

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

**by**

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## ABSTRACT

### CONSTRUCTING AND EVALUATING A CONTINENT-WIDE MIGRATORY SONGBIRD NETWORK ACROSS THE ANNUAL CYCLE

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Information about how migratory animals are spatially connected between periods of the annual cycle is essential for understanding the effects of environmental change and developing optimal conservation strategies. I constructed a migratory network for a songbird, the tree swallow (*Tachycineta bicolor*), using year-round movements derived from 133 light-level geolocators attached to individuals originating from 12 breeding sites across North America. I identified 10 autumn stopover nodes (regions) in North America, 13 non-breeding nodes around the Gulf of Mexico, Mexico, and the Caribbean, and 136 unique migratory pathways connecting these nodes. Using network-based metrics, I ranked the stopover and non-breeding nodes based on their contribution to network connectivity and identified three distinct ‘communities’ of nodes that corresponded to western, central, and eastern flyways. This study highlights how network-based metrics can be valuable for identifying overall network structure and prioritizing specific regions within the network, information that is crucial for effectively conserving migratory species.

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The contents of this thesis are in review at *Ecological Monographs*, co-authored by David W. Bradley, Robert G. Clark, Elizabeth A. Gow, Marc Bélisle, Lisha L. Berzins, Tricia Blake, Eli S. Bridge, Lauren Burke, Russel D. Dawson, Peter O. Dunn, Dany Garant, Geoffrey L. Holroyd, David J. T. Hussell, Olga Lansdorp, Andrew J. Laughlin, Marty L. Leonard, Fanie Pelletier, Dave Shutler, Lynn Siefferman, Caz M. Taylor, Helen Trefry, Carol M. Vleck, David Vleck, David W. Winkler, Linda A. Whittingham, and D. Ryan Norris. D.R.N., D.W.B., R.C.G., and S.M.K. conceived of and designed the study. D.W.B., R.G.C., M.B., L.L.B., T.B., E.S.B., L.B., R.D.D., P.O.D., D.G., G.L.H., D.J.T.H., O.L., A.J.L., M.L.L., F.P., D.S., L.S., C.M.T., H.T., C.M.V., D.V., D.W.W., L.A.W., and D.R.N. conducted fieldwork (geolocator deployment and recovery). D.W.B. downloaded the geolocator data from the geolocators. S.M.K. conducted statistical analyses. S.M.K. wrote the manuscript with support from D.R.N. and E.A.G. All authors had the opportunity to provide feedback on the manuscript. Funding for the study was provided by Leaders Opportunity Fund Grants from the Canadian Foundation for Innovation (D.R.N., R.D.D.), Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants (D.R.N., R.G.C., R.D.D., M.B., D.G., F.P., M.L.L.), an NSERC Research Tools and Instruments Grant (D.R.N., M.B., R.D.D., D.G., M.L.L., F.P., D.S.), an NSERC Industrial Research and Development Fellowship (D.W.B.), an NSERC Alexander Graham Bell Canada Graduate Scholarship (L.L.B), the NSERC Canada Research Chairs Program (M.B, F.P.), the University of Guelph (D.R.N.), Environment and Climate Change Canada (R.G.C., O.L.), Bird Studies Canada (D.W.B., D.J.T.H.), the University of Northern British Columbia (R.D.D.), the British Columbia Knowledge Development Fund (R.D.D.), The Skaggs Foundation (T.B.), a National Science Foundation Grant IOS-0745156 (C.M.V., D.V.), Fonds de Recherche

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## 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 such challenge is describing the patterns of individual movement between populations in different seasons of the annual cycle (Webster and Marra 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, 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 the factors that limit and regulate populations, as well as decisions about how to allocate limited conservation resources, should not be made in isolation, but instead need to incorporate information about how populations are connected between different periods of the annual cycle (Martin et al. 2007, Runge et al. 2014).

For small-bodied organisms, such as songbirds (typically less than 50 g), only recently have individuals been directly followed over the course of an entire year. Developments in the use of archival light-logging geolocators (Stutchbury et al. 2009) and, more recently, archival GPS tags (Hallworth and Marra 2015) have created the opportunity to describe patterns of range-wide connectivity for small migratory animals (Bridge et al. 2013, McKinnon et al. 2013, Knight

and Norris 2016). Geolocator-based studies have documented migratory patterns in a variety of songbirds (e.g., Ryder et al. 2011, Cormier et al. 2013, Finch et al. 2015, Koleček et al. 2016, Ouwehand et al. 2016), as well as highlighted some record-breaking journeys (Bairlein et al. 2012, DeLuca et al. 2015). However, few studies have described connectivity across a species' range, or covered all major regions across a species' range (Fraser et al. 2012, Hobson et al. 2015, Stanley et al. 2015). Furthermore, even fewer capitalized on such information to make inferences about the relative importance of different regions or populations on the breeding and non-breeding grounds (Taylor and Stutchbury 2016).

One approach that can be used to describe and evaluate patterns of 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 about social networks (Scott 2012), metabolic networks (Guimerà et al. 2005a), transportation networks (Guimerà et al. 2005b), 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 modeling metapopulations (Urban et al. 2009). One of the primary advantages of using network theory in landscape ecology is that it can be used to identify the relative importance of habitat patches, represented as nodes, to maintaining 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 (Urban et al. 2009).

A network theory approach can also be applied to migratory networks to evaluate 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 or pathways between nodes. Three basic sets of nodes are represented in a migratory network: breeding nodes, non-breeding nodes (typically areas used during the non-breeding period for extended periods of time) and stopover nodes (temporary sites used during migration; Taylor and Norris 2010). A more complex approach is to develop population models within migratory networks that predict how migratory populations and connections within the network will respond to environmental change (Taylor and Norris 2010, Taylor and Stutchbury 2016, Taylor et al. 2016), as well as to identify 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 not available for all nodes and, therefore, rely on several key assumptions (e.g., density-dependence operating in the breeding and non-breeding season; Taylor and Stutchbury 2016). 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 pathways and nodes (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 my knowledge, basic network metrics have

only been applied once to migratory waterfowl (Buhnerkempe et al. 2016) and never in songbirds – one of the most diverse and abundant migratory taxa in the world.

In this study, I describe a continent-wide 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 connectivity in the network. In doing so, I also provide insight into the stopover and overwintering ecology of this species. Tree swallows are aerial insectivores that breed across northern and central North America and spend the non-breeding season along the Gulf of Mexico, Florida, the Caribbean, Mexico, and Central America (Winkler et al. 2011). By tracking individuals originating from 12 different breeding populations using light-level geolocators, my first goals were to describe how breeding populations were connected to non-breeding sites and stopover sites, and then quantify the overall degree of connectivity in the network. My 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 based on band recoveries: the Atlantic coast, the Mississippi River drainage, the eastern slope of the Rocky Mountains, and the Pacific coast. Because of the spatial coverage of the geocator deployment (no geolocators were deployed between Montana and Colorado), I expected that I would be able to identify the flyways along the Atlantic and Pacific coasts, and along the Mississippi River. My final goal was to use network-based metrics to evaluate the relative importance of non-breeding and stopover regions in the network, in terms of maintaining overall connectivity in the network.

## **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, Lawler and Edwards Jr. 2002) and nest boxes (Holt and Martin 1997, Lawler and Edwards Jr. 2002). Previous studies have shown that tree swallows are declining over the northeastern portion of their breeding range (Nebel et al. 2010, Shutler et al. 2012, Michel et al. 2015). They migrate shortly after the breeding season in July and August (Winkler et al. 2011) and during migration roost in large flocks, usually in cane and reed beds over water (Winkler 2006, Laughlin et al. 2013). They overwinter 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.; Winkler et al. 2011).

#### *Geolocator deployment and retrieval*

Light-logging geolocators are small archival devices that estimate the latitude and longitude of a bird by recording light levels periodically (every 2 or 10 min) in relation to an internal clock (Afanasyev 2004). Estimates of geographic location rely on seasonal 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 (Hill 1994). 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 part way 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 from 2010 to 2014 (Lotek Wireless model MK6440 in 2010 and 2011, MK6740 from 2012-2014, with a 10 mm stalk in all years; Fig. 1). Geolocators were attached to individuals weighing > 20 g (representing less than 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, WA, USA). In total, 140 of the 561 geolocators (25%) deployed were retrieved the following year (Table 1). An additional 35 geolocators developed by E.S.B. 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 from the full deployment period without any malfunctions and were used in this analysis.

In general, though based on only three of the same sites in this study, return rates of tree swallows have been shown to vary across breeding locations (Gómez et al. 2014). Thus, I compared possible differences in return rates between sites for the M-series geolocators using a Fisher's exact test. I could not use a chi-squared test because of low sample sizes at the Fairbanks, AK and Ames, IA breeding sites and I simulated the p-value using Monte Carlo simulation (10,000 replicates) because the contingency table was greater than 2x2 dimensions.

### *Geolocator analysis*

Light data downloaded from geolocators were converted to *.lig* files. Clock drift (where the geolocator 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 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. Light levels for M-series geolocators were recorded on a scale from 0 to 64 with zero indicating complete darkness, and 64 anything above a low level of sunlight (a truncated maximum), while the geolocators developed by E.S.B. recorded light levels on a scale from 0 to 127 (again darkness to anything above a low level of sunlight). 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.B. 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. Twilight times that were not clear due to shading were also removed. I then used the FLightR package (Rakhimberdiev et al. 2015), 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, therefore, 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 in FLightR, a spatial probability distribution was generated for each twilight time and used to compute the most probable track of each individual.

There are two ‘behavioural 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, while they are considered in a ‘sedentary state’ when they move less than 45 km, as per the defaults of the FLightR program. This behavioural model better accounts for migrating birds that stop for prolonged periods, punctuated by rapid migratory movements (Rakhimberdiev et al. 2015). I combined this behavioural model with a mask that allowed individuals to fly over (any movement between twilights greater than 45 km), but not enter a sedentary state (any movement between twilights less than 45 km) when they were over water. The spatial object used for the water mask did not perfectly outline the coast, so some location estimates were slightly offshore and were moved to the closest location on land.

