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Research article

Stopover regions, phenology, and spatiotemporal group dynamics of adult and juvenile common terns *Sterna hirundo* from inland lakes in North America

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Understanding the behavior of migratory birds can help determine levels of connectivity and inform conservation actions for species of conservation concern. The common tern *Sterna hirundo* is a long-distance migratory seabird that is considered a species of conservation concern in the North American Great Lakes region and that has experienced significant declines in breeding numbers across large lakes in Manitoba. To better understand the movement ecology of common terns, we used data from multiple tracking technologies (solar geolocation, GPS tracking, and Motus radio tracking) obtained from individuals ($n = 83$) across five breeding colonies on four inland lakes in North America. We identified key stopover regions used during southward migration and explored how demographics and social interactions influence connectivity. We identified three key stopover regions (Lake Erie, the southern Atlantic Coast, and Florida) and documented, for the first time, differences in post-natal and post-breeding migration for inland nesting terns. Juveniles arrived, on average, three weeks later than unrelated adults to their first major staging area. Although adult female arrival to and departure from Lake Erie was similar to adult males, female schedules became significantly earlier than males as southward migration progressed. Using a graph network to describe the spatiotemporal associations among adults from the same inland lake, individuals appeared to be highly connected, meeting up in different regions throughout the non-breeding season, suggesting that social interactions may play an important role in maintaining spatial connectivity. Despite differences in migration schedules by sex and arrival to the first major staging area by age class, birds appeared to rely on the same key stopover regions during southward migration. The stopover

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regions identified in this study can help identify potential bottlenecks and guide future research aimed at assessing the impacts of climate change and human disturbance on common terns breeding in North America.

Keywords: animal movement, bird migration, geolocation, interaction networks, migratory behavior, spatio-temporal ecology

Introduction

By studying the behavior of migratory birds, we can document how movement is linked to decision-making processes, such as timing of migration, stopover site selection, and establishment of migratory routes (Flack et al. 2022). This information can then be used to identify patterns which can aid in conservation planning, a critical need given the large number of migratory birds that are declining globally (Runge et al. 2015, Rosenberg et al. 2019, Phillips et al. 2022). Migratory connectivity has proven to be a valuable concept to quantify migratory patterns within and across populations and to assess their sensitivity to environmental change (Webster and Marra 2005, Bauer et al. 2016, Skinner et al. 2022). Understanding geographical linkages of migratory birds can indeed identify potential threats (Trierweiler et al. 2014), explain population dynamics (Kürten et al. 2022), and increase our understanding of the general influence of migration behavior on individual and population-specific fitness components (Bauer et al. 2016).

A range of factors influence the strength of migratory connectivity and its consequences, including the geographical setting, such as corridors and barriers (Finch et al. 2015, Lisovski et al. 2021), sex, age, and social behavior (Dittmann and Becker 2003, Nisbet et al. 2011a, Bracey et al. 2018, Dhanjal-Adams et al. 2018, Byholm et al. 2022, Kürten et al. 2022, Verhoeven et al. 2022). Stable isotopes and banding data have often been used to describe migratory connectivity between breeding and wintering sites (Hobson 2005, Horton et al. 2023). However, high resolution tracking data allows us to gain insights into migratory connectivity patterns at a finer scale and across the entire annual cycle, including during migration and stopover periods (Bauer et al. 2016, Bellisario et al. 2023).

Spatiotemporal group dynamics (Dhanjal-Adams et al. 2018) could be another important explanatory factor in understanding migratory connectivity, but it remains poorly understood (DeSimone and Cohen 2023). In fact, social behavior has been shown to influence learning and group structure and to improve navigation, enhance foraging opportunities, and reduce predation risk (Couzin et al. 2005). Many seabirds migrate in large groups (Arnold et al. 2020). However, the composition and stability of these groups (i.e. which individuals from which populations are migrating with whom and for how long) are largely unknown, yet this could have significant population-level implications associated with the transfer of information and survival (Dhanjal-Adams et al. 2018), as well as population genetic structure (Szczyz et al. 2017). Identifying whether migratory interactions between individuals from a mutual breeding population are static or dynamic would not only provide insight on

the role that social interactions play in influencing migration behavior, but may also help identify key stopover regions, patterns of connectivity, and the potential consequences of those behaviors (Dhanjal-Adams et al. 2018).

Many seabird species exhibit individually consistent but highly variable among-individual migration strategies (Brown et al. 2021, Kürten et al. 2022), resulting in low connectivity (Bracey et al. 2018, Merkel et al. 2021, Kleinschmidt et al. 2022). Because of their ability to rest and forage on water en route, seabirds regularly stop during migration (Bonnet-Lebrun et al. 2021), sometimes for long durations (> 2 months; Bracey et al. 2018). Where birds choose to rest and refuel, as well as the frequency and duration of stops, can be influenced by a multitude of factors (Schmaljohann et al. 2022). While not the only measure of the quality or importance of a stopover location; long stopover durations tend to occur in regions with predictable and abundant prey resources (McKnight et al. 2013, Grecian et al. 2016). Therefore, identification of key stopover regions could greatly benefit conservation planning for seabirds (Warnock 2010). Additionally, linking demographic parameters of breeding populations to non-breeding habitats can inform how environmental conditions influence population dynamics, which can also guide conservation planning (Strøm et al. 2021).

In North America, the common tern *Sterna hirundo* is separated into three broadly defined breeding populations (the Atlantic, Central, and Northwest breeding units) based on band recovery data and genetic analysis (Szczyz et al. 2017, Arnold et al. 2020). Across inland North America (i.e. Central breeding unit), common terns appear to be in decline despite intensive management efforts occurring across much of the region (Szczyz et al. 2017, Arnold et al. 2020, 2022). To identify key stopover regions for this population, we combined previously published tracking data ($n=44$ tracks collected across five inland breeding colonies) and new tracking data ($n=40$ tracks collected across three inland breeding colonies; locations which were also included in the previous study). We used multiple on-bird tracking devices, with data from 44 archival solar geolocator (i.e. global location sensors (GLS)) tracks from a previous study (Bracey et al. 2018), and new data collected from archival GLS ($n=3$), archival global positioning system (GPS) tags ($n=10$), and very high frequency (VHF) radio transmitters (hereafter nanotags; $n=27$). Using archival solar geolocators, Bracey et al. (2018) identified the non-breeding distributions, including migratory routes and stopover regions of 46 individuals from five nesting colonies. Data recovered from those geolocators identified 1) coastal Peru as an important wintering location, 2) that females initiated southward migration earlier than males, and 3) that migratory connectivity was low among colonies (Bracey et al.

