



Migration routes, high-use areas, and network connectivity across the annual cycle of an arctic seabird

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Abstract

Understanding how breeding and non-breeding populations are geographically linked across seasons has important behavioral, demographic, and evolutionary implications for migratory animals. We used movement data collected from satellite-tagged Red-throated Loons (*Gavia stellata*) to provide new and more accurate information about spatial use during the full annual cycle for this species in eastern North America. We provide the first complete description of four migration routes used by Red-throated Loons along the U.S. mid-Atlantic coast and their northern breeding grounds. Despite sampling just 5% of the North American Atlantic coast non-breeding range, the birds we sampled exhibited a high degree of population spread across 65% of the breeding range, occurring across 44 degrees of longitude and 23 degrees of latitude. Network analysis identified core stopover areas with high population use and slower movement speeds, as well as migratory corridors associated with faster speeds and higher connectivity between core sites. Some of these high-use areas represent sites where environmental events could impact a majority of the sampled individuals, e.g., some of the migratory corridors and stopover locations were used exclusively by birds breeding in the far eastern breeding range. Our results underscore the possibility that spatial connectivity can exist between the migratory period and one stationary period even when there is not strong migratory connectivity as traditionally measured between stationary periods.

Keywords Migratory connectivity · Network theory · Movement ecology · Annual cycle · Migration · Stopover ecology · *Gavia stellata* · Red-throated Loon

Zusammenfassung

Zugrouten, stark frequentierte Gebiete und Verbindungen untereinander bei einem arktischen Seevogel während eines ganzen Jahres. Zu wissen, wie brütende und nicht brütende Populationen über die Jahreszeiten hinweg geografisch miteinander verbunden sind, bietet wichtige Ansatzpunkte für die Verhaltensbiologie, Demographie und Evolutionsbiologie ziehender Tiere. Wir benutzten über Satelliten erfasste, gesammelte Bewegungsdaten von Sterntauchern (*Gavia stellata*), um neue und genauere Informationen über ihre Bewegungen im Raum während eines ganzen Jahrs im Osten Nordamerikas zu bekommen. Hier geben wir die erste vollständige Beschreibung von vier Zugrouten von Sterntauchern entlang der mittelatlantischen Küste der USA und ihren nördlichen Brutgebieten. Trotz der Stichproben von nur 5% des Nicht-Brutgebiets an der nordamerikanischen Atlantikküste zeigten die von uns erfassten Vögel eine sehr große Populations-Ausbreitung über 65% des Brutgebiets, das sich über ein Gebiet von 44 Längengrade und 23 Breitengrade erstreckte. Eine Analyse des

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Zug-Netzwerks ergab Kerngebiete für Zwischenstopps, die bei langsameren Fluggeschwindigkeiten von den Populationen sehr stark genutzt wurden, sowie Korridore, in denen es höhere Geschwindigkeiten und mehr Verbindungen zwischen den Kerngebieten gab. Einige dieser stark frequentierten Gebiete sind Bereiche, in denen sich Umweltgegebenheiten auf die Mehrheit der erfassten Tiere auswirken könnten, z. B. wurden einige der Zugkorridore und Rastplätze ausschließlich von Vögeln aus den weiter im Osten gelegenen Brutgebieten genutzt. Unsere Ergebnisse unterstreichen die Möglichkeit, dass auch während und außerhalb der Zugzeit eine räumliche Verbindung sogar dann bestehen kann, wenn es nicht den starken Zug-Zusammenhalt gibt, der normalerweise während der Zugzeiten festgestellt wird.

Introduction

Animal populations may be limited by factors operating in any part of their annual cycle, and the limiting factors with the greatest effect on species vital rates will result in the greatest changes in annual and long-term abundance (Newton 2004). For migratory birds making large-scale seasonal movements between disparate breeding and wintering ranges, these effects interact across multiple spatial and temporal scales to influence population dynamics (Nichols 1996). Demographic events experienced during one time or in one place during the annual cycle may result in carryover effects during subsequent seasons, including the timing or capacity to migrate, breed, or survive (Marra et al. 1998; Studds and Marra 2005). The ability for these effects to propagate across an entire population or species, however, is determined by the degree of spatial interconnectivity achieved through individual movements. Effective conservation at the species scale therefore necessitates a full annual cycle research approach (Rushing et al. 2016) that elucidates (A) seasonal variability in where individuals are most likely to be exposed to ecological or evolutionary impacts (i.e., spatial distribution) as well as (B) how likely those impacts will propagate due to exchanges in individuals among areas (i.e., connectivity).

Understanding how breeding and non-breeding populations are geographically linked across seasons for migratory species, i.e., migratory connectivity, is key to understanding how ecological or evolutionary impacts in one location propagate across the annual range (Webster and Marra 2005; Webster et al. 2002; Taylor and Norris 2010; Kays et al. 2015). Migratory connectivity is strongest when populations are highly structured, and most individuals who reside near each other in one period of the year are similarly associated in other residential periods. Consequently, the effects of local environmental conditions will propagate much faster across the entire species for species with high migratory connectivity (McKellar et al. 2013; Ouweland et al. 2016). In contrast, individuals from migratory populations with weak connectivity diffuse across the species range between stationary phases, and individuals from any given locale during one phase may overlap with individuals from across the range during the opposite stationary phase (Webster et al.

2002). The environmental conditions that might influence demographic rates in one locale during one season (and, in turn, the resultant ecological and evolutionary impacts of those conditions) are, thus, diluted across a range of locations for the other season (Cresswell 2014).