### *Network terminology*

I constructed and analyzed the migratory network by adopting terminology from graph theory (Urban and Keitt 2001, Urban et al. 2009, Taylor and Norris 2010). Networks (or graphs) are composed of *nodes* that are connected by *edges* (Urban and Keitt 2001, Taylor and Norris 2010). 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 (Urban et al. 2009), such as the network I developed. Otherwise it is considered *undirected* if individuals migrate in both directions between sets of

nodes (Taylor and Norris 2010). A *weighted* network has varying edge weight. For example, edges could be weighted by the number of individuals moving between nodes or the distance between nodes (Urban et al. 2009, Taylor and Norris 2010). 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 (Urban and Keitt 2001, Taylor and Norris 2010). 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 (Urban et al. 2009). Nodes may also contain attributes (Urban et al. 2009). In this case, they contained geographic coordinates, but nodes may also contain information on demographics or habitat quality (Taylor and Norris 2010).

#### *Elements of the network*

I defined individual stopover and non-breeding sites in this network as the average location an individual occupied over the same general area for greater than two weeks. This cut-off was chosen because short 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 some individuals 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 nodes was not initiated from these sites. In five cases, sites were used as both autumn stopovers by some individuals and non-breeding sites by others. In these circumstances, I classified the node based on its dominant use. Specifically, the Utah/Arizona and the Mid-Atlantic coast sites were mostly used as autumn stopovers; each had only one individual stay the entire non-breeding period (Supplementary Material Fig. S-1). Similarly, some individuals used the Carolinas/Georgia site (Supplementary Material Fig. S-1) in late autumn, but it was mostly used as a non-breeding site. The NW Mexico and SW Mexico sites (Supplementary Material Fig. S-1) were heavily used in autumn, likely as sites for molting, but were classified as non-breeding sites because individuals remained at these sites throughout the non-breeding period. Other than these five cases, there was clear distinction between the stopover and non-breeding nodes. Only half of the swallows (51%) made spring stopovers that were longer than two weeks (all individuals were likely stopping during spring migration, but I did not have the resolution to detect these short stopovers), so spring stopovers were not included in the network.

Clusters of stopover and non-breeding sites were grouped into nodes that represent larger geographic areas for network analysis (Supplementary Material Fig. S-1). When possible, grouping of sites was based on obvious clusters of sites that were separate from other clusters. The 'Northwest Mexico' and 'Southwest Mexico' nodes were separated along the 26° latitude line, and the points in 'Baja California' were assigned a unique node. Locations in the 'Quintana' region of Mexico were separated from the 'East Mexico' node that represents the southern coast of the Gulf of Mexico. The two northern points in the 'Dakotas' node were from poorly calibrated geolocators, due to the high breeding latitude in Alaska and assumed to belong further south in the 'Dakotas' where the other two Alaskan swallows were located. The 'Midwest' node was separated from the 'Louisiana' node along the 35° latitude line. The 'Wisconsin' node was

distinguished from the 'Midwest' node because the 'Wisconsin' node was exclusively used by the breeding populations from Saukville, and was slightly more east than individuals at the 'Midwest' node. The 'Lake Erie' node was exclusively used by individuals from Long Point, and it was separated from the 'Mid-Atlantic coast' at  $-79.7^{\circ}$  longitude where individuals east of this line originated from other breeding sites. The 'Mid-Atlantic coast' was separated from the 'New England coast' along the  $-74^{\circ}$  longitude line. The 'Mid-Atlantic coast' was separated from the 'Carolinas/Georgia' node along the coast at  $34^{\circ}$  latitude and at a diagonal away from the coast. The 'Carolinas/Georgia' node was separated from the 'South Florida' node along the  $31^{\circ}$  latitude line. The 'West Florida' and 'South Florida' nodes were separated along the  $-83.5^{\circ}$  longitude line. One location of an individual thought to be in the Dominican Republic was grouped with the 'Cuba' node. 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, Poisson family), and I found no overdispersion in the data.

#### *Degree of migratory connectivity*

I used a Mantel test to quantify the degree of migratory connectivity between the breeding and first stopover sites visited by individuals, as well as the degree of connectivity between the breeding and non-breeding grounds (Ambrosini et al. 2009). The Mantel test, which is commonly used to estimate the degree of migratory connectivity between songbird populations (e.g., Cormier et al. 2013, Finch et al. 2015, Hallworth and Marra 2015, Stanley et al. 2015, Koleček et al. 2016), measures the correlation between two matrices, each containing pairwise distances between all individuals in the network at two different periods of the annual cycle. For

example, to calculate the Mantel correlation coefficient ( $r_M$ ) between the breeding grounds and autumn stopover sites, I calculated a matrix of pairwise distances between all individuals on the breeding grounds and a matrix of pairwise distances between all individuals at their first stopover sites. I ran two Mantel tests between the breeding and non-breeding grounds, one using the location of the first non-breeding site that an individual visited during the non-breeding season, and one using the location of the last non-breeding site. This was done because, based on my definitions, 56% of individuals visited multiple non-breeding sites. 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 nodes. The randomization procedure was used because the distances between individuals in each matrix are not statistically independent (Ambrosini et al. 2009). 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 and populations are not mixing between these seasons.

### *Network metrics*

I 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 this 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 neighbours (Raghavan et al 2007). At the completion of the algorithm, connected nodes with the same label form a community. In this analysis, there was no

rule that nodes of the same or different sets had to be grouped into ‘communities’ but, in this case, 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.

Related to the community structure analysis, I also calculated two metrics that ranked the importance of nodes for maintaining structure. An *articulation point* (also known as a *cut-node*) is a node, which, if removed, will disconnect a part of the network (Urban and Keitt 2001), thus creating two or more new *components* in the network that were previous not observed (Urban et al. 2009). 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 (Guimerà et al. 2005b). 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 ( $P \leq 0.05$ ; Guimerà et al. 2005b).

Centrality measures are used to identify the most important nodes in the network for maintaining connectivity. *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 two other nodes (Newman 2003, Urban et al. 2009). A node with high betweenness centrality is between many pairs of nodes.

For all network-based analyses, I used the iGraph package (Csardi and Nepusz 2006) in R. Nodes represent all breeding, autumn stopover, and non-breeding locations that individuals visited throughout the annual cycle. I 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.

*Edge weight based on migratory strategy and relative abundance*

The primary step towards building a migratory network is describing which edges (migratory pathways) link different nodes in the network (Fig. 2), but it is difficult to evaluate the importance of nodes (or do demographic analyses) based solely on the number and distribution of edges because the edges are not weighted according to the number of individuals moving along them. The relative weighting of edges can influence their importance in the network, as well as how networks may change via birds' responses to habitat loss (Marra et al. 2006). To weight the network by the number of individuals moving along the edges, I 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). I chose to use BBS data so I could represent a larger region around each of the sampling 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 data were derived. I attempted to find the optimal balance and chose to exclude some breeding areas from the analysis.

I estimated abundance associated with each of the 12 breeding sites by first defining breeding regions from which I could extract BBS data. I 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 I used to calculate relative abundance that were linked to migratory strategies of each breeding site were based on the BCRs that the breeding sites were located in, as well as adjacent BCRs that I thought would contain individuals with similar migration routes (Supplementary Material Fig. S-2). While, collectively, the breeding regions I defined encompassed 46% of the area of tree 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 I 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 this network (Butler 1988), and swallow abundance is relatively low in these areas (Sauer et al. 2014).

To calculate the index of abundance for each region, I obtained a BBS shapefile with indices of relative abundance from 2008–2012 for tree swallows across each of the regions I defined (Sauer et al. 2014). Abundance was estimated using distance-weighted averages of counts along standard BBS survey routes. Using ArcGIS 10.4 (ESRI, Redlands, California, USA), I first summed the indices of relative abundance across all points within the breeding region. These points are based on extrapolating mean counts along 40 km BBS roadside surveys

(Sauer et al. 2014). The index of relative abundance for each breeding region was the sum of all indices of abundance over the breeding region divided by the total abundance across all breeding regions. Some breeding regions contained more than one breeding site, so the index of relative abundance for those breeding regions was divided by the number of breeding sites in that region. The BBS indices of abundance did not reach into the area around Fairbanks because there are few BBS routes in Alaska, so I used the index of abundance from the Boone, NC site because Fairbanks is also on the edge of the breeding range and therefore swallows are likely in low relative abundance there.

Once I had indices of relative abundance (Supplementary Material Table S-1) and proportions for each of the 12 breeding sites, the indices of relative abundance from the breeding regions were propagated through the network. The weight for edges connecting the breeding sites to the first stopovers were calculated by multiplying the proportion of observed individuals moving along that edge by the breeding site's index of relative abundance. The relative abundance of individuals moving along those 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, therefore, 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**

### *Geolocator recovery rates*

M-series geolocator recovery rates ranged from 11–35% among sites, with Saukville, WI having the lowest recovery rate and Sherbrooke, QC the highest (Table 1). However, I found no

significant difference in recovery rates between sites for the M-series geolocators (Fisher's exact test, simulated  $p = 0.12$ ). The E.S.B. geocator recovery rate from Ithaca, NY was 34%.

### *General description of the network*

Overall, I identified 10 autumn stopover and 13 non-breeding nodes for 133 individuals tracked from 12 breeding nodes (Fig. 3a). 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 1–3 autumn stopover nodes (mean =  $1.36 \pm 0.04$  SE, mode = 1; only one individual visiting three stopovers) and stayed for an average of 58 d (SD = 31.64, range 14–204 d). There was no evidence that the number of stopovers individuals visited differed based on their breeding origin (GLM,  $df = 11$ ,  $\chi^2 = 10.35$ ,  $p = 0.50$ ). There was a high degree of connectivity between the breeding sites and the first autumn stopover nodes ( $r_M = 0.75$ ,  $n = 133$ ,  $p < 0.001$ ).