2018). This study provided valuable information about migratory connectivity and non-breeding distributions of adult common terns. However, it was not possible to obtain information about social interactions during migration nor juvenile movement with that dataset. To build upon the broad-scale daily movement locations estimated using solar geolocators, we deployed archival GPS tags on adults and nanotags on both adult and juvenile birds to obtain more spatially explicit location estimates during the non-breeding season.

Although tracking devices have become invaluable resources to researchers, it is necessary to assess the risk of deploying these devices relative to the benefits of collecting data. For example, deployment of tracking devices has been shown to impact flight characteristics of migratory birds resulting in increased energy expenditure and declines in nesting attempts (Barron et al. 2010, Vandenabeele et al. 2014). Entanglement in harness materials has also been associated with lower survival rates in plunge-diving terns (Fijn et al. 2024). However, other studies have found no detectable negative effects on the behavior or fitness of birds fit with tracking devices (Bracey et al. 2018, 2020, Kürten et al. 2019). Because these effects are likely species- and tag-specific, it is important to document potential harmful effects in any study utilizing tracking devices.

With this technology, we aimed to identify key stopover regions used during southward migration of inland nesting common terns and to determine how individuals were linked in space and time during the non-breeding season. We focused on differences in sex, age class, and on individual connectivity to provide a better understanding of life-history strategies and thereby to inform successful conservation planning for this vulnerable species. We also summarized return rates, body condition, and nesting attempts to assess impacts of transmitter deployment.

Material and methods

Study sites

To document phenology, identify important stopover regions, and assess connectivity of common terns, we used three types of on-bird tracking devices: 1) GLS tags, 2) GPS tags, and 3) nanotags (details below). This study includes GLS data collected from five common tern breeding colonies located at inland lakes in North America and GPS and nanotag data collected at two colonies on Lake Superior (Supporting information). The colonies included in our study were located in two Canadian provinces (Manitoba and Ontario [Lake Winnipeg and Lake Huron], respectively) and three US states (Minnesota and Wisconsin [Lake Superior] and New York [Oneida Lake]).

Deployment of tracking devices

Adult common terns were captured on the nest during incubation using either open-bottom walk-in traps or box traps following methods described in Bracey et al. (2018), and

pre-fledged juveniles (< 24 days old) were captured by hand. Handling time was ~15–20 min per bird, including time to attach a tracking device and weigh, measure, and determine the sex of the bird (via blood sample (n=75) or biometric measurements (n=9)). Biometric measurements used to determine sex included tarsus length, head + bill length, bill depth, and wing chord, following Nisbet et al. (2007). Sex was determined for juvenile birds fit with nanotags in 2019 (n = 13) but not in 2020 (n = 30). In years following deployment, tracking devices were removed upon recapture. To determine whether deployment of tracking devices negatively affected survival or fitness, we placed auxiliary markers (i.e. plastic alphanumeric color leg bands) on breeding adults and juveniles not fit with tracking devices to assess differences in return rates. We also weighed birds fit with tracking devices (pre- and post-deployment) to assess differences in body condition. When possible, we determined whether individuals successfully nested (i.e. hatched young) in the year in which tracking devices were deployed by marking nests with unique nest numbers and following the fate (i.e. failed or successfully hatched young). We also documented whether birds fit with tracking devices attempted to nest in the year following deployment (i.e. birds were actively attempting to breed).

Solar geolocators (GLS)

A total of 106 archival GLS tags (Intigeo model W65A9; Migrate Technology, Cambridge, UK and British Antarctic Survey model MK5093; Biotrak, Wareham, UK) were deployed on adult common terns at the five breeding colonies (Supporting information) between 2013 and 2015. GLS tags were deployed using a leg-mounted attachment, which has been shown to have little to no adverse effects on common terns (Nisbet et al. 2011b, Bracey et al. 2018, Kürten et al. 2019). The combined weight of each attachment was \leq 2.0 g [geocator + plastic leg ring or flag + adhesive + auxiliary band], which is <3% body mass of adult birds (range 97–146 g; Arnold et al. 2020). See Bracey et al. (2018) for details regarding colony descriptions and the deployment and retrieval of solar geolocators by colony.

GPS tags

In 2017, a total of 19 archival GPS tags (Lotek: PinPoint-50 ver. V4.16) were deployed on adult common terns breeding at the two Lake Superior colonies (Supporting information) using a leg-loop harness attachment (Mallory and Gilbert 2008), made from 2.5 mm Teflon tape (Bally Ribbon Mills, Bally, Pennsylvania; pattern 8476-.10'). The combined weight of the GPS tag + Teflon tape was ~2.8 g, which is < 3% body mass of adult birds (range 97–146 g; Arnold et al. 2020). This attachment technique has been shown to have no observable negative effects for short-term deployment on common terns (Bracey et al. 2020, Buck et al. 2022). GPS schedules were set to maximize data collection based on estimated battery life over the course of their annual cycle. During autumn migration (1 August–29 November), devices were scheduled for shorter intervals between fixes (i.e. locational data for a specified point) to identify routes with increased spatial accuracy (relative to GLS). Thus, GPS tags were set to record a fix at a

rolling interval between 1 August 2017 and 31 May 2018 based on the following schedule: autumn migration: 1 August–29 November (once every 3–4 days); winter: 1 December–29 March (once every 10–15 days); spring migration: 1 April–15 May (once every 3–4 days); and 16 May–31 May (once daily). Each fix was scheduled to occur at 17:00 in Greenwich Mean Time (GMT). The accuracy of GPS locations varies based on the number of satellites available during an attempted fix, but is generally ± 10 m (Lotek pers comm; 30 September 2015).

