compared to nodes in other communities (Guimera et al. 2005). Nodes with high participation coefficients ($P > 0.80$) are equally connected with all communities and are considered kinless, while there are connector nodes that have many links to other communities than its own ($0.62 < P \leq 0.80$), peripheral nodes with most connections within its own community ($0.05 < P \leq 0.62$), and ultraperipheral nodes with all links within its community ($P \leq 0.05$; Guimera et al. 2005).

Centrality measures are used to identify the most important nodes in the network for maintaining network connectivity. High network connectivity implies that there is extensive mixing between populations due to a highly connected network. *Eigenvector centrality* measures the influence of a node

in a network based on the number of connections and the quality of those connections (Newman 2003). A high quality connection has many connections itself. Nodes with high eigenvector centrality have many connections and/or many high quality connections. *Betweenness centrality* quantifies the number of times a node acts as a bridge along the shortest path between any two other nodes (Urban et al. 2009). A node with high betweenness centrality is between many other pairs of nodes and is, therefore, important because it is along one of the main migratory routes.

For all network-based analyses, we used the *iGraph* package (Csardi and Nepusz 2006) in R version 3.3.1 (R Core Development Team 2015). Nodes contain all breeding, autumn stopover, and non-breeding sites that individuals visited throughout the annual cycle. We added a geographic coordinate attribute to each node for visualization purposes, but this was not accounted for in any network calculations. Each edge represented a directed connection between nodes through migratory movements.

Weighting the network based on migratory strategy and relative abundance

The primary steps toward building a migratory network are defining the nodes and describing edges that connect pairs of nodes in the network (Appendix S1: Fig. S2), but edges also need to be weighted according to the relative abundance of individuals moving along them. The relative weighting of edges can influence their importance in the network and the importance of nodes to which they are connected, as well as how networks respond to habitat loss (Marra et al. 2006). To weight the network by the relative abundance of individuals moving along the edges, we multiplied the proportion of individuals that moved along each edge, as estimated from the geolocator data, by an estimate of abundance derived from Breeding Bird Survey (BBS) data (Sauer et al. 2014). We chose to use BBS data so we could represent a larger region around each of the breeding sites rather than use estimates of abundance based only on the birds monitored at each of the 12 breeding sites, which is likely not reflective of larger areas (Shutler et al. 2012). The trade-off with this approach is that the migration data derived from geolocators may not reflect the larger area from which the BBS indices of abundance were derived. We attempted to find the optimal balance and chose to exclude some breeding areas from our analysis.

To estimate abundance associated with each of the 12 breeding sites, we first defined eight breeding regions from which we could extract BBS data. We used a combination of provincial/state boundaries and Bird Conservation Regions (BCRs; U.S. NABCI Committee 2000). BCRs are based on differences in habitat type and bird community composition and are used in regional analysis of abundance and population trends by the BBS (Sauer et al. 2003). The breeding regions we defined were linked to different migratory strategies across the breeding range, containing the BCRs in which breeding sites were located, as well as adjacent BCRs that we thought would contain individuals with similar migratory strategies (Appendix S1: Fig. S3). Some breeding regions, therefore, contained multiple breeding sites. While, collectively, the breeding regions we defined encompassed 46% of the area of Tree