Bird conservation has advanced greatly in the last twenty years by moving from a focus almost solely on breeding locations to one that includes the demographic impacts from the non-breeding stationary phase as well (Marra et al. 2015). Over the course of their annual cycle, however, migratory animals exploit multiple habitats between those two end points of their overall range (Alerstam et al. 2003). In fact, migration can occupy as much or more of the annual cycle than any stationary phase, and commonly individuals experience a greater degree of habitat heterogeneity and risk to survival during migration than they do during the stationary phases of the year (Klaassen et al. 2014; Newton 2006). Therefore, understanding where species experience ecological disturbances and how the impacts of these events spread across a species requires us to not only define connectivity between the stationary periods, but to instead define a complete annual movement network with all major seasonal sites—e.g., breeding, migratory stopovers, staging, and wintering—that describes where populations may or may not overlap in space and time throughout the year (Taylor and Norris 2010).

The idea of migratory connectivity may apply to migratory routes or stopover location as well as it does to stationary phases in the annual cycle, as these habitats may be used exclusively by a single resident population (high connectivity) or shared to varying degrees among all such populations (lower connectivity). Both high and low connectivity have potential conservation implications. While conservation at the migratory flyway level often focuses on migratory “bottlenecks” within the network (i.e., areas used by individuals from a large majority of stationary phase locations; (Brown et al. 2017; Sherry 2018; Cardenas-Ortiz et al. 2020; Studds et al. 2017), the probability of at least one member of a population encountering risk increases with the number of sites used by the population (Cresswell 2014). Therefore, species that rely upon a suite of sites to complete their annual cycle can experience greater cumulative risk of demographic effect and also may be more or less likely to

propagate impacts from many smaller sites across the species range depending on the degree of connectivity.

Principles of network theory are increasingly being used to evaluate the importance of different sites that comprise the network that migratory populations rely on during the course of their annual cycle (Taylor and Norris 2010; Bastille-Rousseau et al. 2018; Knight et al. 2018; Lamb et al. 2019). The network analysis approach, in comparison to more traditional methods of characterizing animal space use, such as utilization distributions (UDs), allows for the identification of movement corridors. These areas may either be hidden within the core use isopleth of a traditional UD surface (Benhamou and Riote-Lambert 2012; Bastille-Rousseau and Wittemyer 2021) or may be associated with less intensive use and classified as areas of low importance by UD methods, even though they provide important bridges for connectivity within the migratory flyway.

We used movement data collected from satellite-tagged Red-throated Loons (*Gavia stellata*) to accomplish three goals. First, we provide new and more accurate information about spatial use during the full annual cycle for this species in eastern North America. The Red-throated Loon is listed by the U.S. Fish and Wildlife Service (USFWS) as a species of conservation concern in much of its Arctic breeding range and wintering areas in the Atlantic Flyway. Second, we examined the strength of migratory connectivity and the degree of population spread between breeding and wintering areas using traditional methods (i.e., Mantel test) to compare this species to others that have been described in this way. Third, we used network theory and behavioral cluster analysis to construct a movement network for the species to obtain a better understanding of how spatial use and spatial connectivity might affect these birds throughout the annual cycle.

Methods

Study area and field efforts

Red-throated Loons were captured from January to March (2012–2015) while on their wintering areas in waters off the U.S. mid-Atlantic coast, with capture efforts focused in Delaware Bay, Chesapeake Bay, and Pamlico Sound. Birds were captured using night-lighting techniques, i.e., birds were approached at night by boat with a spotlight and captured with a dip net (Whitworth et al. 1997). All captured birds were fitted with a USFWS aluminum band and those aged “after second year” (ASY) via the methods described in (Pyle 2008) were considered primary candidates for PTT implantation. To minimize stress related to capture and handling, individuals were administered 2 mg/kg of mild sedative, midazolam hydrochloride IM, prior to

being transported to land-based surgery locations. Surgical implantations of intra-abdominal PTTs with external antenna were conducted by qualified veterinarians following techniques described elsewhere (Spiegel et al. 2017). Satellite transmitters weighed approximately 49 g and comprised <4% of the average body mass of birds deployed ($\bar{x} = 1853 \pm 256$ g).

Data collection and management

We used multiple transmitter duty cycles to extend battery life to approximately one year to ensure coverage over multiple stages of the birds’ annual cycles: (1) 4 h on and 13 h off for the period of 1 November to 31 May; (2) 2 h on and 5 days off from 31 May to 31 August; and (3) 4 h on and 24 h off from 31 August to 01 November. Location data for all active PTTs was downloaded from Argos servers every five days and filtered with the Douglas Argos Filter (DAF), which filters out improbable locations in satellite-tracking data that do not pass a spatial redundancy test and a movement rate and turning angle test (Douglas et al. 2012). More technical details on data preparation can be found in (Spiegel et al. 2017).

Animal movement behavior may be affected during the period immediately following the procedure, and data collected during the post-surgery period should be censored from data sets to limit surgery-related bias (Mulcahy and Esler 1999; Sexson et al. 2014). To determine the number of days to censor from the Red-throated Loon data set, we calculated daily survival probabilities for the 30-day post-surgery period using daily survival models in RMark (Laake 2013) as described in (Blomberg et al. 2018). We modeled the influence of potential group effects on daily survival—such as sex, capture year, and capture location—and explored threshold models to determine if there was a point where survival probability showed a marked increase, which would indicate the appropriate day to left-censor the data (Blomberg et al. 2018). AIC model selection results indicated support for threshold models for days 12, 13, 15, and 16 ($\Delta AIC_c \leq 2$); therefore, we chose the most conservative option and censored days ≤ 16 post-release for each bird.