Nanotags

We deployed 1.45 g coded VHF nanotags (model NTQB2-6-1; Lotek Wireless, Newmarket, Ontario, Canada) on adults in 2019 ($n=16$) and juveniles in 2019 ($n=13$) and in 2020 ($n=30$) at one of the colonies in Lake Superior (Interstate Island; Supporting information). Transmitters were attached using a leg-loop harness. For adults, the harness material was made from 2.5 mm Teflon tape (the same material as used to attach GPS tags) and for juveniles we used a 1.5 mm diameter elastic (Stretch Magic brand) jewelry cord (Pepperell Braiding Company, Pepperell, Massachusetts, USA). We chose to use elastic cord on juveniles to increase the probability that transmitters would fall off over time, given these individuals were less likely to be recaptured due to deferred breeding and natal dispersal. This attachment technique has been shown to have no observable negative effects for deployment on both adult and juvenile common terns (Buck et al. 2022). The combined weight of the nanotag+Teflon tape or elastic jewelry cord was ≤ 2.0 g, which is $< 3\%$ body mass of adult birds (range 97–146 g; Arnold et al. 2020). All transmitters broadcast on the same frequency (166.380 MHz) with a burst interval of 29.30 s and an expected battery life of 1047 days.

The nanotag data were obtained from the Motus Wildlife Tracking System, which is an international network of coordinated automated radio telemetry stations (Taylor et al. 2017). Because data are collected remotely, at each station (i.e. without needing to recapture tagged individuals), we were able to use this method to track the movement of juveniles during the non-breeding season. The detection radius from automated radio telemetry receiving stations available on the Motus Wildlife Tracking System network varies depending on the characteristics of the antenna array, but typically ranges from 1–15 km (Taylor et al. 2017). A total of 315 Motus stations were active during the deployment period (2019 and 2020) and were expected to remain active throughout the estimated battery life of the transmitters (2023). Another 311 Motus stations were active but subsequently terminated at some point during the study period (2019–2023). Details regarding the activity of all Motus stations available during the study period can be found at <http://www.motus.org/data/receivers>.

Data processing

GLS

We used the R package ‘TwGeos’ (Lisovski 2016) to annotate twilight events based on a light threshold, and used

on-bird calibration periods when birds were known to be at the breeding colony. On-bird calibration periods at a known location (i.e. the breeding colony) are used to match the light intensities with the position of the sun (solar angle), a necessary step for subsequent location estimation. We then used the R package ‘FLightR’ (Rakhimberdiev and Saveliev 2016) to derive location estimates. Here, initial location estimates were refined using a particle filter (Rakhimberdiev et al. 2015). The particles ($n=1 \times 10^6$) are simulated locations based on the increasing and decreasing light during each twilight (Rakhimberdiev et al. 2015) and weights the outcome based on a movement model and a spatial mask. This results in a posterior probability distribution which estimates daily locations and the corresponding uncertainty (Rakhimberdiev et al. 2015). See Bracey et al. (2018) for details about how raw light data were filtered, processed, and analyzed. Note that the same analytical methods and versions of software were used to process the three geolocators that were retrieved after 2018.

GPS tags

Data were downloaded from the GPS tags using the PinPoint Host software and USB interface reader. Locational data included latitude, longitude, date and time of fix (GMT), an indicator of GPS position quality (dilution of precision [DOP]), and the number of satellites used for a fix).

Nanotags

Initial standardized filtering of data occurred using the filtering rules described in the R: Motus users online manual (Brzustowski and LePage 2019). This included; 1) reviewing detections that were initially identified as potentially being false (i.e. run lengths < 3), 2) removing ambiguous detections (i.e. multiple active tags with the same tag ID) and detections likely associated with tag aliasing (i.e. when tag signals overlap and can be misinterpreted as another tag that is not actually present), and 3) manually inspecting all detections assumed to be true to identify any potential false positives (e.g. detection of a juvenile outside the breeding colony before it fledges). We summarized the resulting filtered data by Motus station ID (unique to each station) and included Tag ID (unique to each bird), receiver location (latitude and longitude) and date of detection. The final dataset of nanotag detections included in this study consisted of detections occurring between 31 May 2019 (date of first deployment) and 23 August 2021 (date of final data download from Motus).

Data analyses

Phenology and stopover regions

Areas of high use during winter were previously summarized in Bracey et al. (2018) and due to tag failure; data for northward migration was scarce. Therefore, we describe the phenology of southward migration by summarizing GLS and nanotag data occurring within high use areas identified during this period (i.e. July–November). We included some of

the 'last detection' dates for juveniles, which occurred outside of this period (i.e. one bird was last detected in December) to show that juvenile birds were detected there into winter months. GPS tags were scheduled to take a fix on specified days, therefore, without daily recordings we could not determine with certainty arrival and departure dates by region and so excluded GPS data from the summary of migration schedules.

We used ArcGIS Pro 3.1 (ArcGIS Desktop 2020) to visualize data. During southward migration, we identified clusters of data points based on visual point cloud inspection to identify stopover regions. We visually estimated where the centroid of each cluster should be, and manually created a point feature on the map. Each newly created point feature (i.e. regional centroid) was then buffered by 250 km, to account for scatter that could be both GLS uncertainty (Halpin et al. 2021) and the extent of the region that was used by birds during this period. In each region, > 60% of birds tracked moved through the area (Supporting information). We then summarized southward migration phenology as arrival to and departure from these identified regions. We report mean arrival and departure dates and ranges for adults by sex and region (Table 1). We used Welch two sample t-tests to determine whether arrival and departure dates varied significantly (< 0.05) by sex and paired sample t-tests to determine differences between pre- and post-deployment weights for males and females (Table 1). Due to the low number of nanotag detections occurring in two of the three stopover regions, we conducted significance tests for the nanotag data only in the first major stopover region (Lake Erie; Table 1). We report the median and range of first and last detection by age class (adult versus juvenile) for movements occurring outside of the first stopover region and we do not perform any statistical tests of significance in these regions with nanotag-only data (Table 1). Similarly, we report only median and range for arrival to or first detection at the first major stopover region for adults based on sex and nest fate in the year of deployment (Table 1).