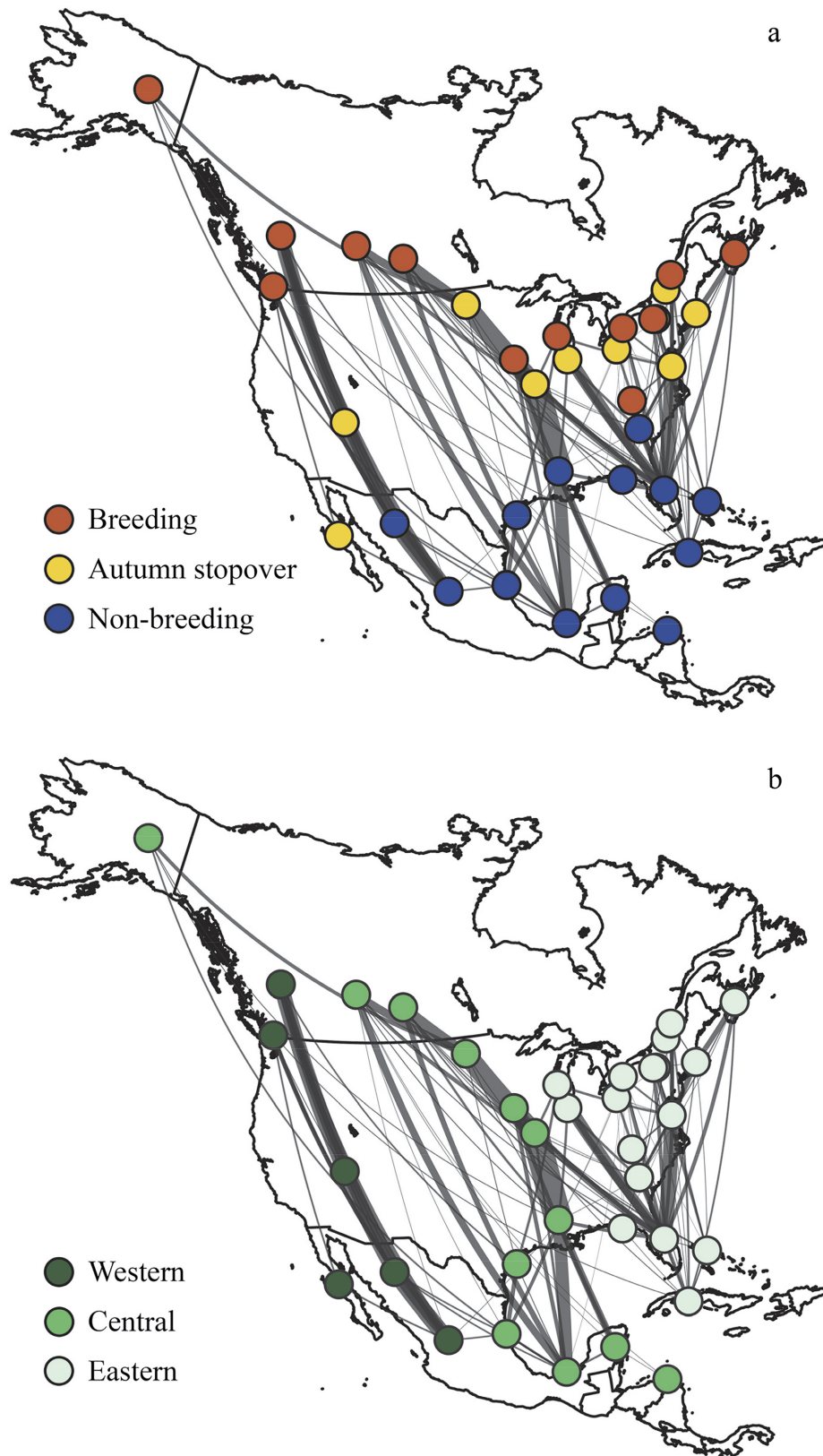


FIG. 2. (a) Migratory network for Tree Swallows showing breeding, autumn stopover, and non-breeding nodes. (b) The same network showing three major migratory flyways (west of the Rocky Mountains, down the Mississippi River valley, and along the Atlantic coast), determined by label propagation. Edges connect the nodes but do not represent the actual migratory route. Edges are weighted by the proportion of individuals moving between nodes multiplied by an index of relative abundance from the previous node. The map is a World2-Hires map (Becker and Wilks 1993) with an Albers Equal-Area projection.

Swallow breeding range, by far the largest region that was excluded was the Canadian boreal forest, which, based on the few BBS routes in boreal regions, has a relatively low abundance of Tree Swallows (Sauer et al. 2014). The other regions we chose to exclude were the U.S. southwest (encompassing parts of California, Nevada, Utah, Colorado, and New Mexico) and some of the U.S. Midwest (encompassing parts of Iowa, Missouri, Arkansas, Tennessee, and Kentucky) because it is possible that individuals from these regions have different migration strategies from those represented in our network (Butler 1988), and there is relatively low abundance of swallows in these areas (Sauer et al. 2014).

To calculate the index of relative abundance for each region, we obtained a BBS shapefile with indices of relative abundance from 2008 to 2012 for Tree Swallows across their breeding range (Sauer et al. 2014). These abundances were estimated from BBS data by extrapolating distance-weighted averages of counts along standard 40 km BBS survey routes. Using ArcGIS 10.4 (ESRI, Redlands, California, USA), we summed indices of relative abundance across all points within each breeding region. The index of relative abundance for each breeding region was the total abundance over the breeding region divided by the total abundance across all breeding regions. Since some breeding regions contained more than one breeding site, the index of relative abundance for those breeding regions was divided by the number of breeding sites in that region to obtain the index of abundance for each breeding site. The BBS indices of abundance did not reach into the area around Fairbanks, so we used the index of abundance from the Boone, North Carolina site because Fairbanks is also on the edge of the breeding range and therefore likely has a low relative abundance.