For this study, we include position data from approximately one complete annual cycle for 36 Red-throated Loons. Location data per bird encompassed at least 300 days to ensure spatial coverage from capture on the non-breeding grounds to the establishment of breeding home ranges and return to the wintering range. Satellite transmitters had an average battery life of 378 ± 48 days; therefore, it was not possible to collect multiple years of data on individuals. We then used R package *foieGras* to filter observed locations with a continuous-time state-space model to account for error in the Argos telemetry, to estimate true animal

locations, and to regularize the filtered locations to a 24-h time interval (Jonsen et al. 2019).

Full annual cycle spatial use

Regularized tracks for each loon were uploaded into the R package *adehabitatLT* and stored as trajectory objects (Calenge 2006). Shapefiles of each trajectory were created using R package *rgdal* and exported for further analysis in ArcGIS (Bivand et al. 2019; ESRI 2011). Summaries of the general patterns of migratory routes were written after visually inspecting plots of each trajectory over the World Ocean Base map in ArcMap 10.8.1 (ESRI 2011).

Traditional migratory connectivity

Mantel tests

We measured migratory connectivity with the Mantel test in Program R package *MigConnectivity* by measuring the correlation of pairwise distances between individual breeding territory locations and capture locations in the non-breeding range (Mantel 1967; Ambrosini et al. 2009; Cohen et al. 2018). Population spread on the breeding and non-breeding grounds was estimated by calculating the range and mean of pairwise distances for both the breeding locations and the winter capture locations.

Sampling coverage

Capture of Red-throated Loons was limited to the mid-Atlantic region of their winter range, while the full winter range extends the length of the U.S. Atlantic Coast. Ideally, estimates of migratory connectivity are based on sampling that occurs across the entirety of one stationary range to limit potential sampling bias (Finch et al. 2017). To ascertain the degree of potential sampling bias in our migratory connectivity estimates, we compared the sampled winter range to an estimate of the percentage of the Atlantic Flyway breeding range occupied by our sampled birds. We defined the breeding range occupied by our sampled population as the area of the minimum convex hull encompassing the centroids of all individual breeding home ranges. We then calculated the percentage of overlap between this area and the full breeding range of North American Red-throated Loons in the Atlantic Flyway, where small overlap would indicate potential sampling bias or migratory connectivity at a scale larger than our winter sampling area. To estimate the Atlantic Flyway breeding range, we used a subset of the full North American breeding range (BirdLife International and Handbook of Birds of the World 2020) with Alaska and British Columbia removed, because results from other tracking studies indicate that Red-throated Loons breeding in these areas are solely members of the North

America–Pacific or Asia–Pacific flyways (McCloskey et al. 2018). We repeated this approach to estimate bias in the wintering range. Capture locations of the birds tracked were used to construct a minimum convex hull of the winter sampling area using the coordinates of each bird's capture location. The percentage of area overlap was then calculated between the winter capture area and the North American Atlantic portion of the non-breeding range (BirdLife International and Handbook of Birds of the World 2020).

Network connectivity

Principles of graph theory were employed to analyze the movement network of Red-throated Loons in eastern North America. When applied to animal tracking data, the structural component of the network, or *nodes*, are the animal relocations on the landscape, and the connections within the network, or *edges*, represent movement between nodes (Bastille-Rousseau et al. 2018; Jacoby and Freeman 2016). Weighting the edges according to the frequency of movement between nodes can provide insight, either at the individual or population level, regarding the intensity of use of sites that make up the network (Jacoby and Freeman 2016). Other metrics, such as edge betweenness, measure the number of shortest paths connecting two sites, and can be used to identify movement “corridors” on the landscape that are critical for maintaining overall connectivity of the network.

We followed methods outlined in Bastille-Rousseau and Wittemyer (2021) and the associated R package, *moveNT*, to build the network. A gridded raster of the regularized and filtered location data for 36 Red-throated Loons was used to build the network. Each pixel in the raster represented a node and movement between nodes represented edges. Nodes of the rasterized network were squares with 19.6 km sides, a distance equal to the median step length—i.e., total distance moved between 24-h relocations—of all individual trajectories. Node-level metrics were calculated for each pixel to assess intensity of use and its importance in connecting other nodes within the network. These included: (1) weight (total number of times any individual used a node); (2) degree (number of other nodes it is connected to); and (3) betweenness (the number of times a node bridges the shortest path between any two other nodes in the network). Movement metrics, including mean (4) speed of movement and (5) turning angle, were also calculated for each node to gain additional insight on movement behavior that could be used to differentiate whether the node served as a residential home range, a migration stopover, or a movement corridor.