Strength of connectivity among individuals

We used a simple interaction network representation to determine the extent to which individuals breeding at the Lake Superior colonies were linked together during the non-breeding season. In the network, a node represents an individual and the links represent the number of close encounters (≤ 150 km AND ≤ 2 days) with another individual within a defined region. Due to the degree of error associated with GLS data and the stationary nature of the nanotag data, only GPS data were used for the interaction network (Table 1). The defined distance of 150 km was large enough to reflect individual mobility and thus potential associations occurring during the non-breeding season when individuals are highly mobile. Although each GPS unit was set to collect fixes at the same interval (date and time), using two days allowed us to account for any delays in timing of GPS fixes that would fall within a 24 hour period. The spatial and temporal threshold were chosen a-priori in the context of data structure and

research question. Fixes around the breeding colonies (radius of $4^\circ = 444$ km) were excluded because we would expect a high degree of association to occur between individuals at or near the breeding colony. The strength of the relationships are depicted by line thickness, with stronger associations being represented by thicker lines and weaker associations by thinner lines. The graph network was created using the `ggraph` function of the R Package 'ggraph' with layout 'igraph' and algorithm 'kk', which places nodes using the spring-based algorithm by Kamada and Kawai (Pedersen 2024). If not stated otherwise, data were analyzed using R ver. 4.1.3 (www.r-project.org).

Results

Return rates and body condition

GLS

A total of 67/106 (63%) birds returned to the colony where they were fitted with GLS tags (Table 2). Of these, 60 (57%) were recaptured (2014–2020). Of these, 55 tags were recovered (i.e. five birds returned without geolocators attached) and 49 had usable tracks (i.e. we were unable to extract data from four tags and two failed on the breeding grounds). Of these, 22 recorded data for a full year and the remaining 27 stopped recording data at different times throughout the course of the year (Table 2). Three of the geolocators deployed at Oneida Lake, New York in 2014 were recovered after 2017. Two of the three tags retrieved collected data for > 1 year. Data from these three geolocators were not available for inclusion in Bracey et al. (2018) but are included in the geolocation summary here (Fig. 1b). Based on similarities in return rates of control birds (i.e. mates of birds fitted with geolocators; Supporting information) and on non-significant differences in pre- and post-deployment weights for males and females (females: $t = -1.4$, $p = 0.17$, $n = 25$ and males: $t = 0.9$, $p = 0.37$, $n = 16$; Bracey et al. 2018), fitness of geolocator-marked individuals appeared to be similar to unmarked individuals. The breeding colony where return rates were lowest (i.e. Lake Winnipeg; Supporting information) was likely due to terns nesting at other nearby colonies where it was not logistically feasible to look for geolocator-marked birds).

GPS tags

In 2018, we recaptured 14/19 (74%) birds fitted with GPS tags but were unable to extract data from four tags. Of the remaining 10 tags, three collected data for a full year and the remaining seven tags stopped recording data at different times throughout the course of the year. A total of 362 fixes were recorded (Fig. 1c). The DOP (measure of accuracy) suggested that 98% of the fixes were considered to have high accuracy (i.e., low precision error; $DOP \leq 5$) and the remaining 2% were excluded from the analysis. Weight measurements were taken for 12 of 14 birds post-deployment. There were no significant differences between pre- and post-deployment weights for males ($t = -1.46$, $p = 0.24$; $n = 4$) or females (t

Table 1. Summary of sample sizes associated with each type of analysis or data summary by tag type. The tag types included solar geolocators (GLS), global positioning system tags (GPS), and Motus radio transmitters (nanotag). For body condition, pre- and post-deployment weights in grams (g) were compared for all tag types. For the phenology and stopover by region (Lake Erie, Atlantic Coast, and Florida) summaries, we compared arrival and departure dates by sex (F = female or M = male) for adults by combining GLS and Nanotag data. We also compared first and last detection by age class (AD = adult and Juv = juvenile) and region. Adult arrival to Lake Erie was summarized for adults of known sex and associated nest fate (Successful = S or Failed = F). For family groups, we summarized nanotag data by sex and nest fate. For the strength of connectivity, we used year-round GPS data to describe individual interactions (i.e. the number of close encounters occurring between individuals in a given region). All numeric values represent sample sizes associated with each summary or analysis by region, where applicable, and bold indicates statistical significance.

	variables (dependent ~ independent)	Tag type	Lake Erie	Atlantic Coast	Florida	Year round	Analysis
Body condition: bird weight	pre- and post-deployment weight (g)	GLS, GPS, Nanotags					Paired sample t-test
Phenology and stopover by region	region ~ sex	GLS + Nanotag	F = 23; M = 19	F = 26; M = 17	F = 25; M = 13		Welch two sample t-test (all regions)
	region ~ age class	Nanotag	AD = 9; Juv = 11	AD = 7; Juv = 5	AD = 3; Juv = 3		Welch two sample t-test (Lake Erie only)
	adult arrival date (Lake Erie) ~ sex + nest fate	GLS + Nanotag	F = 13 (S) & 4 (F); M = 10 (S) & 4 (F)	-	-		Median and range summarized (no statistical tests performed)
	family group ~ sex + nest fate	Nanotag	F = 1 (S) & 3 (F); M = 5 (F)	F = 2 (F); M = 1 (S) & 2 (F)	F = 2 (S) & 1 (F); M = 0		Median and range summarized (no statistical tests performed)
Strength of connectivity	individual bird ~ region + number of encounters	GPS				F = 5; M = 5	Network analysis

= 1.53, $p = 0.17$; $n = 8$). Average pre- and post-deployment weights \pm SD for adults fit with GPS tags in 2017 were 129 ± 3 g and 132 ± 5 g for males, respectively and 138 ± 11 g and 129 ± 8 g for females, respectively. When removing the GPS tags, only one bird showed signs of minor chafing under one leg. Therefore, we felt relatively confident that the harness attachment method did not greatly influence fitness. All GPS-marked birds successfully nested in the year following deployment. Additionally, 10 of 18 control birds (56%) were resighted in the year following deployment, so return rates were higher for GPS-marked birds in 2018 (Supporting information).