Individuals occupied between 1–3 non-breeding nodes (mean =  $1.54 \pm 0.06$  SE, mode = 1) and stayed for an average of 80 d (SD = 48.33, range 14–186 d). Eleven individuals returned to a particular node more than once within the non-breeding season (for example moving from NW Mexico to SW Mexico and back). There was no evidence that the number of non-breeding nodes individuals visited differed based on their breeding origin (GLM,  $df = 11$ ,  $\chi^2 = 5.80$ ,  $p = 0.89$ ). In contrast to the connectivity between breeding sites and autumn stopover nodes, there was a moderate degree of connectivity among breeding sites and first-visited non-breeding nodes ( $r_M = 0.52$ ,  $n = 133$ ,  $p < 0.001$ ) and a similar degree of connectivity among breeding sites and the last-visited non-breeding nodes ( $r_M = 0.51$ ,  $n = 133$ ,  $p < 0.001$ ).

### *Community structure*

Using label propagation to identify community structure, I 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 eastern 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. 3b). There were no articulation points within the network, meaning that the network could not be disconnected by the removal of any single node. 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  $0.62 < P \leq 0.80$ ; Guimerà et al. 2005b) 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).

### *Relative importance of nodes*

I used two centrality measures to determine the most and least important nodes in the network for maintaining 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 ( $\leq 0.01$ ; 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 (594), 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 results between the weighted (Table 3) and unweighted network (Table 4) were very similar for betweenness centrality. The only exception to this was that the Cuba and Southwest Mexico nodes were ranked above Louisiana and East Mexico 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**

This study, using tracks from individual tree swallows spanning over 5000 km from Alaska to Nova Scotia, provides the most comprehensive description and evaluation of a migratory songbird network published to date. By applying network metrics to this continent-wide sample, I provide 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, and the Mantel correlation coefficient from breeding to non-breeding nodes suggested a moderate degree of mixing, I also identified three distinct ‘communities’ that represented major ‘flyways’ down the west, center, and east of the continent. This suggests that, while there is some consistency in the migratory routes and non-breeding sites used by a given breeding population,

some individuals adopt ‘alternative’ migratory strategies and use different non-breeding sites, yet return to the same breeding site the following year. The community structure, combined with a lack of articulation points in the network (no node would disconnect the network if removed), supports my inference about consistent mixing throughout the network overlaid on a distinct, broad-scale structure. It remains to be determined whether other migratory songbird networks follow a similar pattern when examined across their range.

I also provide evidence that the degree of connectivity changes over the course of the annual cycle. I found a high degree of migratory connectivity between the breeding and first stopover sites individuals visited, but only a moderate degree of connectivity between the breeding and both the first and final non-breeding sites. This suggests that regional breeding populations of tree swallows are mostly segregated from other breeding areas 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. Koleček et al. (2016) also found only a very slight decrease in the degree of migratory connectivity between the first and final non-breeding sites of great reed warblers (*Acrocephalus arundinaceus*; Table 5). This suggests that mixing occurs throughout the non-breeding season in other species, though previous studies have not considered connectivity with the autumn stopover sites as I did in this study. The Mantel test provides a means to compare the degree of connectivity between different periods of the annual cycle, something that is useful for describing spatio-temporal patterns in complex networks.

Determining the degree of mixing between breeding and non-breeding populations has important implications for predicting how populations will respond to environmental change. The degree of connectivity in tree swallows between breeding and non-breeding sites falls

approximately in the middle of those previously reported in past studies (Table 5), while the degree of connectivity between breeding and autumn stopover sites falls at the high end. A high degree of connectivity between the 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; moderate mixing between the breeding and non-breeding grounds suggests that events that occur at any non-breeding site will likely have an effect on multiple breeding populations (Taylor and Norris 2010). However, the size of the species' range and the distance between sampled populations are important to consider when comparing results among studies, as connectivity between neighbouring populations likely will 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 (e.g., Stanley et al. 2015; Table 5) than if deployment sites are farther apart (e.g., Koleček et al. 2016; Table 5).

#### *Priority of 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, I identified six nodes that were highly used by individuals from multiple breeding populations, are important for maintaining overall connectivity in the network, and facilitate flow in the network. Maintaining a connected network may be desirable over a disconnected network as it may provide a buffer against global population declines (Taylor and Norris 2010, Betini et al. 2015). These important nodes are the Midwest, the Dakotas, the Mid-Atlantic coast, South Florida, Louisiana, and East Mexico. This study confirms sites that were 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 I identified above were not previously recognized as important sites. Individuals from five of the 12 populations moved through the Midwest stopover node, coming from the 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 between nodes. The propagating labels algorithm that I used constructed communities that spanned the annual cycle and contained nodes of all three types, even though the network was made of up a single component. Buhnerkempe et al. (2016) also used network metrics to determine migratory flyways that spanned the annual cycle in four species of

waterfowl. The flyways that they identified differed among species and were distinct from those currently used in waterfowl management, which are based on political boundaries (Buhnerkempe et al. 2016).

The tree swallow network consisted of three communities that span across 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. 3b). Western breeding populations migrate west of the Rocky Mountains to overwinter mostly in NW and SW 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 et al. 1988) to spend the non-breeding season, for the most part, around the Gulf of Mexico. Eastern populations migrate down the Atlantic coast to overwinter in Florida, Cuba, and the Bahamas. The migratory flyways that I 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 geolocators were not deployed in these states, I cannot confirm this flyway.

The strong 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). Since 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 was done here using community detection, would be more effective.

### *Stopover ecology*

This 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 day refueling stopovers, short stopovers are difficult to identify given the spatial resolution of geolocators. Thus, I only identified stopovers that were visited for greater than 2 weeks. These extended autumn stopovers averaged 58 days, and so individuals were clearly not using these sites solely for refueling (Alerstam 1991). Tree swallows finish breeding in June or July (Winkler et al. 2011), depart the breeding grounds within 1–2 weeks after fledging young (all authors, unpublished), 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, during which individuals remain at stopover sites for extended periods, is one strategy to decrease the energetic costs of molt. 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 overwinter in South America and complete molt on the non-breeding grounds (Niles 1972), the harsher northern

winters 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 (Stutchbury and Rohwer 1990), but it is unlikely they experience severe time constraints that would prevent this from occurring as 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 (Winkler et al. 2011), which has the benefit of reducing predation risk and thus energetic demand during this long molt period. However, large roosts can also have density-dependent effects on resource acquisition, which may force some birds to molt at sites farther from the breeding grounds.

While tree swallows likely use autumn stopover sites for molt, there also appears to be a range of stopover strategies across the continent. Individuals from some breeding sites (Ames, Saukville, Long Point, Ithaca) stopped very close to the breeding grounds, while individuals from other breeding sites (Fairbanks, Vancouver, Prince George) travelled thousands of kilometers before reaching their first stopover site, and others travelled intermediate distances (Beaverhill, Saskatoon, Boone, Sherbrooke, Wolfville). Some individuals, predominantly in the eastern breeding regions, may begin an uninterrupted molt before leaving the breeding grounds, while others begin molt after migrating to roosting sites near the breeding grounds (Stutchbury and Rohwer 1990). Conversely, individuals from Vancouver and Prince George went directly from the breeding to the western non-breeding regions in Mexico, and presumably molted at these non-breeding sites (Stutchbury and Rohwer 1990).

Molt migration is well documented in several avian groups such as waterfowl and shorebirds, but is rarely documented in passerines (reviewed in Leu and Thompson 2002, Pyle et al. 2009). Tree swallows may travel short distances to molt near their breeding site, or travel long

distances, often over 3000 km, to reach molting sites. This dichotomy in the distances to molting sites is particularly interesting because it can provide insights into the variance in molt migration strategies across and within species. Molt is energetically demanding and, coupled with the changes in aerodynamics and physiology during this period, may influence the seasonal timing and location of molt (reviewed in Leu and Thompson 2002). Thus, the main hypothesis about why individuals of some populations or species leave the breeding grounds to molt relates to insufficient food, forcing birds to delay molt until they reach sites with 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 at this time of year (Leu and Thompson 2002, Bortolotti et al. 2011) and all individuals migrate to Mexico, or in one case Utah/Arizona, before beginning molt. The NW and SW 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, Pyle et al. 2009) that rapidly increase food abundance and attract molting individuals to these regions (Méndez-Barroso et al. 2009).

### *Overwintering ecology*

Given that half of the individuals moved between multiple (2–3) widely separated non-breeding nodes, remaining for an average of 80 d at each node, these results challenge the notion of a ‘stationary’ non-breeding period. Intratropical, or non-breeding, movements have been found in previous studies of 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 (Stutchbury et al. 2016). Furthermore, because temperature influences the food availability of aerial insects (Taylor 1963, McCarty and Winkler 1999b), this could be driving tree swallows farther south as the non-breeding season progresses. The individuals that persist in some of the more northern overwintering 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 moving throughout the non-breeding season as they track the abundance of bayberries. These shrubs/small trees produce waxy berries that only a few species of animals, including tree swallows, can digest (Place and Stile 1992). They ripen in the autumn and persist well into winter (Place and Stile 1992), 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 overwinter so far north (Place and Stiles 1992). It also explains how one individual from Saukville was able to overwinter along the Mid-Atlantic coast, where small numbers of tree swallows have been previously observed to overwinter and were believed to have been persisting on a diet of bayberries (Winkler et al. 2011). It appears, therefore, that individuals can have vastly different non-breeding strategies.

*Implications for 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 I was able to, post hoc, systematically sample across the breeding range of tree swallows. I 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.