We used Gaussian mixture model clustering with the five movement metrics in *moveNT* to identify unique classifications of movement behavior among nodes in the network for each individual (Bastille-Rousseau and Wittemyer 2021). The cluster analysis was constrained to

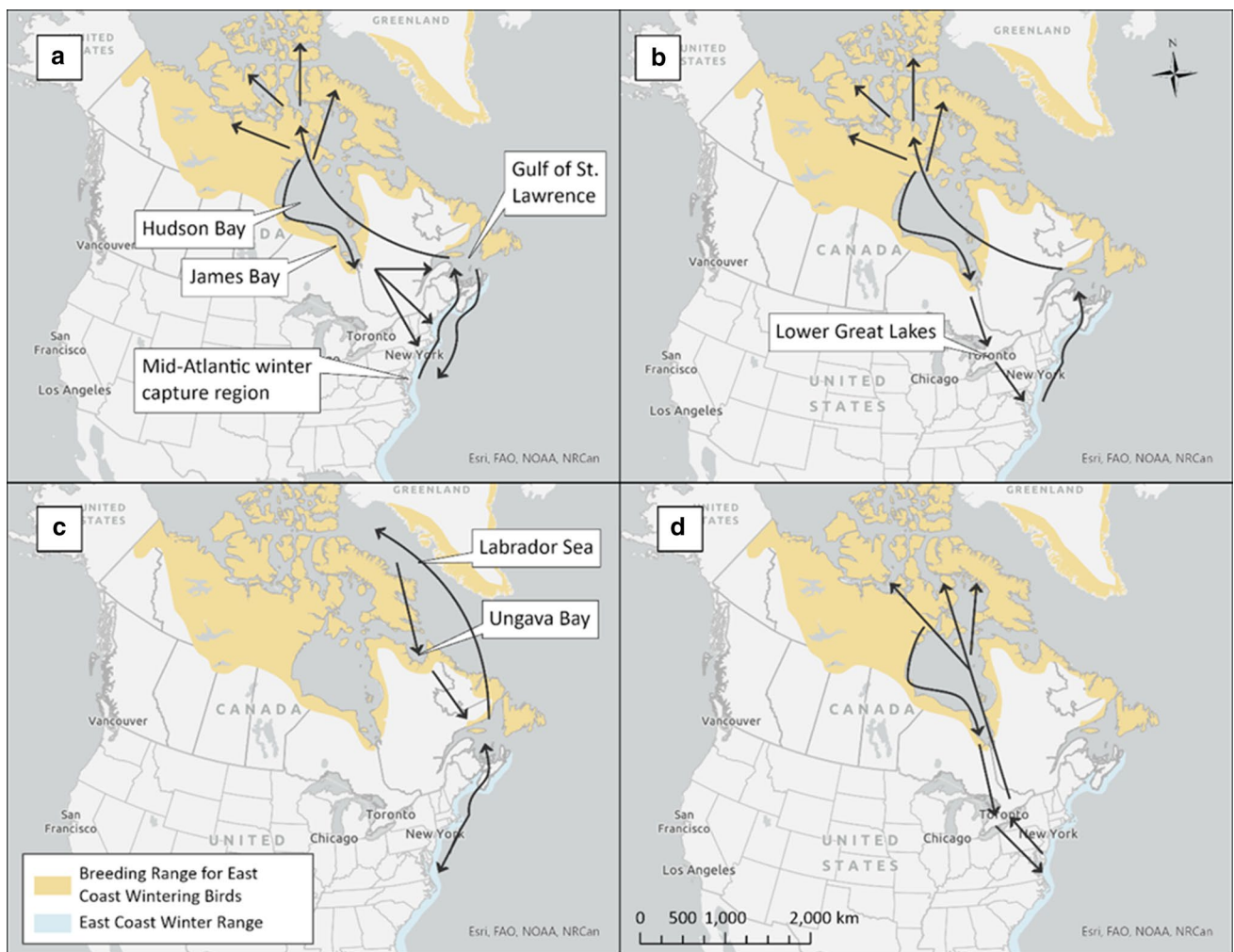


Fig. 1 Four primary spring and autumn migration routes of satellite-tracked Red-throated Loons ($n=36$) captured on wintering area offshore of the U.S. mid-Atlantic coast: **a** 16 birds followed the Atlantic coast north in spring to the Gulf of St. Lawrence before spreading north over Hudson Bay to Arctic breeding territories. Birds returned to northern Hudson Bay in early autumn and moved south to James Bay, from where they made rapid flights overland to points along the east coast, before turning south to return to the mid-Atlantic region;

b 10 birds followed a route similar to Route A in spring and early autumn, but made stopovers in the lower Great Lakes, before returning directly to the mid-Atlantic region; **c** 6 birds followed a more eastern route north when departing the Gulf of St. Lawrence and returned through Ungava Bay in autumn; **d** 4 birds took an inland route north through the Great Lakes en route to the Arctic and returned through this area in autumn when returning to the mid-Atlantic

differentiate up to a maximum of 8 qualitative classifications: fast or slow movements in high-use, medium-use, or low-use sites, and fast or slow movements in movement corridors. This provided estimates for each bird location's (individual use of a node) probability of belonging to each of the classification categories. We then calculated the population-level probability that a node was used for a discrete type of behavior by averaging the individual probabilities for each node. Our primary interest was the identification of nodes in the network that were associated with the greatest intensities of use (e.g., residential ranges or migratory stopover locations) and those that served as movement corridors (e.g., areas with fast movements).

Results

Full annual cycle spatial use.