Nanotags

In 2020, we resighted 8/16 (50%) adults and recaptured seven adults fitted with nanotags in 2019 (Table 2). The remaining eight adult birds were not observed at the colony in any years post-deployment. We have not re-encountered any of the juvenile birds fitted with nanotags as of August 2023, which is not unexpected due to deferred breeding and natal dispersal. A total of 341 detections from 29 individual birds occurred at stations outside of the breeding colony (Fig. 1c). Of these, two juvenile birds were detected outside of the migration period in the year following deployment and were not included in the summary. This included one juvenile that was detected on the Atlantic Coast 24–30 June and one juvenile detected in Florida 23 March and 3 August. A total of 15 adult birds were marked as controls in 2019 (Supporting information). Of these, eight (53%) were recaptured or resighted in 2020 (Supporting information). Therefore, return rates were similar for adults fit with nanotags and control birds. Average pre- and post-deployment weights \pm SD for adults fit with nanotags in 2019 were 133 ± 7 g and 126 ± 8 g for males ($n = 5$) and 151 ± 1 g and 127 ± 0 g for females ($n = 2$). Because we did not weigh control birds in 2020 (i.e. most birds were resights only), we are not able to determine if pre- and post-deployment weights of control birds were similar to birds fit with nanotags. However, weights appear to be generally lower for both sexes post-deployment. All recaptured birds that were fit with nanotags in 2019 attempted to nest in 2020 and five of eight nests successfully hatched young. Additionally, aside from the apparent weight reduction, none of the birds fit with nanotags showed physical signs of wearing the tags (e.g. no obvious chafing or feather loss).

Tag integrity

GLS

Five of 60 birds fitted with geolocators returned without the devices still attached. This was likely due to issues with the adhesive. An additional six tags were also non-functioning resulting in 11% of the tags failing to collect data (Table 2).

GPS

Nine of the fourteen tags retrieved were missing the antenna and for most, the batteries were still functioning upon

Table 2. Tracking devices were deployed across five common tern breeding colonies located on four inland lakes in North America (2013–2020). The tag types included solar geolocators (GLS), global positioning system tags (GPS), and Motus radio transmitters (nanotag). The number of tags deployed by age class (Adult or Juvenile), the number of tagged birds that returned to the breeding colony (Return rates) and the number of tagged birds that were recaptured (Recaptures) are provided by tag type. The number of tags that were retrieved and had usable data (i.e. locational data that could be extracted from a device (GLS or GPS)) or the number of tags that were detected by at least one Motus station (nanotags) outside the breeding area are also provided. The percentage of tags that were recovered that had total failure rates (i.e. no extractable data) are also provided by tag type for GLS and GPS tags only. Since nanotags are non-archival, we could not differentiate between the number of tags that failed versus those that remained undetected by Motus stations. The percentage of tags that failed relative to their expected longevity is also provided. This includes tags that had usable data but data collection failed during the course of its expected lifespan, which is also provided. *Five birds recaptured without geolocators attached, 4 tags where data could not be extracted, 2 tags failed on the breeding grounds.

Tag type	Deployment	No. tags deployed	Return rates	Recaptures	No. tags with usable data	% tags total failure	% tag failure/life expectancy
GLS	2013–2015	106 (Adult)	67 (7 observed only) (63%)	60 (57%)	49/55* (89%)	6/55* (11%)	27/49 (55%) / < 1 year
GPS	2017	19 (Adult)	14 (74%)	14 (74%)	10/14 (71%)	4/14 (29%)	11/14 (79%) / < 1 year
Nanotag	2019–2020	16 (Adult)	8 (Adult; 1 observed only) (50%)	7 (Adult; 44%)	12/16 (75%)	NA	7/7 (100%) / < 2 year
Nanotag	2019–2020	43 (Juvenile)	0 (Juvenile) (0%)	0 (Juvenile; 0%)	15/43 (35%)	NA	NA

retrieval. Therefore, they likely stopped collecting data due to a missing antenna rather than to battery failure. This resulted in 29% of the tags failing to collect data (Table 2).

Nanotags

Two of the eight nanotags were missing antennae when retrieved and none of the tags were still functioning. There was an active Motus station located on the island where the transmitters were deployed; however, no detections were recorded. This suggests that battery failure or corrosion of the tags led to a significant reduction in expected longevity of these tags. Since nanotags are non-archival, we could not determine which tags failed versus those that remained active but undetected by Motus stations and could therefore not provide a tag failure rate (Table 2).

Based on the expected longevity of each of the tracking devices (1 year for both geolocators and GPS tags and 2+ years for nanotags), solar geolocators performed best followed by GPS tags and then nanotags (Table 2). The GLS were the highest functioning with 89% of the tags ($n=49$) containing usable data, 45% of which ($n=22$) collected data for an entire year. Of the GPS tags recovered ($n=14$), 71% contained usable data but only 21% ($n=3$) collected data for an entire year. Based on the nanotags (which are not archival), zero of the tags removed from adult birds ($n=7$) were still functioning upon retrieval (Table 2).

Phenology and stopover region by sex

We identified three areas of high use during southward migration: 1) Lake Erie, 2) coastal South Carolina and Georgia (hereafter southern Atlantic Coast), and 3) Florida. Mean arrival of adult common terns to Lake Erie ($n=43$) was 15 August (range: 16 July–28 September) and mean departure was 16 September (range: 24 July–6 November; Fig. 1d). Based on the 19 males and 23 females of known sex (i.e. one adult of unknown sex not included), arrival to Lake Erie did not vary significantly by sex ($t=1.68$, $df=29.96$, $p=0.10$).

Similarly, departure from Lake Erie did not vary significantly by sex ($t=1.64$, $df=38.98$, $p=0.11$). Based on nest fate and sex, median arrival to Lake Erie for females that successfully hatch young in the year of deployment was 14 August (range: 16 July–9 September; $n=13$) and for males was 15 August (range: 27 July–28 September; $n=10$). Median arrival to Lake Erie for females with failed nests was 4 August (range: 26 July–11 August; $n=4$) and for males was 18 August (range: 31 July–4 September; $n=4$).