One drawback to tracking animal movements using geolocators is that they have to be retrieved in order to obtain the data, and so the patterns I observed were biased toward individuals who returned to their breeding site from the previous year. Some individuals may have gone to a different breeding site that was not monitored (though the high site fidelity in tree swallows suggests this is likely not a major problem; e.g., Lagrange et al. 2014), or died before returning to the breeding grounds. If individuals who did not return had alternate migratory strategies, important patterns could be missing from the network I described. For example, if some individuals overwintered in an area I did not identify in the network analysis, but did not survive to return to the breeding grounds, I would be missing a key node that acts as a sink for the tree swallow population. New technologies that do not require tracking devices to be retrieved (e.g., ICARUS; Wikelski et al. 2007) will eventually overcome this drawback in small songbirds.

It is also important to note that the number of stopover and non-breeding nodes identified in a network are 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 at sites where few geolocators were recovered, some stopover or non-breeding nodes may have been missed. In this study, it seems that, for sites with small sample sizes (few retrieved geolocators), there was a lower probability of missing stopover sites than non-breeding sites, because the number of stopover nodes was not related to sample size (linear regression,  $\beta = 0.060 \pm 0.039$ ,  $t = 1.540$ ,  $p = 0.155$ ; Supplementary Material Fig. S-3), while the number of non-breeding nodes was higher for breeding sites with larger sample sizes (linear regression,  $\beta = 0.201 \pm 0.063$ ,  $t = 3.203$ ,  $p = 0.009$ ; Supplementary Material Fig. S-3). Although this analysis was able to identify many non-breeding sites, one should be cautious of the limitations of determining non-breeding sites when using small sample sizes. Small samples sizes can be overcome, however, with wide spatial coverage of the network, such as was done in this study. In this way, I described a fully connected migratory network, where an individual at any node can theoretically reach any other node in the network.

### *Conclusion*

This study represents a comprehensive examination of year-round movements from a single species across its North American breeding range. My results demonstrate that tree swallows have a highly connected network where populations increasingly mix as they move from the breeding to non-breeding season. I 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, I also show that there are three distinct migratory flyways that tree swallows use during autumn and spring migration.

I show that network metrics can be a relatively easy way to identify important features of a network if tracking data (or even mark-recapture data) are available, including overall spatial structure and important nodes for maintaining 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 this will be critical for building year-round, range-wide population models designed to predict how a species will respond to environmental change.

**LITERATURE CITED**

- Adams, D. K., and A. C. Comrie. 1997. The North American monsoon. *Bulletin of the American Meteorological Society* 78:2197-2213.
- Afanasyev, V. 2004. A miniature daylight level and activity data recorder for tracking animals over long periods. *Memoirs of National Institute of Polar Research. Special Issue* 58:227-233.
- Alerstam, T. 1991. Bird flight and optimal migration. *Trends in Ecology and Evolution* 6:210–215.
- Ambrosini, R., A. P. Møller, and N. Saino. 2009. A quantitative measure of migratory connectivity. *Journal of Theoretical Biology* 257:203-211.
- Ambrosini, R., J. J. Cuervo, C. du Feu, W. Fiedler, F. Musitelli, D. Rubolini, B. Sicurella, F. Spina, N. Saino, and A. P. Møller. 2016. Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin *Erithacus rubecula*: a continent-wide analysis. *Journal of Animal Ecology* 85:749-760.
- Arlt, D., P. Olsson, J. W. Fox, M. Low, and T. Pärt. 2015. Prolonged stopover duration characterises migration strategy and constraints of a long-distance migrant songbird. *Animal Migration* 2:47-62.
- Bairlein, F., D. R. Norris, R. Nagel, M. Bulte, C. C. Voigt, J. W. Fox, D. J. T. Hussell, and H. Schmaljohann. 2012. Cross-hemisphere migration of a 25 g songbird. *Biology Letters*:rsbl20111223.
- Becker, R. A., and A. R. Wilks. 1993. Maps in S. AT&T Bell Laboratories Statistics Research Report 93.2:1-21.
- Betini, G. S., M. J. Fitzpatrick, and D. R. Norris. 2015. Experimental evidence for the effect of habitat loss on the dynamics of migratory networks. *Ecology Letters* 18:526-534.

- Bortolotti, L. E., V. B. Harriman, R. G. Clark, and R. D. Dawson. 2011. Can changes in provisioning by parent birds account for seasonally declining patterns of offspring recruitment?. *Canadian Journal of Zoology* 89:921-928.
- Bradley, D. W., R. G. Clark, P. O. Dunn, A. J. Laughlin, C. M. Taylor, C. Vleck, L. A. Whittingham, D. W. Winkler, and D. R. Norris. 2014. Trans-Gulf of Mexico loop migration of tree swallows revealed by solar geolocation. *Current Zoology* 60:653-659.
- Bridge, E. S., J. F. Kelly, A. Contina, R. M. Gabrielson, R. B. MacCurdy, and D. W. Winkler. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology* 84:121-137.
- Brower, L. 1996. Monarch butterfly orientation: missing pieces of a magnificent puzzle. *Journal of Experimental Biology* 199:93-103.
- Buhnerkempe, M. G., C. T. Webb, A. A. Merton, J. E. Buhnerkempe, G. H. Givens, R. S. Miller, and J. A. Hoeting. 2016. Identification of migratory bird flyways in North America using community detection on biological networks. *Ecological Applications* 26:740-751.
- Butler, R. W. 1988. Population dynamics and migration routes of tree swallows, *Tachycineta bicolor*, in North America (dinámica de poblaciones y rutas de migración de *Tachycineta bicolor* en norte america). *Journal of Field Ornithology* 59:395-402.
- Calabrese, J. M., and W. F. Fagan. 2004. A comparison-shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment* 2:529-536.
- Cormier, R. L., D. L. Humple, T. Gardali, and N. E. Seavy. 2013. Light-level geolocators reveal strong migratory connectivity and within-winter movements for a coastal California Swainson's thrush (*Catharus ustulatus*) population. *Auk* 130:283-290.

- Cormier, R. L., D. L. Humple, T. Gardali, and N. E. Seavy. 2016. Migratory connectivity of Golden-crowned Sparrows from two wintering regions in California. *Animal Migration* 3:48-56.
- Csardi, G, and T. Nepusz. 2006. The igraph software package for complex network research. *InterJournal, Complex Systems* 1695:1-9.
- Dancose, K., D. Fortin, and X. Guo. 2011. Mechanisms of functional connectivity: the case of free-ranging bison in a forest landscape. *Ecological Applications* 21:1871-1885.
- Decout, S., S. Manel, C. Miaud, and S. Luque. 2012. Integrative approach for landscape-based graph connectivity analysis: a case study with the common frog (*Rana temporaria*) in human-dominated landscapes. *Landscape Ecology* 27:267-279.
- DeLuca, W. V., B. K. Woodworth, C. C. Rimmer, P. P. Marra, P. D. Taylor, K. P. McFarland, S. A. Mackenzie, and D. R. Norris. 2015. Transoceanic migration by a 12 g songbird. *Biology Letters* 11:20141045.
- Dingle, H. 2014. *Migration: the biology of life on the move*. Oxford University Press, New York, NY, USA.
- Dobkin, D. S., A. C. Rich, J. A. Pretare, and W. H. Pyle. 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin. *Condor* 97:694-707.
- Dray, S., and A. B. Dufour. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of statistical software* 22:1-20.
- Estrada, E., and Ö. Bodin. 2008. Using network centrality measures to manage landscape connectivity. *Ecological Applications* 18:1810-1825.

- Ferrer i Cancho, R., C. Janssen, and R. V. Solé. 2001. Topology of technology graphs: Small world patterns in electronic circuits. *Physical Review E* 64:046119.
- Finch, T., P. Saunders, J. M. Avilés, A. Bermejo, I. Catry, J. de la Puente, T. Emmenegger, I. Mardega, P. Mayet, D. Parejo, E. Račinskis, J. Rodríguez-Ruiz, P. Sackl, T. Schwartz, M. Tiefenbach, F. Valera, C. Hewson, A. Franco, and S. J. Butler. 2015. A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. *Diversity and Distributions* 21:1051-1062.
- Fraser, K. C., B. J. M. Stutchbury, C. Silverio, P. M. Kramer, J. Barrow, D. Newstead, N. Mickle, B. F. Cousens, J. C. Lee, D. M. Morrison, T. Shaheen, P. Mammenga, K. Applegate and J. Tautin. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proceedings of the Royal Society B: Biological Sciences* 279:1749. doi: 10.1098/rspb.2012.2207.
- Gómez, J., C. I. Michelson, D. W. Bradley, D. R. Norris, L. L. Berzins, R. D. Dawson, and R. G. Clark. 2014. Effects of geolocators on reproductive performance and annual return rates of a migratory songbird. *Journal of Ornithology* 155:37-44.
- Guimera, R., and L. A. N. Amaral. 2005a. Functional cartography of complex metabolic networks. *Nature* 433:895-900.
- Guimera, R., S. Mossa, A. Turttschi, and L. A. N. Amaral. 2005b. The worldwide air transportation network: Anomalous centrality, community structure, and cities' global roles. *Proceedings of the National Academy of Sciences* 102:7794-7799.
- Hahn, S., S. Bauer, and F. Liechti. 2009. The natural link between Europe and Africa—2.1 billion birds on migration. *Oikos* 118:624-626.