Four primary migration routes were identified that Red-throated Loons used to move between wintering areas offshore of the U.S. mid-Atlantic region and their Canadian breeding grounds (Fig. 1). All birds departed the mid-Atlantic wintering area between mid-April and early May. The most frequently traveled route (A), with 44% ($n=16$) of birds using, followed the Atlantic coast north, with a 2–4-week stopover in Nantucket Shoals off the coast of southern

New England and/or a 2–4-week stopover in the Gulf of St. Lawrence. In early June, birds then fanned north and northwest to arrive in breeding territories across Nunavut in mid-June. In early September, birds moved to Hudson Bay before continuing south towards James Bay. Between mid-November and mid-December, individuals made rapid flights overland to points along the northeastern Atlantic coastline, before continuing southward to return to the mid-Atlantic wintering area. The next most utilized route (B) followed a similar pattern, i.e., coastal route north in spring and autumn return through Hudson and James Bays; however, birds using this route ($n = 10$) departed James Bay between late September and mid-November, then traveled to the lower Great Lakes, where they stayed until early to mid-December, before making direct rapid flights over New York and Pennsylvania to the mid-Atlantic coast. Route C was used by 17% ($n = 6$) of sampled birds, and, like routes A and B, followed the Atlantic coast north to the Gulf of St. Lawrence in spring, but then continued north in early June along a more eastern route through the Labrador Sea and over Baffin Island to points north. These birds returned south through Ungava Bay in early September, in lieu of Hudson Bay, before returning to the Gulf of St. Lawrence in late September. These birds departed the Gulf of St. Lawrence from late November to mid-December and then south along the coast toward the mid-Atlantic. Route D ($n = 4$) took an inland route north through the Great Lakes, where they stayed until late May before spreading to points north and northwest in the breeding range. Three of these birds returned through Hudson/James Bay before returning to the lower Great Lakes en route to the mid-Atlantic wintering area (i.e., like route B). One bird returning from a breeding location in the Northwest Territories, however, kept further south and west after departure from the breeding area, moving through Lake Winnipeg and the western Great Lakes in September and October before arriving in lower Great Lakes and continuing on to the mid-Atlantic in late November. All the birds we tracked arrived back in the mid-Atlantic wintering grounds between mid-November and mid-December each year.

Traditional migratory connectivity.

Mantel tests

The distance between capture locations of individuals sampled in the mid-Atlantic portion of the wintering range ranged from < 1 km to 444 km ($\bar{x} = 195$ km). The population spread of those individuals during the breeding season ranged from 37 km to 2,506 km ($\bar{x} = 943$ km). Overall, the distance between two individuals during the non-breeding season was poorly correlated (-0.03) with the distance between the same individuals during the breeding season,

suggesting low connectivity and random spatial structure in winter.

Sampling coverage

The area of the Red-throated Loon wintering range sampled due to capture locations ($x = 22,284$ km²) comprised only 5% of the total North American east coast winter range ($x = 474,820$ km²) (Fig. 2). The breeding territories of the birds that were captured, however, spread out over an area of 15,012,145 km², comprising 65% of the total Atlantic flyway breeding range ($x = 38,739,315$ km²). Source breeding locations ranged from 66°W to 110°W longitude and 58°N to 81°N latitude, and included the Northwest Territories, Nunavut, Manitoba, and northwest Greenland (Fig. 2).

Network connectivity

Cluster analysis on the node-level metrics of weight, degree centrality, betweenness, speed, and turning angle resulted in the identification of seven types, or clusters, of movement behavior across the migratory network (Table 1). Nodes designated to clusters 2, 4, and 6 together comprised the majority of nodes in the network (35.1%, 3.4%, and 13.7%, respectively), and were indicative of high-use areas, sites with the highest values for weight and moderate to high connectivity with other nodes (degree) (Fig. 3). Among these nodes, however, cluster 2 had the lowest use and degree of connectivity, suggesting more peripheral nodes in high-use areas. Cluster 4 was differentiated among these three clusters by faster relative movement behavior, higher betweenness, and more directed movement (i.e., less turning angle) values than clusters 2 and 6. This suggests that nodes designated as cluster 4 were end points for corridors, where birds typically departed from or arrived when engaging in stopover behavior. Speed, betweenness, and directed movement were greatest for clusters 5 and 7, which accounted for 8.2% and 12.6% of all nodes within the network (Fig. 3). Together with their lower use, this indicates that these sites are important corridors for facilitating movement between high-use areas. Movement in corridors was directed and fast, with speeds being slightly slower in cluster 7 nodes than in cluster 5. Clusters 1 and 3, representing 15.5% and 11.5% of all nodes, represented sites of low use, low connectivity, and were not considered primary stopover or migration corridors for the birds we sampled.

Discussion

We provide the first complete description of four broad migration routes used by Red-throated Loons to move between wintering areas along the U.S. mid-Atlantic coast