Once we had indices of relative abundance (Appendix S1: Table S1) for each of the regions around the 12 breeding sites, the indices of relative abundance were propagated

TABLE 2. Participation coefficients (P) > 0 for nodes in the Tree Swallow network, ranked in order of decreasing P .

Node	Node type	P
Texas coast	Non-breeding	0.67
Louisiana	Non-breeding	0.54
Saukville	Breeding	0.50
Midwest	Stopover	0.48
Southwest Mexico	Non-breeding	0.48
East Mexico	Non-breeding	0.45
Wisconsin	Stopover	0.44
Bahamas	Non-breeding	0.38
Dakotas	Stopover	0.38
Western Florida	Non-breeding	0.38
South Florida	Non-breeding	0.36
Northwest Mexico	Non-breeding	0.32
Lake Erie	Stopover	0.28
Cuba	Non-breeding	0.24
Carolinas/Georgia	Non-breeding	0.22

Notes: P is a measure of how many of the edges connected to a given node are linked to other nodes within its community vs. nodes in other communities (for communities, see Fig. 2b). Texas coast is the only connector node (many links to other communities; $0.62 < P \leq 0.80$). The remaining nodes are peripheral nodes (most connections within their own communities; $0.05 < P \leq 0.62$) and ultraperipheral nodes (all links within their communities; $P \leq 0.05$; not listed in this table).

through the network. Weights for edges connecting breeding sites to first stopovers were calculated by multiplying the proportion of individuals moving along that edge by the breeding site's index of relative abundance. The relative abundance of individuals moving along edges from the breeding sites were then summed with all other edge abundances ending at the same node to get an index of relative abundance at each of the first stopover nodes. The remaining edges were weighted using the proportion of individuals moving between nodes multiplied by an index of relative abundance from the previous node so the indices of relative abundance propagated through the network.

RESULTS

General description of the network

Overall, we identified 10 autumn stopover and 13 non-breeding nodes for 133 individuals tracked from 12 breeding sites (Fig. 2a). The network consisted of 136 edges and was made up of one component, meaning there was no part of the network that was completely disconnected. Individuals occupied between 0 and 3 autumn stopover nodes (1.35 ± 0.04 [mean \pm SE], mode = 1; only one individual visited zero or three stopovers) and stayed for an average of 57 d (SD = 29.82 d, range 14–132 d). There was no evidence

TABLE 3. Eigenvector centrality and betweenness centrality scores from the Tree Swallow migratory network for stopover and non-breeding nodes, weighted by population indices of relative abundance.

Node	Eigenvector centrality	Betweenness centrality
Stopover nodes		
Midwest	1.00	549
Dakotas	0.58	253
Mid-Atlantic coast	0.20	275
Wisconsin	0.19	143
Lake Erie	0.04	0
New England coast	0.04	33
Utah/Arizona	0.02	0
South New York	0.01	1
Baja California	0.01	0
Northern New York	0.00	0
Non-Breeding nodes		
Louisiana	0.85	389
South Florida	0.44	638
East Mexico	0.43	327
Quintana, Mexico	0.19	33
Northwest Mexico	0.19	241
Southwest Mexico	0.16	33
Carolinas/Georgia	0.12	0
Western Gulf of Mexico	0.11	195
Cuba	0.07	0
Texas coast	0.05	118
Bahamas	0.04	19
Western Florida	0.03	0
Honduras	0.01	0

Notes: Nodes are ranked by eigenvector centrality from high to low. Nodes with high eigenvector or betweenness centrality are important for maintaining network connectivity.

that the number of stopovers individuals visited differed based on their breeding origin (GLM, $df = 11$, $\chi^2 = 10.80$, $P = 0.46$). The Mantel correlation coefficient for the entire network suggested there was strong migratory connectivity between the breeding sites and the first autumn stopover sites ($r_M = 0.75$, $n = 133$, $P < 0.001$, 95% CI [0.71, 0.79]). The MC value was slightly lower (MC = 0.68, $n = 133$, 95% CI [0.65, 0.70]), suggesting moderate-strong migratory connectivity between breeding sites and first autumn stopover sites.