Adult arrival to the southern Atlantic Coast varied significantly by sex ($t=3.62$, $df=38.35$, $p<0.001$) with a mean arrival date for females of 16 September (range: 17 August–27 October) [$n=26$] and for males, 8 October (range: 12 September–9 November; $n=17$; Fig. 1d). Departure also varied significantly by sex ($t=4.06$, $df=40.99$, $p<0.001$) with mean departure for females on 28 September (range: 19 August–15 November) and for males, 26 October (range: 22 September–27 November; Fig. 1b).

Adult arrival to Florida varied significantly by sex ($t=3.48$, $df=29.71$, $p<0.001$) with a mean arrival for females of 22 September (range: 20 August–1 November; $n=25$) and for males, 17 October (range: 10 September–9 November; $n=13$; Fig. 1d). Departure also varied significantly by sex ($t=3.95$, $df=35.46$, $p<0.001$) with a mean departure for females of 8 October (21 August–14 November) and for males, 5 November (range: 26 September–28 November; Fig. 1d).

Phenology and stopover region by age class

Adult first detection at Lake Erie varied significantly from unrelated juvenile first detection ($t=-2.77$, $df=17.74$, $p=0.01$). Median first detection for adults at Lake Erie was 6 August (range: 26 July–4 September; $n=9$) and for unrelated juveniles was 27 August (range: 1 August–14 October; $n=11$; Fig. 2). However, last detection from Lake Erie did not vary significantly by age class ($t=-0.46$, $df=17.23$, $p=0.65$). Median last detection at Lake Erie was 4 October (range: 30 August–3 November) for adults and for unrelated juveniles

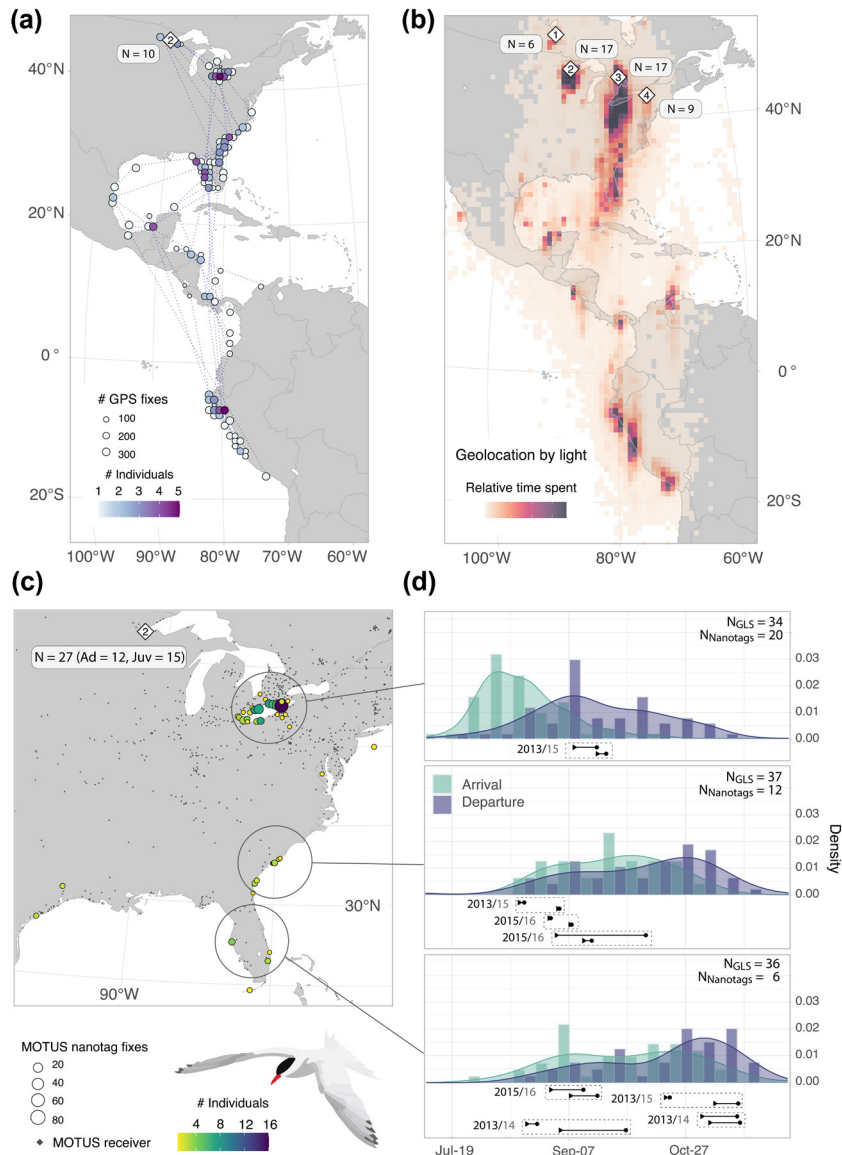


Figure 1. Tracks of common terns fitted with GPS tags (a), solar geolocators ‘GLS’ (b), and MOTUS nanotags (c). Sample sizes are labeled on plots (a)–(c) as (n =) and in plot (d) as (N_{tag type} =), i.e. N_{GLS} = or N_{Nanotags} =. GPS and MOTUS nanotag fixes were summarized on a grid (0.75 × 0.75°). GLS location estimates (a million particles per day per individual) were summarized on the same grid, providing a measure of relative time spent accounting for the spatial inaccuracy of the method. Panel (d) provides a summary of migration schedules by region (Lake Erie, southern Atlantic Coast, and Florida; top to bottom) for birds fitted with GLS and MOTUS nanotags. Beneath each phenology density plot by region, triangles (arrival) and circles (departure) grouped by dashed grey rectangles, show individuals with at least two tracks from different years. Breeding colony locations where tracking devices were deployed are indicated by white diamonds with black outline and include: 1) Lake Winnipeg, 2) Lake Superior, 3) northern Lake Huron and 4) Oneida Lake. Map made with Natural Earth.

was 16 October (range: 1 August–9 November; Fig. 2). The number of detections for both age classes declined as birds continued southward migration. Median first and last detection for adults (n = 7) at Motus stations on the Atlantic Coast was 29 September (range: 8 September–29 October; Fig. 2). Median first detection for juveniles (n = 5) was 1 October (range: 28 August–24 October) and median last detection was 2 October (range: 9 September–24 October). Median first detection for adults (n = 3) at Motus stations in Florida was 22 September (range: 7 September–3 October) and for

juveniles (n = 3) was 16 November (range: 14 September–17 November; Fig. 2). Median last detection for adults in Florida was 26 September (range: 7 September–3 October) and for juveniles was 16 November (range: 26 September–17 November; Fig. 2).