- Halls, L. K. 1977. Southern fruit producing woody plants used by wildlife. US Department of Agriculture Forest Service General Technical Report SO-16. New Orleans, Louisiana, USA.
- Hallworth, M. T., and P. P. Marra. 2015. Miniaturized GPS tags identify non-breeding territories of a small breeding migratory songbird. *Scientific reports* 5:11069.
- Harris, G., S. Thirgood, J. G. C. Hopcraft, J. P. G. M. Cromsigt, and J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research* 7:55-76.
- Heckscher, C. M., S. M. Taylor, J. W. Fox, and V. Afanasyev. 2011. Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. *Auk* 128:531-542.
- Hill, R. D. 1994. Theory of geolocation by light levels. Pages 227-236 in J. Burney, B. J. Le Boeuf, R. M. Laws, editors. *Elephant seals: population ecology, behaviour, and physiology*. University of California Press, Berkeley, California, USA.
- Hobson, K. A., K. J. Kardynal, S. L. Van Wilgenburg, G. Albrecht, A. Salvadori, M. D. Cadman, F. Liechti, and J. W. Fox. 2015. A continent-wide migratory divide in North American breeding Barn Swallows (*Hirundo rustica*). *PloS one* 10:e0129340.
- Holland, R. A., M. Wikelski, and D. S. Wilcove. 2006. How and why do insects migrate?. *Science* 313:794-796.
- Holt, R.F., and K. Martin. 1997. Landscape modification and patch selection: the demography of two secondary cavity nesters colonizing clearcuts. *Auk* 114:443-455.
- Knight, S., and D. R. Norris. 2016. Light-logging archival geolocators: opening the door to a new era of songbird migration science. *Ontario Birds* 34:134-140.

- Koleček, J., P. Procházka, N. El-Arabany, M. Tarka, M. Ilieva, S. Hahn, M. Honza, J. de la Puente, A. Bermejo, A. Gürsoy, S. Bensch, P. Zehindjiev, D. Hasselquist, and B. Hansson. 2016. Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. *Journal of Avian Biology* 47:1-12. doi:10.1111/jav.00929.
- Lagrange, P., R. Pradel, M. BÉlisle, and O. Gimenez. 2014. Estimating dispersal among numerous sites using capture–recapture data. *Ecology* 95:2316-2323.
- Laughlin, A. J., C. M. Taylor, D. W. Bradley, D. Leclair, R. G. Clark, R. D. Dawson, P. O. Dunn, A. Horn, M. Leonard, D. R. Sheldon, D. Shutler, L. A. Whittingham, D. W. Winkler, and D. R. Norris. 2013. Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. *Auk* 130:230–239.
- Lawler, J. J., and T. C. Edwards Jr. 2002. Composition of cavity-nesting bird communities in montane aspen woodland fragments: the roles of landscape context and forest structure. *Condor* 104:890-896.
- Leu, M., and C. W. Thompson. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: a review for neotropical migrants. *Biological Conservation* 106:45-56.
- Lincoln, F. C. 1935. The waterfowl flyways of North America. U.S. Department of Agriculture, circular 342. Washington, DC, USA.
- Marra, P. P., D. R. Norris, S. M. Haig, M. Webster, and J. A. Royle. 2006. Migratory connectivity. Pages 157-183 *in* K. R. Crooks and M. Sanjayan, editors. *Connectivity Conservation*. Cambridge University Press, Cambridge, UK.
- Martin T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham, and D. R. Norris. 2007. Optimal conservation of migratory species. *PLoS ONE* 2:e751.

- McCarty, J. P. and D. W. Winkler. 1999a. Foraging ecology and diet selectivity of tree swallows feeding nestlings. *Condor* 101:246-254.
- McCarty, J. P. and D. W. Winkler. 1999b. Relative importance of environmental variables in determining the growth of nestling Tree Swallows *Tachycineta bicolor*. *Ibis* 141:286–296.
- McKinnon, E. A., K. C. Fraser, and B. J. M. Stutchbury. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. *Auk* 130:211-222.
- Méndez-Barroso, L. A., E. R. Vivoni, C. J. Watts, and J. C. Rodríguez. 2009. Seasonal and interannual relations between precipitation, surface soil moisture and vegetation dynamics in the North American monsoon region. *Journal of hydrology* 377:59-70.
- Michel, N. L., A. C. Smith, R. G. Clark, C. A. Morrissey, and K. A. Hobson. 2015. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. *Ecography* 38: 1-13.
- Minor, E. S., and D. L. Urban. 2007. Graph theory as a proxy for spatially explicit population models in conservation planning. *Ecological Applications* 17:1771-1782.
- Nebel, S., A. Mills, J. D. McCracken, and P. D. Taylor. 2010. Declines of aerial insectivores in North America follow a geographic gradient. *Avian Conservation and Ecology* 5: 1.
- Newman, M. E. 2003. The structure and function of complex networks. *SIAM review* 45:167-256.
- Nicol, S., R. Wiederholt, J. E. Diffendorfer, B. J. Mattsson, W. E. Thogmartin, D. J. Semmens, L. López-Hoffman, and D. R. Norris. 2016. A management-oriented framework for selecting metrics used to assess habitat-and path-specific quality in spatially structured populations. *Ecological Indicators* 69:792-802.
- Niles, D. M. 1972. Molt cycles of Purple Martins (*Progne subis*). *Condor* 74:61-71.

- Norris, D. R., P. P. Marra, G. J. Bowen, L. M. Ratcliffe, J. A. Royle, and T. K. Kyser. 2006. Migratory connectivity of a widely distributed songbird, the American Redstart (*Setophaga ruticilla*). *Ornithological Monographs* 61:14-28.
- Ouwehand, J., M. P. Ahola, A. N. M. A. Ausems, E. S. Bridge, M. Burgess, S. Hahn, C. M. Hewson, R. H. G. Klaassen, T. Laaksonen, H. M. Lampe, W. Velmala, and C. Both. 2016. Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. *Journal of Avian Biology* 47:69–83.
- Place, A. R., and E. W. Stiles. 1992. Living off the wax of the land: Bayberries and Yellow-rumped Warblers. *Auk* 109:334–345.
- Poor, E. E., C. Loucks, A. Jakes, and D. L. Urban. 2012. Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. *PLoS One* 7:e49390.
- Proctor, M. F., S. E. Nielsen, W. F. Kasworm, C. Servheen, T. G. Radandt, A. G. Machutcheon, and M. S. Boyce. 2015. Grizzly bear connectivity mapping in the Canada–United States trans-border region. *The Journal of Wildlife Management* 79:544-558.
- Pyle, P., W. A. Leitner, L. Lozano-Angulo, F. Avilez-Teran, H. Swanson, E. G. Limón, and M. K. Chambers. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. *Condor* 111: 583-590.
- Quinney, T. E., and C. D. Ankney. 1985. Prey size selection by tree swallows. *Auk* 102:245-250.
- Raghavan, U. N., R. Albert, and S. Kumara. 2007. Near linear time algorithm to detect community structures in large-scale networks. *Physical review E* 76:036106.
- Rakhimberdiev, E., D. W. Winkler, E. Bridge, N. E. Seavy, D. Sheldon, T. Piersma, and A. Saveliev. 2015. A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. *Movement Ecology* 3:1-15.

- Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines (Nuevo Diseño de Arnés para Atar Transmisores a Passeriformes Pequeños). *Journal of Field Ornithology* 62:335-337.
- Rohwer S., L. K. Butler, and D. R. Froehlich. 2005. Ecology and demography of east-west differences in molt scheduling in Neotropical migrant passerines. Pages 87-105 in R. Greenberg and P. P. Marra, editors. *Birds of two worlds*. Johns Hopkins University Press, Baltimore, MD, USA.
- Runge, C. A., T. G. Martin, H. P. Possingham, S. G. Willis, and R. A. Fuller. 2014. Conserving mobile species. *Frontiers in Ecology and the Environment* 12:395-402.
- Ryder, T. B., J. W. Fox and P. P. Marra. 2011. Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark-recapture data. *Auk* 128:448-453.
- Sauer, J. R., J. E. Fallon, and R. Johnson. 2003. Use of North American Breeding Bird Survey data to estimate population change for bird conservation regions. *The Journal of wildlife management* 67:372-389.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2014. *The North American Breeding Bird Survey, Results and Analysis 1966 - 2013*. Version 01.30.2015 USGS Patuxent Wildlife Research Center, Laurel, MD, USA.
- Scott, J. 2012. *Social network analysis*. Sage, London, United Kingdom.
- Shutler, D., D. J. T. Hussell, D. R. Norris, D. W. Winkler, R. J. Robertson, F. Bonier, W. B. Rendell, M. Bélisle, R. G. Clark, R. D. Dawson, N. T. Wheelwright, M. P. Lombardo, P. A. Thorpe, M. A. Truan, R. Walsh, M. L. Leonard, A. G. Horn, C. M. Vleck, D. Vleck, A. P. Rose, L. A. Whittingham, P. O. Dunn, K. A. Hobson, and M. T. Stanback. 2012.

- Spatiotemporal patterns in nest box occupancy by tree swallows across North America. *Avian Conservation and Ecology* 7:3.
- Stach, R., S. Jakobsson, C. Kullberg, and T. Fransson. 2012. Geolocators reveal three consecutive wintering areas in the Thrush Nightingale. *Animal Migration* 1:1-7.
- Stanley, C. Q., E. A. Mckinnon, K. C. Fraser, M. P. Macpherson, G. Casbourn, L. Friesen, P. P. Marra, C. Studds, T. B. Ryder, N. E. Diggs, and B. J. M. Stutchbury. 2015. Connectivity of wood thrush breeding, wintering, and migration sites based on range-wide tracking. *Conservation Biology* 29:164–174.
- Stutchbury, B. J., and S. Rohwer. 1990. Molt patterns in the tree swallow (*Tachycineta bicolor*). *Canadian Journal of Zoology* 68:1468-1472.
- Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323:896.
- Stutchbury, B. J. M., R. Siddiqui, K. Applegate, G. T. Hvenegaard, P. Mammenga, N. Mickle, M. Pearman, J. D. Ray, A. Savage, T. Shaheen, and K. C. Fraser. 2016. Ecological causes and consequences of intratropical migration in temperate-breeding migratory birds. *American Naturalist* 188:S28-S40.
- Sutherland W. J., and P. M. Dolman. 1994. Combining behaviour and population dynamics with applications for predicting consequences of habitat loss. *Proceedings of the Royal Society B: Biological Sciences*: 255:133–138.
- Taylor, L. R. 1963. Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology* 32:99-117.