Individuals occupied between 1 and 3 non-breeding nodes (1.55 ± 0.06 [mean \pm SE], mode = 1) and stayed for an average of 81 d (SD = 48.88 d, range 14–204 d). Eleven individuals returned to a particular node more than once within the non-breeding season (for example moving from Northwest Mexico to Southwest Mexico and back). There was no evidence that the number of non-breeding nodes individuals visited differed based on their breeding origin (GLM, $df = 11$, $\chi^2 = 5.37$, $P = 0.91$). In contrast to the migratory connectivity between breeding sites and autumn stopover sites, the Mantel correlation coefficient for the entire network suggested that there was moderate migratory connectivity between the breeding sites and first-visited non-breeding sites ($r_M = 0.53$, $n = 133$, $P < 0.001$, 95% CI [0.48, 0.57]) as well as moderate migratory connectivity between breeding sites and the last-visited non-breeding sites ($r_M = 0.51$, $n = 133$, $P < 0.001$, 95% CI [0.47, 0.56]). Correspondingly, the MC value calculated between the breeding and first-visited non-breeding sites (MC = 0.54, $n = 133$, 95% CI [0.49, 0.60]) and between the breeding and last-visited non-breeding sites (MC = 0.51, $n = 133$, 95% CI [0.44, 0.59]) also suggested moderate migratory connectivity.

Community structure

Using label propagation to identify community structure, we identified three “communities” in the weighted network: a western community that consisted of nodes west of the Rockies and into western Mexico, a central community that primarily consisted of nodes between the Rockies and the Great Lakes and south into East Mexico, and an eastern community that was made up of nodes from the Great Lakes east to the Atlantic coast and south to Florida and Cuba (Fig. 2b). Based on the participation coefficients for the weighted network, the only node that was considered a connector node between communities (i.e., a score between $0.62 < P \leq 0.80$; Guimera et al. 2005) was the Texas coast ($P = 0.67$; Table 2). All other nodes in the network were considered ultraperipheral ($P \leq 0.05$) or peripheral ($0.05 < P \leq 0.62$; Table 2). The Mantel correlation coefficients for the community subsets suggested weak to moderate migratory connectivity within communities between breeding and autumn stopover sites, and weak migratory connectivity within communities between breeding and non-breeding sites (Appendix S1: Table S2).

Evaluation of node importance

We used two centrality measures to determine the most and least important nodes in the network for maintaining network connectivity. The most important autumn stopover nodes based on weighted eigenvector centrality were the

Midwest (1.00) and the Dakotas (0.58; Table 3). The top ranked non-breeding nodes based on the weighted eigenvector centrality were Louisiana (0.85), South Florida (0.44), and East Mexico (0.43; Table 3). Utah/Arizona, South New York, Baja California, North New York, and Honduras had the lowest eigenvector centrality scores (≤ 0.01 ; Table 3) indicating that they had the fewest connections and were connected to other nodes with low eigenvector centrality. Based on betweenness centrality, the top ranked autumn stopover nodes were the Midwest (549), the Mid-Atlantic coast (275), and the Dakotas (253; Table 3), while the top ranked non-breeding nodes were South Florida (638), Louisiana (389), and East Mexico (327; Table 3). Several nodes in the network had a betweenness centrality score of 0, indicating that they did not act as bridges along the shortest path between other nodes (Table 3).

The rankings of the nodes between the weighted (Table 3) and unweighted network (Appendix S1: Table S3) were very similar for betweenness centrality. However, the Southwest Mexico and Carolinas/Georgia nodes had a much higher ranking in the unweighted network. There were greater differences between the weighted and unweighted network for eigenvector centrality, however. In the unweighted network, the Mid-Atlantic coast was the top ranked stopover node for eigenvector centrality. As for the non-breeding nodes, the Carolinas/Georgia, Cuba, and Bahamas nodes had a much higher ranking in the unweighted network, though South Florida was still the top non-breeding node.

DISCUSSION

Our study, using tracks from individual Tree Swallows spanning over 5,000 km from Alaska to Nova Scotia, provides the most comprehensive description and evaluation of a migratory songbird network to date. By applying network metrics to this continent-wide sample, we provide convincing evidence of both a high degree of mixing throughout the network, as well as large-scale regional structuring. While the Tree Swallow network was made up of one component, meaning that an individual at any node could theoretically travel along edges to any other node in the network, we also identified three distinct “communities” that represented major “flyways” down the west, center, and east of the continent. This suggests that although there is some consistency in the migratory routes and non-breeding nodes used by a given breeding population, some individuals adopt “alternative” migratory strategies and use different non-breeding nodes, yet return to the same breeding site the following year. A highly connected network also implies a greater chance that individuals have the opportunity to use alternative migratory routes, which could be important for buffering populations from environmental change. The community structure supports this notion of consistent mixing throughout the network overlaid on top of a distinct, broad-scale structure. It remains to be determined whether other migratory songbird networks follow a similar pattern when examined across their range.