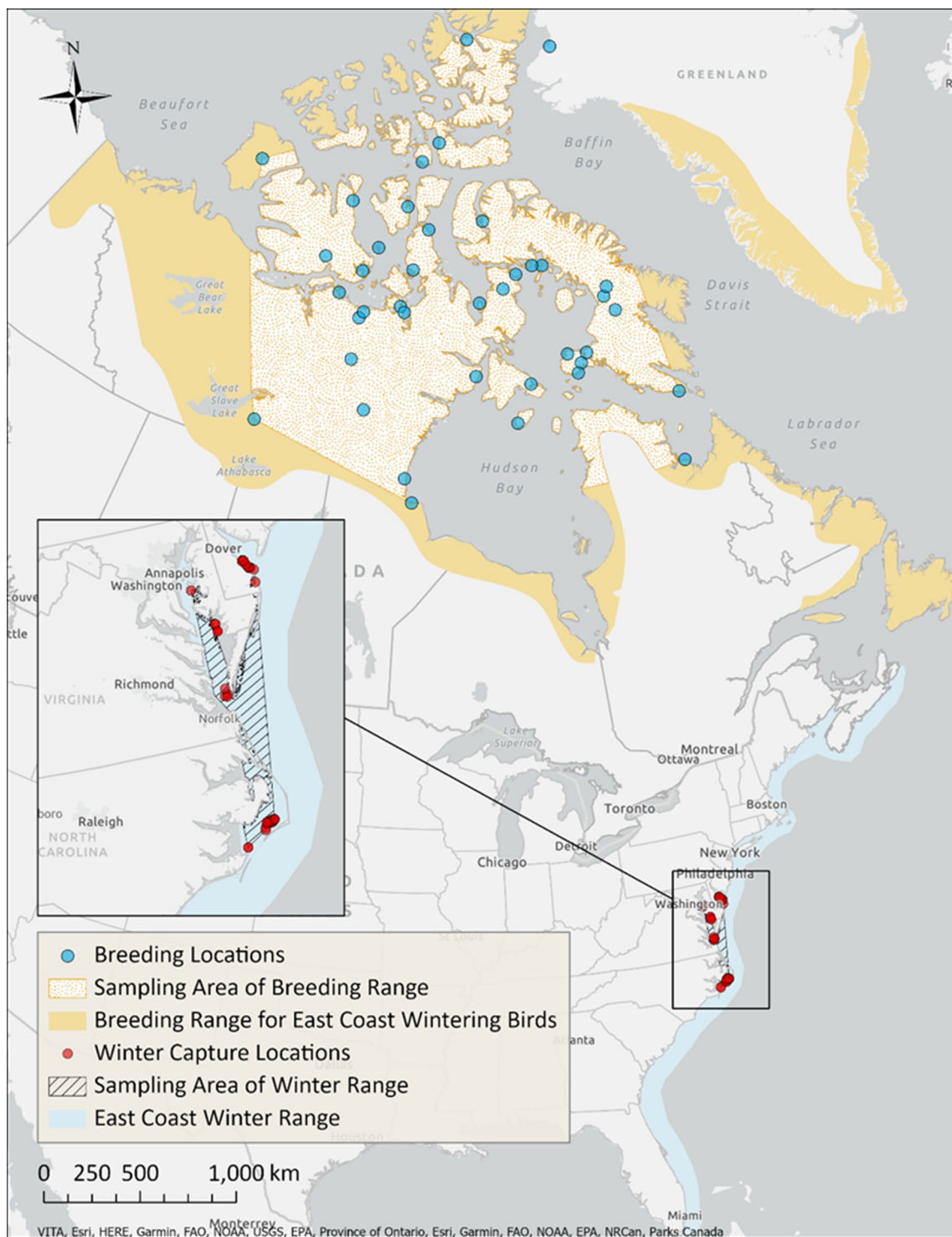


Fig. 2 Capture and breeding locations of satellite-tracked Red-throated Loons ($n=36$) wintering offshore of U.S. mid-Atlantic coastline in January–April, 2012–2015. Winter range sampling area coverage denotes the proportion of the east coast North American non-breeding range we sampled. Breeding range sampling area cov-

erage denotes the proportion of the North American breeding range (minus Alaska and British Columbia) the birds we sampled covered. Note: the individual with breeding territory in northwest Greenland was not included in the sampling area calculation because it did not overlap with the officially mapped breeding range for this population

Table 1 Summary of Gaussian mixture model classifications applied to network analysis and movement metrics of satellite-tracked Red-throated Loons ($n=36$) in eastern North America, 2012–2015.

Metric	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Cluster 7
Weight	− 0.361	0.427	− 0.228	3.190	− 0.284	3.162	− 0.364
Degree	− 0.499	0.889	− 0.218	2.347	− 0.323	2.754	− 0.498
Betweenness	− 0.116	− 0.141	− 0.254	0.155	0.422	0.052	0.642
Speed	− 0.186	− 0.381	− 0.304	0.254	2.750	− 0.450	0.896
Turning angle	0.073	− 0.269	− 0.877	− 0.633	0.015	− 0.187	0.601
% of network	0.155	0.351	0.115	0.034	0.082	0.137	0.126
Movement type	Low use (slow)	Med. use (slow-est)	Low use (slow-est)	High use (slow)	Corridor (fastest)	High use (slow-est)	Corridor (fast)

Network metrics were based on a gridded raster with a pixel size of 19.6 km that classified pixels as one of seven clusters based on five metrics that included: weight—number of relocations in a pixel; degree—number of other pixels to which a pixel is connected; betweenness—number of shortest paths in pixel relative to total shortest paths, i.e., importance of pixel in facilitating flow of network; movement speed—average velocity in a pixel; and turning angle—mean cosine of all turning angles in pixel.

and their northern breeding grounds. Most birds followed the Atlantic Coast north to the Gulf of St. Lawrence in spring before fanning out in multiple directions to reach breeding grounds distributed across a wide swath of Canada and Greenland. In autumn, birds associated with more eastern breeding locations, e.g., northwest Greenland, tended to track further east through Ungava Bay, but most birds across nearly the entire Canadian Arctic east of Yukon returned through Hudson and James Bay. The primary distinguishing factor in migration routes among the birds we sampled was whether they traveled from Hudson/James Bay directly to points along the Atlantic Coast or if they instead moved to the lower Great Lakes for extended stopovers. All but one of the birds that moved through the Great Lakes exhibited an elliptical migration pattern with different northward and southward routes, which has not been documented in other parts of the species' range; however, it has been observed in other Arctic-breeding birds that utilize the Atlantic Flyway (Brown et al. 2017).