Phenology and stopover region by family group

We had planned to track family groups in 2019, however, due to extensive nest failure, only three of eight nesting pairs

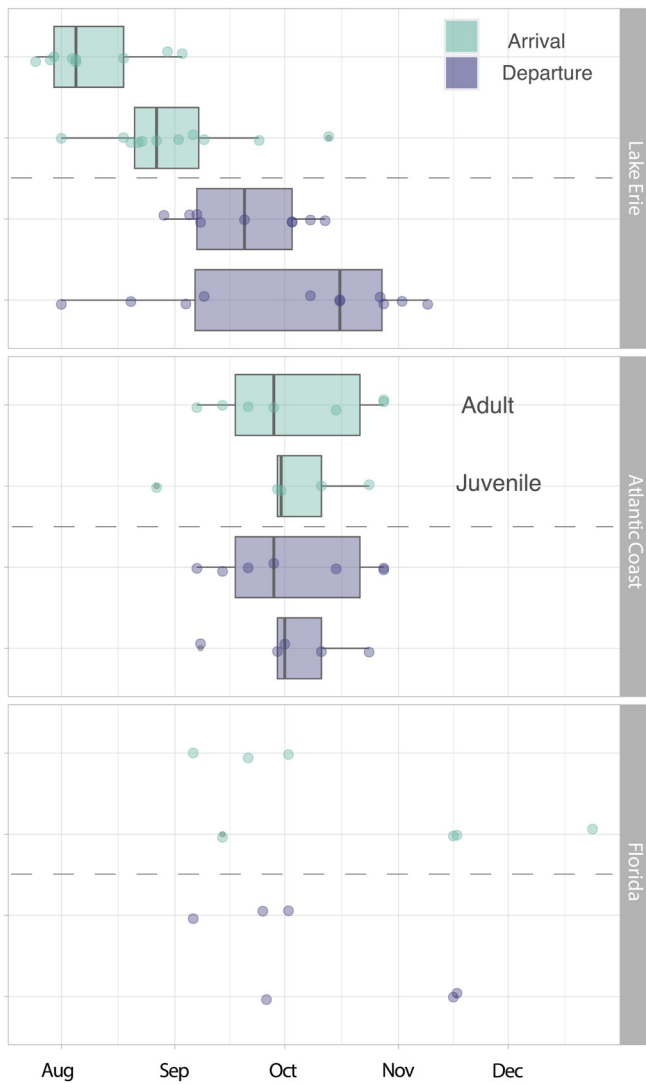


Figure 2. Box plots of arrival (first detection) and departure (last detection) of adult and juvenile common terns by region (Lake Erie ($n = 9$ Adult; $n = 11$ Juvenile), southern Atlantic Coast ($n = 7$ Adult; $n = 5$ Juvenile), and Florida ($n = 3$ Adult; $n = 3$ Juvenile)). Midline values represent median date (Julian day). The upper and lower limits of the boxes represent the 75th and 25th quartiles, respectively, with whiskers representing minimum and maximum values ($< 1.5 \times$ inter-quartile range). Only raw data points are shown for both adult and juvenile birds in Florida where only three individuals of each age class were detected.

fitted with nanotags successfully hatched young at the Lake Superior colony. Of those, only two adult pairs successfully fledged one young each, both of which were fitted with nanotags and only one was detected outside of the breeding season. Therefore, the remainder of the juveniles fitted with nanotags in this study were not associated with a family group. Although we were unable to document differences in phenology for family groups as planned (i.e. adult nesting pairs and fledged young), we were able to document movement for seven family groups in 2019, including for one pair that successfully fledged one young and six that did not (Supporting

information). For the pair that did successfully fledge one young (M1; Supporting information), the adult female was first detected at Lake Erie on 19 August and the juvenile female was first detected at Lake Erie ~ five weeks later (Supporting information). The adult female was last detected at Lake Erie ~ 2 weeks before the juvenile female arrived. The male was not detected at Lake Erie but was detected at a station along the Atlantic Coast on 22 September. The adult female was also detected at a station in Florida on 3 October. For the six pairs that did not successfully fledge young, arrival to Lake Erie ranged from 26 July–6 August for females ($n = 3$) and 30 July and 4 September for males ($n = 5$; Supporting information). For the Atlantic Coast, females ($n = 2$) arrived between 8 September–29 September and for males, 16 October–29 October ($n = 3$; Supporting information). For adults, arrival to and departure from Florida all occurred on the same day and all detections ($n = 3$) were for females and occurred between 7 September–3 October (Supporting information).