Migratory connectivity

We provide evidence that the strength of migratory connectivity changes over the course of the annual cycle. Based on

TABLE 4. A summary of the strength of migratory connectivity between the breeding and non-breeding grounds from past studies of songbirds, along with the estimate in this study.

Species	Mantel correlation coefficient (r_M)	Study
Ovenbird (<i>Seiurus aurocapilla</i>)	0.84	Hallworth and Marra (2015)
Swainson's Thrush (<i>Catharus ustulatus</i>)	0.72	Cormier et al. (2013)
Golden-Crowned Sparrow (<i>Zonotrichia atricapilla</i>)	0.66	Cormier et al. (2016)
Great Reed Warbler (<i>Acrocephalus arundinaceus</i>)	0.53–0.56	Koleček et al. (2016)
Tree Swallow (<i>Tachycineta bicolor</i>)	0.51–0.53	This study
European Roller (<i>Coracias garrulus</i>)	0.50	Finch et al. (2015)
European Robin (<i>Erithacus rubecula</i>)	0.48	Ambrosini et al. (2016)
Wood Thrush (<i>Hylocichla mustelina</i>)	0.33	Stanley et al. (2015)
Barn Swallow (<i>Hirundo rustica</i>)	0.22	Ambrosini et al. (2009)

Note: Values are based on the Mantel correlation coefficient and range from strong ($r_M = 1$) to weak ($r_M = 0$).

both the Mantel correlation coefficients and MC on the entire network, we found strong migratory connectivity between the breeding and first stopover sites individuals visited ($r_M = 0.75$, MC = 0.68), but only moderate migratory connectivity between the breeding sites and both the first ($r_M = 0.53$, MC = 0.54) and final ($r_M = 0.51$, MC = 0.51) non-breeding sites. However, we also show (solely based on r_M) that, within communities, there was extensive mixing (weak migratory connectivity) between the breeding sites and other periods of the annual cycle (Appendix S1: Table S2). Though incorporating uncertainty around the geolocator estimates and estimates of relative abundance with the MC metric, we found only minor differences in the strength of connectivity when compared to the Mantel correlation coefficients.

Together, these results suggest that regional breeding populations of Tree Swallows are mostly segregated from other breeding populations at the first stopover site they visit in the autumn, but then increasingly mix as they move away from their breeding grounds, creating overlap between populations on the non-breeding grounds. This may not be surprising given the large geographic spread of the deployment sites and that previous studies, using the Mantel test, have shown a similar pattern in other species (Koleček et al. 2016, Table 4). However, determining the degree of mixing throughout the annual cycle does have important implications for predicting how populations will respond to environmental change. Based on the Mantel test as well as the MC metric, the strength of migratory connectivity in Tree Swallows between breeding and non-breeding sites falls approximately in the middle of those previously reported in past studies (Table 4), whereas the strength of migratory connectivity between breeding and autumn stopover sites falls on the strong end. The strong migratory connectivity that we found between breeding and autumn stopover sites implies that events, such as habitat loss, at stopover sites may influence abundance of one or a few breeding populations, whereas moderate mixing between the breeding and non-breeding grounds suggests that events that occur at any non-breeding site will likely affect multiple breeding populations (Taylor and Norris 2010).

It is important to note, however, that the size of the species' range and the distance between sampled populations is important to consider when comparing Mantel test results among studies. This is because estimates of migratory connectivity between close neighboring populations will likely

yield very different results from widely separated populations (Cormier et al. 2013, Trierweiler et al. 2014). For instance, shorter distances between deployment sites may lead to more mixing during the non-breeding season (Stanley et al. 2015, Table 4) than if deployment sites are farther apart (Koleček et al. 2016, Table 4). Furthermore, the Mantel tests within community subsets confirmed that sampling within only a portion of the range can dramatically increase the estimated amount of mixing within the network, as measured by r_M (Appendix S1: Table S2). These limitations to the Mantel test highlight the benefit to using the MC metric, which is standardized so it can be compared across species with different range sizes and incomplete sampling (Cohen et al. 2017).