The birds we sampled exhibited a high degree of population spread in the breeding range, occurring across 44 degrees of longitude and 23 degrees of latitude. It is unclear, however, if this represents a continuous breeding range or disjunct breeding populations that mix in the wintering area. When considered as one continuous population, the random spatial distribution of individuals during the breeding and non-breeding seasons indicated a pattern of low migratory connectivity. Estimates derived from the Mantel test, however, may not be robust to small sample size, uneven sampling efforts, and location error uncertainty (Cohen et al. 2018; Finch et al. 2017). New methods that account for variation in population abundance in the breeding and wintering areas may help to fine-tune migratory connectivity estimates (Cohen et al. 2018); although, abundance estimates are not yet available for our sampled population.

Despite sampling just 5% of the North American Atlantic coast non-breeding range, an area equivalent to just 0.001% of the presumed Atlantic flyway breeding range, the birds spread out across 65% of that breeding range. These results support the notion that the mid-Atlantic region constitutes the core of the non-breeding range for Red-throated Loons that winter on the Atlantic coast (Root 1988; Forsell 1999), that traditional migratory connectivity is low, and that anthropogenic disturbance or changing environmental conditions in this relatively small area could have consequences across much of the North American breeding range.

The four discrete migratory routes highlight the importance of considering the migratory range during investigations of connectivity, even for species that show low traditional migratory connectivity. While Mantel Tests revealed little to no migratory connectivity as traditionally described (Ambrosini et al. 2009), we revealed four discrete migratory pathways each used by only a subset of the birds. This opens up the possibility of spatial structure during one period of the annual cycle. Further, one (Route C) was used only by birds breeding in the far eastern summer range. Birds found at stopover sites in Labrador and Ungava Bay are thus far more likely to originate from breeding locations in the eastern part of the range than elsewhere, which indicates connectivity among these disparate geographic areas. Individuals that use these matched breeding and migratory locations, however, mix extensively with individuals from across the breeding range during the non-breeding stationary phase. Multi-year data are necessary to determine whether the four routes are consistently used by the same individuals among years (high spatial structure) or whether individuals use different routes among years (low spatial structure). The difference between these two possibilities is important for understanding how easily ecological disturbances