- Taylor, C. M., and D. R. Norris. 2010. Population dynamics in migratory networks. *Theoretical Ecology* 3:65-73.
- Taylor, C. M., and B. J. M. Stutchbury. 2016. Effects of breeding versus winter habitat loss and fragmentation on the population dynamics of a migratory songbird. *Ecological Applications* 26:424–437.
- Taylor, C. M., A. J. Laughlin, and R. J. Hall. 2016. The response of migratory populations to phenological change: a migratory flow network modelling approach. *Journal of Animal Ecology* 85:648–659.
- Tøttrup, A. P., R. H. G. Klaassen, R. Strandberg, K. Thorup, M. W. Kristensen, P. S. Jørgensen, J. Fox, V. Afanasyev, C. Rahbek, and T. Alerstam. 2012. The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society of London B: Biological Sciences* 279:1008-1016.
- Trierweiler, C., R. H. Klaassen, R. H. Drent, K.M. Exo, J. Komdeur, F. Bairlein, and B. J. Koks. 2014. Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences* 281:20132897.
- Urban, D., and T. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. *Ecology* 82:1205-1218.
- Urban D. L., E. S. Minor, E. A. Treml, and R. S. Schick. 2009. Graph models of habitat mosaics. *Ecology Letters* 12:260–273.

- U.S. NABCI Committee. 2000. North American bird conservation initiative: bird conservation region descriptions. U.S. Fish and Wildlife Service, Division of Bird Habitat Conservation, Washington, DC, USA.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76–83.
- Wells, J. V. 2011. Boreal birds of North America: a hemispheric view of the conservation links and significance. *Studies in Avian Biology* 41. University of California Press, Oakland, USA.
- Wiederholt, R., L. López-Hoffman, J. Cline, R. A. Medellín, P. Cryan, A. Russell, G. McCracken, J. Diffendorfer, and D. Semmens. 2013. Moving across the border: modeling migratory bat populations. *Ecosphere* 4:1-16.
- Wikelski, M., R. W. Kays, N. J. Kasdin, K. Thorup, J. A. Smith and G. W. Swenson. 2007. Going wild: what a global small-animal tracking system could do for experimental biologists. *Journal of Experimental Biology* 210:181-186.
- Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: is animal migration disappearing. *PLoS Biol* 6:e188.
- Winkler, D. W. 2006. Roosts and migrations of swallows. *El Hornero* 21:85-97.
- Winkler, D. W., K. K. Hallinger, D. R. Ardia, R. J. Robertson, B. J. Stutchbury, and R. R. Cohen. 2011. Tree Swallow (*Tachycineta bicolor*). In *Birds of North America Online* (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Available at [bna.birds.cornell.edu/bna/species/011](http://bna.birds.cornell.edu/bna/species/011).
- Wotherspoon, S., M. Sumner, and S. Lisovski. 2013. BASTag: basic data processing for light based geolocation archival tags. Version 0.1–3.

Table 1. Summary of 561 M-series geolocators deployed between 2010 and 2014 across 12 breeding sites, and 35 E.S.B. geolocators deployed in 2011 in Ithaca, NY. In total, 140 M-series and 12 E.S.B. geolocators were recovered.

<b>Location</b>	<b>Province/State</b>	<b>Latitude (°N), Longitude (°W)</b>	<b>Years geolocators deployed</b>	<b>Number of geolocators deployed</b>	<b>Number of geolocators retrieved</b>
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	Quebec	45.55, -72.60	2012, 2014	51	18
Wolfville	Nova Scotia	45.10, -64.39	2011, 2012	60	12

Table 2. Participation coefficients ( $P$ )  $> 0$  for nodes in the tree swallow network, ranked in order of decreasing  $P$ .  $P$  is a measure of how many of the edges connected to a given node are linked to other nodes within its community versus nodes in other communities (for communities, see Fig. 3b). A high  $P$  value indicates that nodes have a relatively high number of connections to nodes outside its community.

<b>Node</b>	<b>Node type</b>	<b>P</b>
Texas coast	Non-breeding	0.67
Louisiana	Non-breeding	0.54
Saukville	Breeding	0.50
Midwest	Stopover	0.48
SW Mexico	Non-breeding	0.48
E Mexico	Non-breeding	0.45
Wisconsin	Stopover	0.44
Bahamas	Non-breeding	0.38
Dakotas	Stopover	0.38
W Florida	Non-breeding	0.38
S Florida	Non-breeding	0.36
NW Mexico	Non-breeding	0.32
Lake Erie	Stopover	0.28
Cuba	Non-breeding	0.24
Carolinas/Georgia	Non-breeding	0.22

Table 3: Eigenvector centrality and betweenness centrality scores from the tree swallow migratory network for autumn stopover and non-breeding nodes, weighted by population indices of relative abundance. Nodes are ranked by eigenvector centrality from high to low.

<b>Node</b>	<b>Eigenvector centrality</b>	<b>Betweenness centrality</b>
<b>Stopover nodes</b>		
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	0.01	0
S New York	0.01	1
Baja California	0.01	0
N New York	0.00	0
<b>Non-Breeding nodes</b>		
Louisiana	0.85	389
S Florida	0.44	638
E Mexico	0.43	327
Quintana, Mexico	0.19	33
NW Mexico	0.16	241
SW Mexico	0.14	33
Carolinas/Georgia	0.12	0
W Gulf of Mexico	0.11	195

Cuba	0.07	0
Texas coast	0.05	118
Bahamas	0.04	19
W Florida	0.03	0
Honduras	0.01	0

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Table 4: Unweighted eigenvector centrality and betweenness centrality scores for autumn stopover nodes and non-breeding nodes. Nodes are ranked by eigenvector centrality from high to low.

<b>Node</b>	<b>Eigenvector centrality</b>	<b>Betweenness centrality</b>
<b>Stopover nodes</b>		
Mid-Atlantic coast	0.76	142
Midwest	0.44	260
Lake Erie	0.44	43
S New York	0.41	11
New England coast	0.34	7
Dakotas	0.26	121
Wisconsin	0.25	27
N New York	0.12	0
Utah/Arizona	0.03	1
Baja California	0.02	6
<b>Non-Breeding nodes</b>		
S Florida	1.00	189
Carolinas/Georgia	0.89	107
Cuba	0.70	138
Bahamas	0.53	35
Louisiana	0.53	151
W Florida	0.49	10
E Mexico	0.31	126
W Gulf of Mexico	0.18	96

SW Mexico	0.16	173
Quintana, Mexico	0.14	34
NW Mexico	0.10	98
Texas coast	0.10	38
Honduras	0.05	0

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Table 5. 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. Values are based on the Mantel correlation coefficient and range from strong ( $r_M = 1$ ) to weak ( $r_M = 0$ ).

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> )	0.51-0.52	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

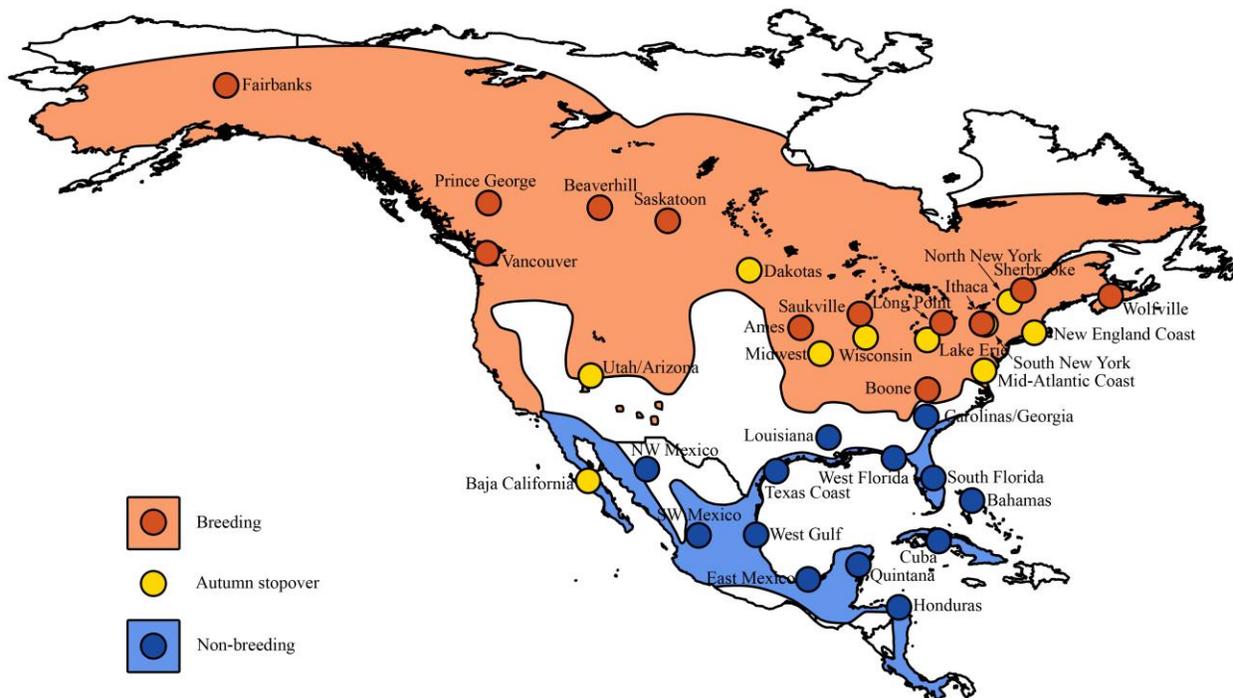


Figure 1. Breeding (dark orange), autumn stopover (yellow) and non-breeding (dark blue) nodes, superimposed on a map showing the breeding (orange) and non-breeding (blue) ranges of tree swallows (BirdLife International and NatureServe 2015). Breeding nodes represent the 12 sites where geolocators were deployed, while the stopover and non-breeding nodes represent locations determined through geocator tracking and network analyses. I used a World2Hires Pacific-centered Mercator projection for the map (Becker and Wilks 1993).