Prioritizing regions for optimal conservation

Network analysis can be used to prioritize regions for conservation based on the key nodes highlighted by centrality metrics. Based on this method, we identified six nodes that were highly used by individuals from multiple breeding populations and are important for maintaining network connectivity. Maintaining a connected network is desirable over a disconnected network because it may provide a buffer against range-wide population declines (Taylor and Norris 2010, Betini et al. 2015). These important nodes were the Midwest, the Dakotas, the Mid-Atlantic coast, South Florida, Louisiana, and East Mexico. Our study confirms sites previously identified as major non-breeding sites for Tree Swallows, such as Florida (Winkler et al. 2011), Louisiana (Laughlin et al. 2013), and East Mexico (Bradley et al. 2014); however, the major stopover sites we identified above were not previously recognized as important sites. Individuals from 5 of the 12 populations moved through the Midwest stopover node, coming from breeding regions with some of the highest indices of abundance, and moving to non-breeding nodes from East Mexico to South Florida. South Florida itself had individuals from nine of the 12 breeding sites visit during the non-breeding period and is the node with the most connections (22) in the network. However, there are drawbacks to this method of determining important nodes for conservation based solely on the structure and weighting in the network. First, these metrics do not address which region throughout the annual cycle is most critical for a particular breeding population. Second, these centrality measures fail to take into consideration the

habitat quality of nodes, missing an important component of evaluating regions in a network. However, other approaches based on network theory can incorporate information on habitat quality if it is available (Urban and Keitt 2001, Taylor and Norris 2010).

Communities represent distinct migratory flyways

Network-based community detection algorithms are an alternative method for identifying migratory flyways. Previously, flyways have been identified visually using bird banding records and were constrained by political boundaries (Lincoln 1935). Community detection algorithms are a quantitative way to estimate flyways that are strictly biological by considering the connections among nodes. The propagating labels algorithm that we used constructed communities that spanned the annual cycle and contained nodes of all three types, even though the network was made up of a single component. Buhnerkempe et al. (2016) also used network metrics to determine migratory flyways that spanned the annual cycle quantitatively in waterfowl, but used a slightly different community detection algorithm.

Our network consisted of three communities that span the full annual cycle, each including nodes of all three sets, and represent three distinct flyways that Tree Swallows use to migrate between the breeding and non-breeding grounds (Fig. 2b). Western breeding populations migrate west of the Rocky Mountains to spend the non-breeding season mostly in Northwest and Southwest Mexico. Most Tree Swallows likely avoid migrating over the Rocky Mountains, thus separating the migratory routes of populations west and east of the Rockies. The Alaskan breeding population joins the central breeding populations to migrate through the center of the continent (likely along the Mississippi River Valley; Butler 1988) to spend the non-breeding season, for the most part, around the Gulf of Mexico. Eastern populations migrate down the Atlantic coast to Florida, Cuba, and the Bahamas. The migratory flyways that we identified support three of the four Tree Swallow flyways identified in an analysis of band-recapture data (Butler 1988). The fourth possible route that Butler (1988) identified was individuals breeding in Montana and Colorado then migrating east of the Rocky Mountains and straight south to Mexico, but because we did not deploy geolocators in these states, we cannot confirm this flyway.

The community structure in this network means that these flyways could be considered separate management units. Based on the participation coefficient, the Texas coast was the only node in the network that was considered a connector node between the three communities and all other nodes in the network had most connections within their own community (Table 2). Because habitat loss at a node in one of these flyways will have a greater effect on the populations within that flyway than the network as a whole, management units based on flyways would be useful for coordinating efforts at a biologically relevant scale. For waterfowl, the flyways identified by Lincoln (1935) are still largely used as management units, though Buhnerkempe et al. (2016) argue that a more quantitative and biological measurement of flyways, as we have done here using community detection, would be more effective.

Stopover ecology

Our study demonstrates that Tree Swallows make multiple, long stopovers in the autumn en route to their non-breeding grounds. Though it is possible that they also make short 1–3 d refueling stopovers, short stopovers are difficult to identify given the spatial resolution of geolocators. Thus, we only identified stopovers that were visited for longer than 2 weeks. These extended autumn stopovers averaged 58 d, and so individuals were clearly not using these sites solely for refueling (Alerstam 1991). Adults finish breeding in June or July (Winkler et al. 2011), depart the breeding grounds within 1–2 weeks after fledging young (additional analysis of geocator data; all authors, *unpublished data*), and then migrate directly to stopover sites where they likely complete a full molt from mid-July to early November (Stutchbury and Rohwer 1990). These autumn stopover sites may, therefore, be more appropriately called short-term molting, or short-term residency, sites (Stach et al. 2012, Tøttrup et al. 2012, Arlt et al. 2015).