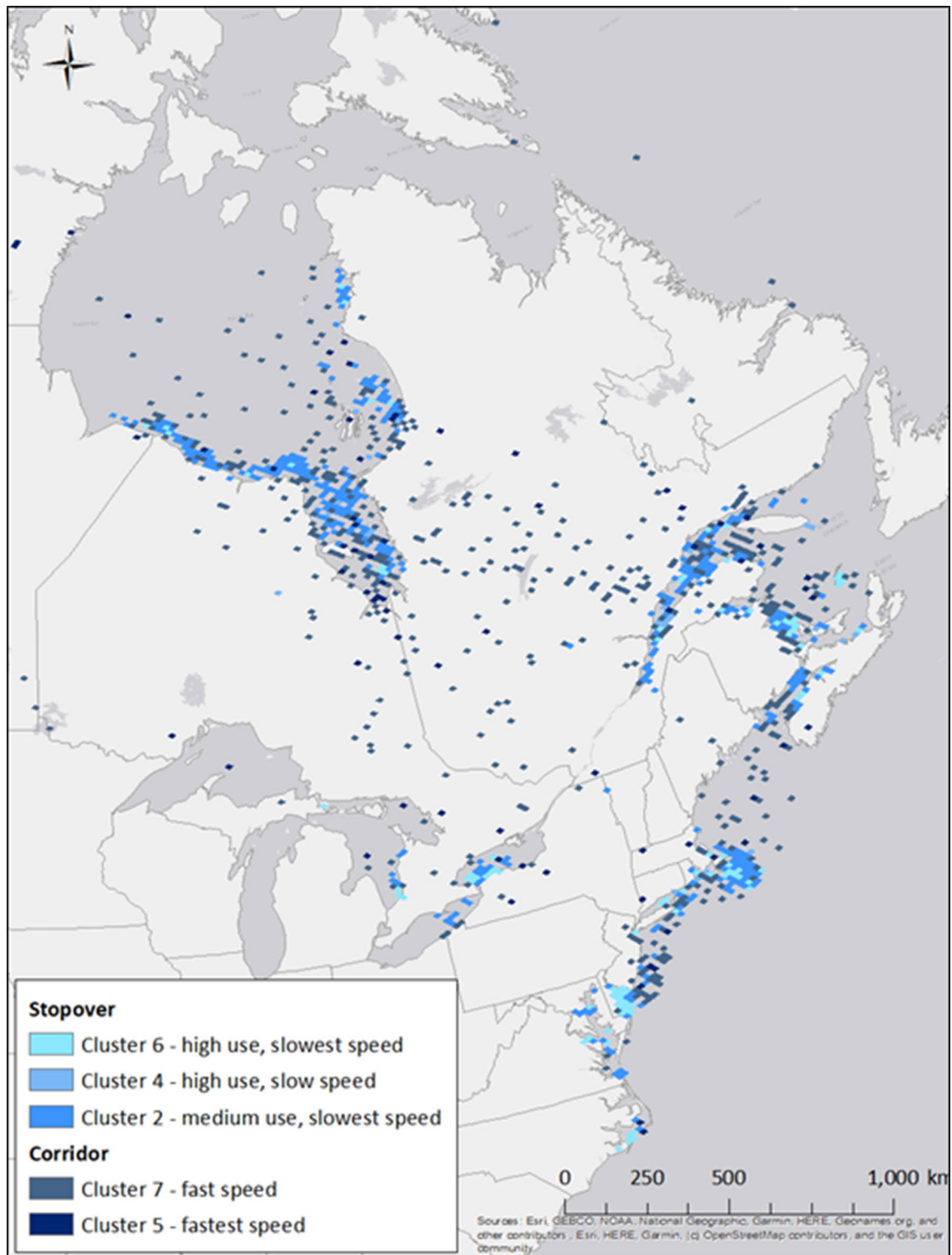


Fig. 3 Map of the movement network of satellite-tracked Red-throated Loons ($n=36$) in eastern North America, September–May, 2012–2015. Cells within the network with moderate to high intensity use and characterized by slow rates of movement are represented

by Clusters 2, 4, and 6. Cells classified as movement corridors with fast and slow rates of movement are represented by Clusters 5 and 7, respectively

during the migratory period propagate among breeding and non-breeding populations.

Low migratory connectivity between wintering and breeding ranges (i.e., relative panmixia) and the use of several varied migration routes likely dilute the demographic impacts from any one residential location across the annual network. There are, however, multiple points in the network where anthropogenic disturbances or changing environmental conditions have the potential to influence birds from across their North American breeding range. For example, 90% of the birds we tracked in spring and 61% in autumn relied on core use areas (and the corridors that connected them) along the Atlantic coast of the northeastern U.S. and Canadian Maritimes. Potential limiting factors on loon demography in coastal non-breeding areas include: inclement weather and oceanographic conditions (Schmutz 2014); exposure to contaminants (Schmutz et al. 2009; Evers et al. 2014) and oil spills (Sperduto et al. 2003; Evers et al. 2019; Paruk et al. 2020); risk of collision mortality and habitat displacement from offshore wind farms (Bradbury et al. 2014; Heinänen et al. 2020; Stenhouse et al. 2020); and the threat of bycatch mortality associated with fishing nets (Warden 2010; Żydelis et al. 2013). This highlights the possibility that species without strongly structured residential populations (i.e., without high traditional migratory connectivity) might still be sensitive to environmental changes in small portions of their migratory ranges, a finding that requires an annual cycle approach which includes the migratory period.

Network analysis of Red-throated Loon satellite tracking data allowed for the identification of core use areas across the annual cycle (clusters 2, 4, and 6) that provide critical stopover area, wintering habitat, and movement corridors (clusters 5, 7), which facilitate connectivity across the range. The major sites identified as core use areas included lower Hudson Bay and James Bay, the lower Great Lakes, the Gulf of St Lawrence, Nantucket Shoals, and the major bays of the mid-Atlantic region, where birds were captured in winter, including Delaware Bay, Chesapeake Bay, and Pamlico Sound. Interestingly, our cluster analysis found strong similarities in loon behavior between sites used during migratory stopover and the overwintering so-called “stationary” period. Many loons in our study periodically changed home ranges during the winter months in a way that was similar (at least for the metrics we measured) to switching between stopover sites during migration, which highlights the possibility that the behavior underlying dispersal and migration could be impacted by similar physiological mechanisms.

Movement corridors are also critical components of the network and link disjunct core use areas that are used for foraging and rest (LaPoint et al. 2013; Bastille-Rousseau and Wittemyer 2021). Prominent movement corridors were evident from southern Hudson Bay and James Bay extending to points south and southeast, primarily the lower Great Lakes

and the Gulf of St. Lawrence. Hudson/James Bay provides important autumn core use stopover habitat but is also of high importance as a movement corridor during both the spring and autumn migrations. Most of the birds we tracked relied on the waters of southern Hudson and James Bays for one-quarter to one-third of their annual cycle. It was also the final staging area before they embarked on non-stop flights of more than 1000 km across eastern Ontario and Quebec. This may have important conservation implications as conditions at important stopover locations can have considerable effects on individual survival, and potentially population size (Newton 2006).

This study revealed considerable sympatry of wintering Red-throated Loons from a wide swath of the breeding range and used a network approach to identify several important migratory stopover locations and movement corridors. These sites were used by a high proportion of the birds we tracked, despite their use of multiple, clearly discrete, migration routes. Understanding the effect of changing environmental conditions in the non-breeding range on Red-throated Loon populations will require a better understanding of whether individuals closely adhere to these spatial patterns from year to year or if they are more flexible in their movement patterns. However, by documenting these locations, we hope to both inform the conservation of this species as well as to underscore the importance that large-scale migratory spatial structure might play for otherwise panmictic taxa.

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Author contributions Data used in this paper were obtained secondarily from a satellite-tracking study of Red-throated Loons while in their wintering area offshore of the U.S. Mid-Atlantic Coast (Spiegel et al. 2017). CG and BO conceived the idea for this analysis; CG analyzed the data; CG led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication. Both authors read and approved the final manuscript.

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Data availability The data that support the findings of this study are available from Movebank's Arctic Animal Movement Archive (https://www.movebank.org/cms/webapp?gw_fragment=page=studies,path=study37025629) but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available. Data are, however, available from the authors upon reasonable request and with permission of the Bureau of Ocean Energy Management.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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