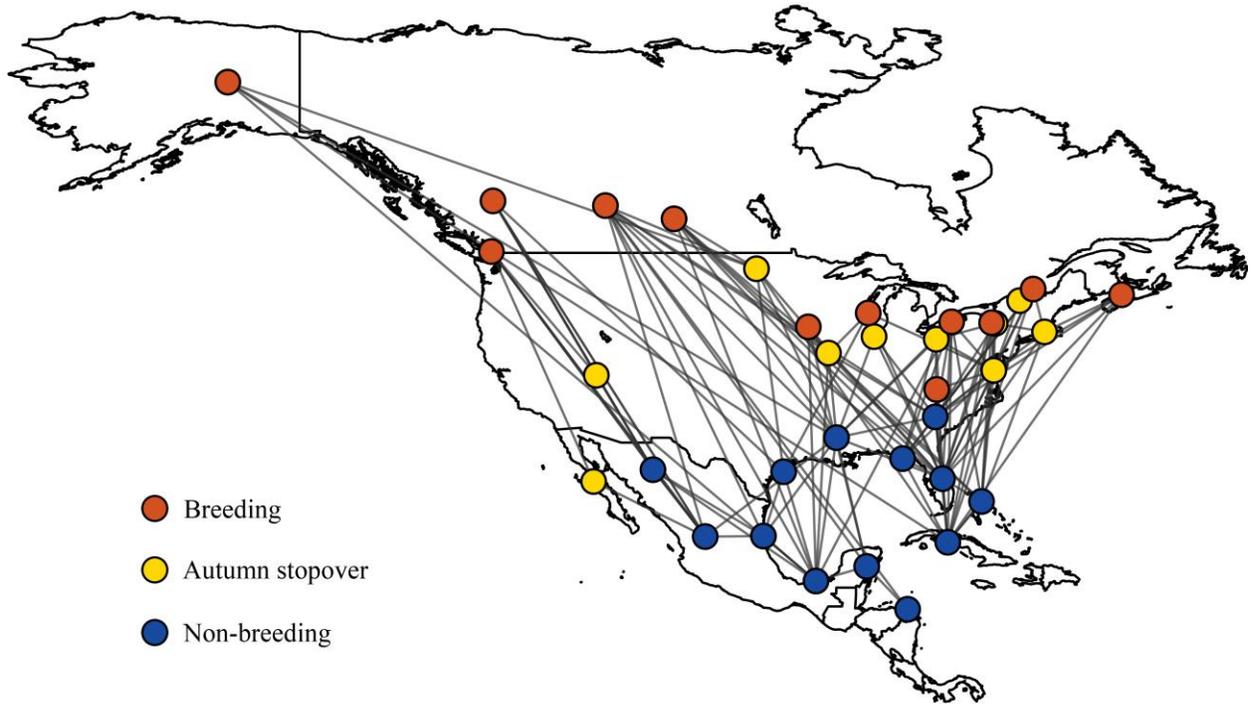


Figure 2. Migratory network for tree swallows showing breeding, autumn stopover, and non-breeding nodes. Edges connect the nodes, but do not represent the actual migratory path. I used a World2Hires Pacific-centered Mercator projection for the maps (Becker and Wilks 1993).

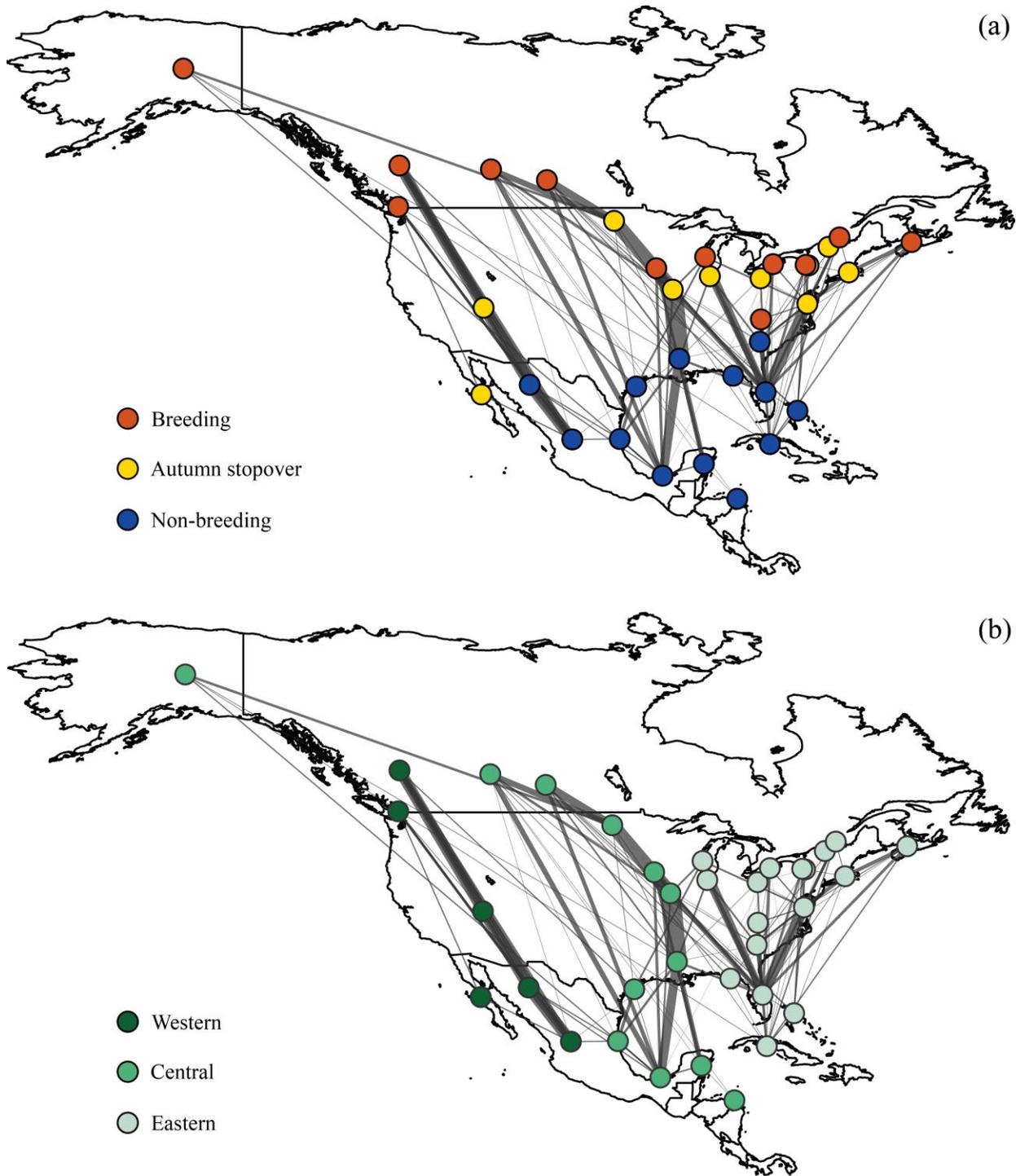


Figure 3. (a) Migratory network for tree swallows showing breeding, autumn stopover, and non-breeding nodes. (b) The same network showing three major migratory flyways (east of the Rocky Mountains, down the Mississippi River valley, and along the Atlantic coast), determined

by label propagation. Edges connect the nodes but do not represent the actual migratory path. Edges are weighted by the proportion of individuals moving between nodes multiplied by an index of relative abundance from the previous node. I used a World2Hires Pacific-centered Mercator projection for the maps (Becker and Wilks 1993).

**SUPPLEMENTARY MATERIAL**

Table S-1: Indices of relative abundance for each breeding site in the network estimated from BBS data

<b>Breeding site</b>	<b>Index of relative abundance</b>
Fairbanks	3.31
Vancouver	5.93
Prince George	17.37
Beaverhill	10.90
Saskatoon	10.90
Ames	10.90
Saukville	14.11
Boone	3.31
Long Point	5.67
Ithaca	5.67
Sherbrooke	5.97
Wolfville	5.97