Molt migration, where individuals remain at stopover sites for extended periods, is one strategy to decrease the energetic costs of molt. It is well documented in several avian groups, such as waterfowl and shorebirds, but is less common in passerines (reviewed in Leu and Thompson 2002, Pyle et al. 2009). For aerial foragers such as Tree Swallows, reduced flight abilities and foraging costs associated with molt may increase the time it takes to complete molt compared to many other songbirds (Rohwer et al. 2005). However, unlike other North American swallows, such as the Purple Martin (*Progne subis*), that spend the non-breeding period in South America and complete molt on the non-breeding grounds (Niles 1972), the harsher northern climate may pose an energetic constraint, forcing Tree Swallows to complete molt before reaching the non-breeding grounds (Stutchbury and Rohwer 1990). They also do not complete their molt on the breeding grounds, but it is unlikely they experience severe time constraints that would prevent this from occurring because Tree Swallows typically finish breeding relatively early in the summer (Winkler et al. 2011). Rather, it seems that Tree Swallows congregate at autumn roosting sites during molt, which has the benefit of reducing predation risk and thus energetic demand during this long molt period.

Tree Swallows may travel short distances to molt near their breeding site, or travel long distances, often over 3,000 km, to reach molting sites. The main hypothesis explaining why individuals of some populations or species leave the breeding grounds to molt is insufficient food resources, forcing them to delay molt until they reach sites that have adequate resources (Leu and Thompson 2002). This is likely the case for the populations of Tree Swallows breeding in British Columbia, where available resources are thought to be lower (Bortolotti et al. 2011) and all individuals migrate to Mexico, or in one case Utah/Arizona, before beginning molt. The northwestern and southwestern regions of Mexico are part of a major molt-stopover region used by several western populations of songbird species due to monsoons and heavy rains in these areas (Adams and Comrie 1997, Rohwer et al. 2005) that rapidly increase food abundance and attract molting individuals to these regions (Méndez-Barroso et al. 2009).

Non-breeding ecology

Given that 51% of the individuals moved between multiple (two or three) widely separated non-breeding sites, remaining for an average of 80 d at each site, our results challenge the notion of a “stationary” non-breeding period. Intratropical, or non-breeding, movements have been observed in previous studies of migratory songbirds such as Veeries (*Catharus fuscescens*; Heckscher et al. 2011), Great Reed Warblers (Koleček et al. 2016), and Purple Martins (Stutchbury et al. 2016). Moving to another non-breeding site could occur due to increasing densities of roosts at the first non-breeding sites (Stutchbury et al. 2016). However, the more temperate regions that Tree Swallows occupy have more extreme seasonal shifts in resources compared to tropical regions, meaning that the benefits of moving to another non-breeding site may outweigh the energetic and mortality costs of migration. Furthermore, because temperature influences the food availability of aerial insects (Taylor 1963, McCarty and Winkler 1999b) and most individuals who moved made southbound movements, temperature could be driving Tree Swallows farther south as the non-breeding season progresses. Individuals that persist in some of the more northern non-breeding areas for the entire non-breeding season may be able to do this because of decreased roost density and decreased competition for limited resources as others move south.

Tree Swallows may also be tracking abundance of bayberries throughout the annual cycle. These shrubs/small trees produce waxy berries that only a few species of animals, including Tree Swallows, can digest (Place and Stiles 1992). They ripen in the autumn and persist well into the non-breeding season, with the autumn and non-breeding distribution of Tree Swallows matching the distribution of several species of bayberry (including *Myrica pensylvanica* and *Myrica cerifera*) in the eastern United States (Halls 1977). This ability to persist on bayberries may be why they can successfully spend the non-breeding season so far north. It also explains how one individual from Saukville remained along the Mid-Atlantic coast during the non-breeding season, where small numbers of Tree Swallows were previously seen persisting on a diet of bayberries (Winkler et al. 2011).

Designing connectivity studies

Designing connectivity studies presents several challenges, such as time constraints in sampling protocols, and how to systematically sample across a species' range. By using combinations of Bird Conservation Regions (BCRs) to represent larger breeding regions we were able to, post hoc, systematically sample across the breeding range of Tree Swallows (Appendix S1: Fig. S3). We propose that incorporating BCRs is one way to design connectivity studies to systematically sample populations from across a species' range. BCRs also have additional benefits because they can allow for targeting of declining populations within flyways to help prioritize conservation efforts. We show that failing to sample from across a species' range can also give misleading results about the strength of migratory connectivity within the entire network (Appendix S1: Table S2).

One drawback to using geolocators is the uncertainty in location estimates. Latitudinal error can be over 300 km, particularly around the equinox when there is little variation in day length across the globe. We attempted to acknowledge this uncertainty by grouping individual locations into larger regions (nodes), but this approach assumes individuals actually did use the same area. Given that Tree Swallows roost in large aggregations outside of the breeding season (Winkler 2006, Laughlin et al. 2013), this may have been a valid assumption in most cases, but it is still possible individuals used different areas or habitats within a small geographic region. Other long-distance tracking methods may provide opportunities to derive more precise location estimates from small birds. For example, MOTUS is an automated telemetry array that now covers large parts of North America and is expanding into Central and South America (Taylor et al. 2017), while ICARUS is a satellite-based telemetry tracking system that is due to launch in 2018 (ICARUS Initiative 2018).

Another drawback to tracking animal movements using geolocators is they have to be retrieved to obtain their data, and so the patterns we observed were only from individuals who returned to their breeding site from the previous year. Some individuals may have gone to a different breeding site that we were not monitoring (though high site fidelity in Tree Swallows suggests this is likely not a major problem; Lagrange et al. 2014), or died before returning to the breeding grounds. If individuals who did not return had alternate migratory strategies, we could be missing some important patterns from the network we described. For example, if some individuals spent the non-breeding season in a region we did not identify in our network analysis, but did not survive to return to the breeding grounds, we would be missing a key node that acts as a sink for the Tree Swallow population. Devices that do not need to be retrieved to acquire the data, such as MOTUS (although towers have incomplete coverage; Taylor et al. 2017) and ICARUS (Wikelski et al. 2007) can overcome this drawback to research on small songbirds.

It is also important to note that the number of stopover and non-breeding nodes identified in a network is influenced by the number of geolocators recovered at a given breeding site. Even if a similar number of geolocators are deployed per site, recapture and return rates and geocator failure rates can vary among populations (Gómez et al. 2014). The variance in sample sizes across breeding populations in this study could mean that for sites where few geolocators were recovered, some stopover or non-breeding nodes may have been missed. In our study, it seems that, for sites with small sample sizes, there was a lower probability of missing stopover nodes than non-breeding nodes, because the number of stopover nodes was not significantly related to sample size (linear regression, $\beta = 0.06 \pm 0.04$, $t = 1.54$, $P = 0.16$; Appendix S1: Fig. S4), whereas the number of non-breeding nodes was significantly higher for breeding sites with larger sample sizes (linear regression, $\beta = 0.20 \pm 0.06$, $t = 3.20$, $P = 0.01$; Appendix S1: Fig. S4). Model selection results (Appendix S1: Table S4) indicated that quadratic models fit to the data (Appendix S1: Fig. S4) had considerably less support than the linear models. Although our analysis identified many non-breeding nodes, one should be cautious of the limitations of determining non-breeding nodes when

using small sample sizes. The strength of migratory connectivity results may also be influenced if we do not have a good representation of all non-breeding nodes that individuals from a given population used. Small sample sizes can be overcome, however, with wide spatial coverage of the network, such as was done in this study. In this way, we described a fully connected migratory network, where an individual at any node can theoretically reach any other node in the network.

CONCLUSION

Our study represents a comprehensive examination of year-round movements of a single species across its North American breeding range. Our results demonstrate that Tree Swallows have a highly connected network where populations increasingly mix as they move from the breeding to non-breeding season. We also show that Tree Swallows make long stopovers in the autumn, likely to molt, and then move between multiple sites during the non-breeding season. Despite such extensive mixing in the network, we also show that there are three distinct migratory flyways that Tree Swallows use during autumn and spring migration.

We show that network metrics can be a relatively easy way to identify important features of a network, including overall spatial structure and important nodes for maintaining network connectivity. This approach is computationally less intensive than other methods and, aside from building the structure of the network, has few additional data requirements. Such an approach could be effective for making conservation decisions where it is not feasible to collect additional data (Runge et al. 2014, Nicol et al. 2016). Nevertheless, when additional data are available, the construction of a network such as ours will be critical for building year-round, range-wide population models designed to predict how a species will respond to environmental change.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1298/full>

DATA AVAILABILITY

Data associated with this study are available from Movebank at <https://doi.org/10.5441/001/1.25551gr6>