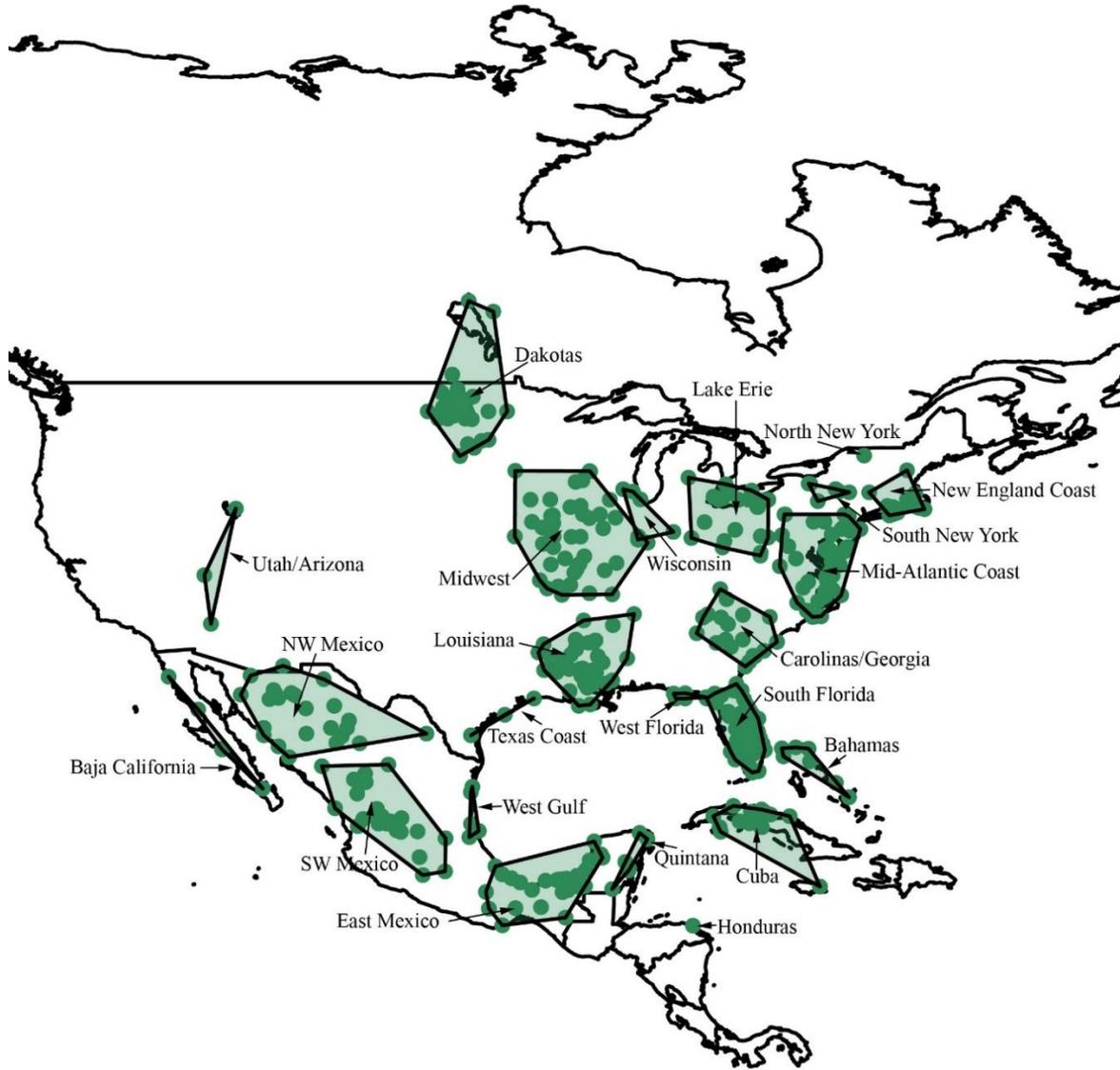


Figure S-1. Minimum convex polygons showing the stopover and non-breeding node areas. All stopover and non-breeding sites identified for 133 tree swallows are shown by the green points.

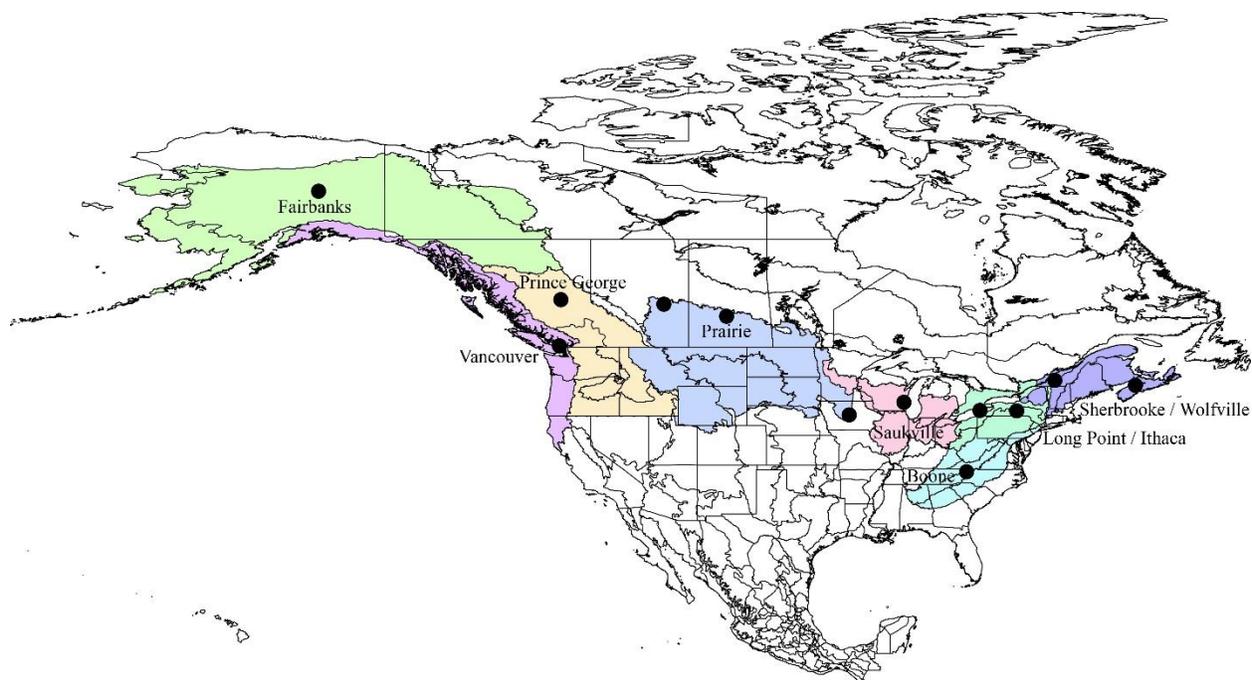


Figure S-2. Bird Conservation Regions (BCR) for each breeding site (shown as points on the map). The Fairbanks breeding region was composed of BCR 2 (Western Alaska) and BCR 4 (Northwestern Interior Forest). The Vancouver breeding region was composed of BCR 5 (Northern Pacific Rainforest). The Prince George breeding region consisted of the BC, Washington, Idaho, and Oregon portions of BCR 10 (Northern Rockies), and the BC, Washington, Idaho, and Oregon portions of BCR 9 (Great Basin). The Beaverhill, Saskatoon, and Ames (Prairie) breeding region was composed of BCR 11 (Prairie Potholes), BCR 17 (Badlands and Prairies), and the Montana, Wyoming, and Colorado portions of BCR 10. The Saukville breeding region included BCR 23 (Prairie Hardwood Transition), and the Illinois, Indiana, and Ohio portions of BCR 22 (Eastern Tallgrass Prairie). The Long Point and Ithaca breeding region was composed of the Ontario and American portions of BCR 13 (Lower Great Lakes/St. Lawrence Plain), as well as the Ohio, Pennsylvania, New York, and New Jersey portions of BCR 28 (Appalachian Mountains). The Sherbrooke and Wolfville breeding region was composed of BCR 14 (Atlantic Northern Forest) and the Quebec portion of BCR 13 (Lower

Great Lakes/St. Lawrence Plain). The Boone breeding region was composed of the remaining states in BCR 28 (Appalachian Mountains) and BCR 29 (Piedmont).

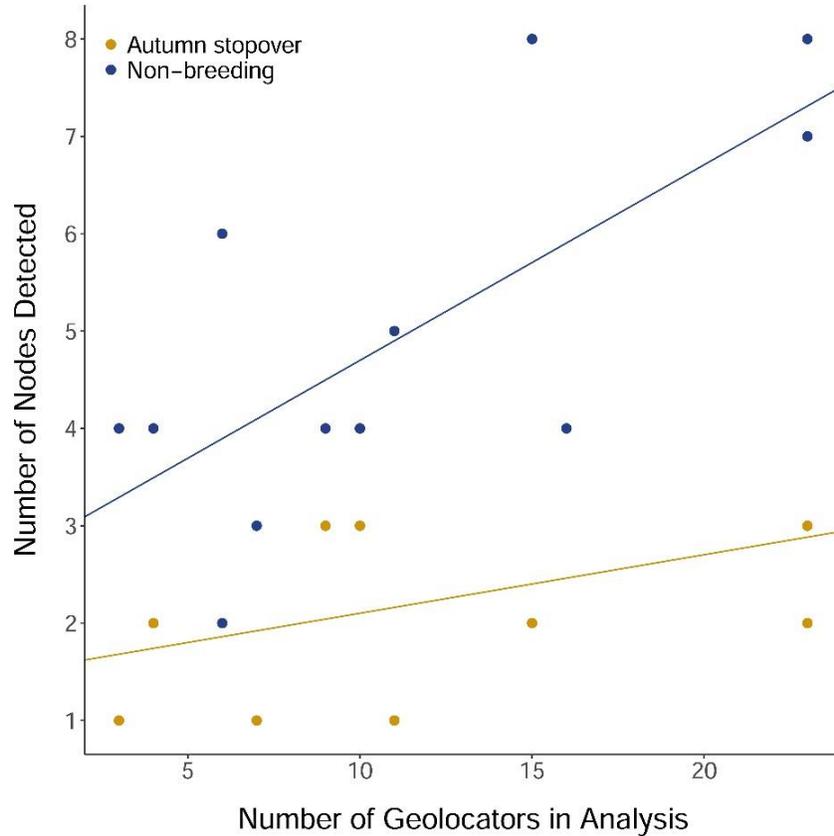


Figure S-3. Number of autumn stopover nodes (gold) and non-breeding nodes (blue) detected based on the number of geolocators retrieved and used for analysis (sample size) at each breeding site. There was no significant difference in the number of stopover nodes that I was able to detect based on sample size (linear regression,  $\beta = 0.060 \pm 0.039$  SE,  $t_{10} = 1.540$ ,  $p = 0.155$ ). Sample size did have a statistically significant effect on the number of non-breeding nodes that I was able to detect for each breeding population (linear regression,  $\beta = 0.201 \pm 0.063$  SE,  $t_{10} = 3.203$ ,  $p = 0.009$ ).