Strength of connectivity among individuals

Of the 10 adult common terns with recovered GPS tracks from Lake Superior, six were from the Interstate Island colony ($n = 3$ males and $n = 3$ females) and four were from the Ashland colony ($n = 2$ males and $n = 2$ females; Supporting information). After excluding fixes within 444 km of each breeding colony, we identified spatial interactions, i.e. same sites used within a radius of 150 km across the entire non-breeding season, which revealed nearly 5000 links (Fig. 3a). These spatial associations show that all tagged individuals were spatially linked to varying degrees regardless of sex or colony location (Fig. 3a). Applying a temporal filter to maintain associations, we found all birds maintained connectivity with a minimum of four and up to eight individuals during this period (Fig. 3b). When assessing spatiotemporal associations by region (Fig. 3c), we identified five locations with links between individuals; 1) Lake Erie, US, 2) the southern Atlantic Coast of the US, 3) the western coast of Florida, US, 4) the northwestern coast of the Yucatan Peninsula, Mexico, and 5) the northwestern coast of Peru, primarily near the Port of Bayóvar and along the coast near Chiclayo (Fig. 3c). Spatiotemporal interactions were strongest among individuals in Lake Erie followed by Florida, the southern Atlantic Coast, Peru, and the Yucatan Peninsula. No particular pattern emerged between individuals but rather a fission–fusion dynamic with individual links at only one or at several sites, e.g. 735 and 743 had links to other individuals within the western coast of Florida compared to links along the coast of Peru, and 725 showed a link with 740 in the Lake Erie region and only again along the coast of the Yucatan Peninsula (Fig. 3c).

Discussion

Integrating different tracking technologies provided both complementary and additive information about the migratory behavior of common terns breeding at inland lakes in

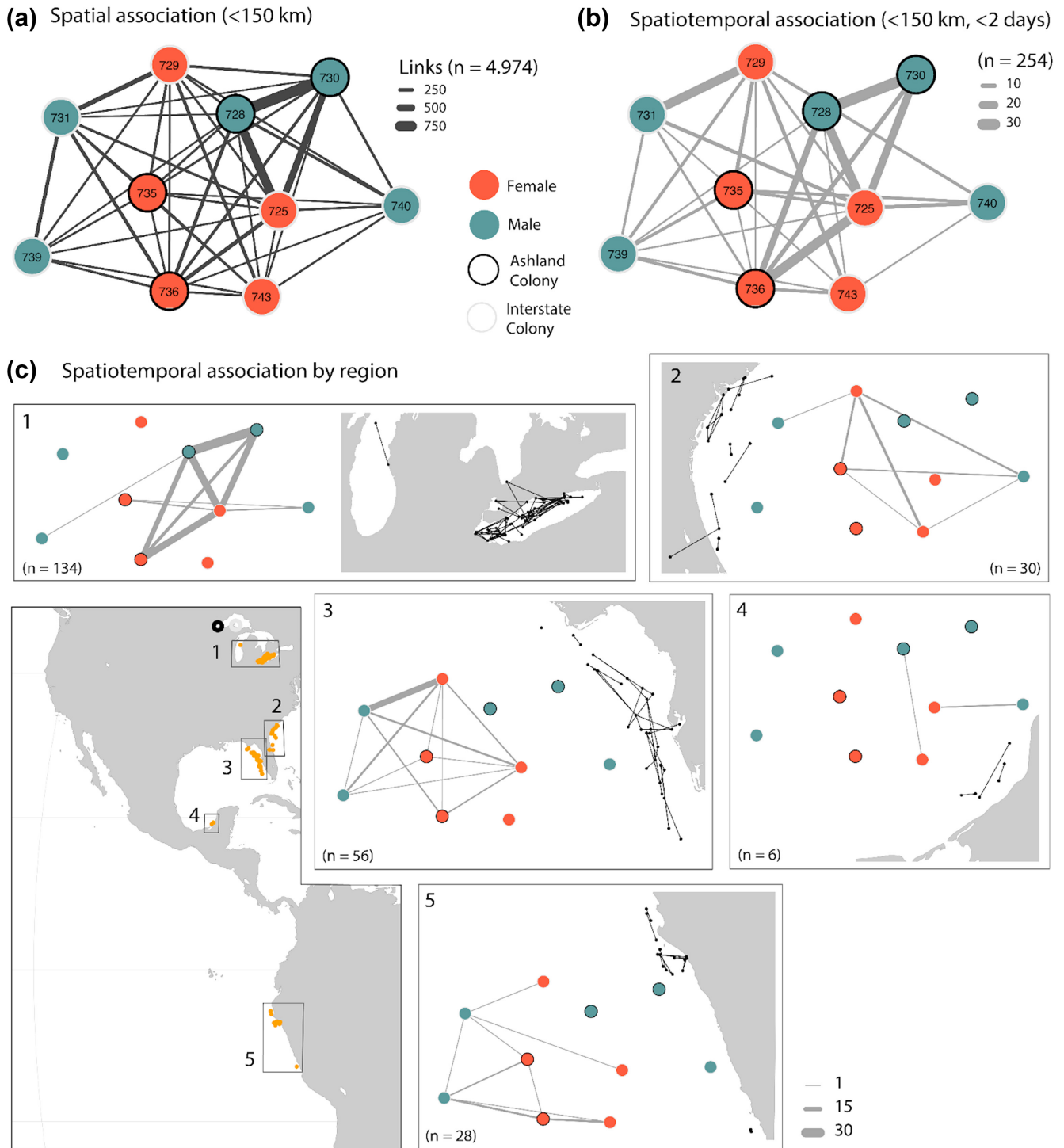


Figure 3. Graph network showing spatial (a), spatiotemporal (b), and region-specific spatiotemporal associations (c) of adult common terns breeding at two colonies on Lake Superior (thick black and grey circles) during the non-breeding season. Nodes represent individuals (with numeric ids) differentiated by sex and breeding colony location (color) within western Lake Superior (Minnesota and Wisconsin, USA). The links provide spatial and spatiotemporal associations among individuals. The network structure (e.g. relative location of nodes/individuals) is fixed to the location of individuals from the spatial association network (a). The regional maps in (c) provide the filtered links between two fixes of different individuals that occurred within a period of 2 days. The total number of links is given for each network. The regional maps describe regions in North America (1) Lake Erie, (2) southern Atlantic Coast, and (3) western coast of Florida, in Mexico (4) northwestern coast of the Yucatan Peninsula and in South America (5) northwestern coastal Peru. Map made with Natural Earth.

North America. Most importantly, the collected data indicate relatively high synchrony during the early stages of migration, with individuals gathering at Lake Erie, without strong differences between sexes. However, as adults continued south from Lake Erie, differences in timing of migration between sexes became significant. In addition, while juvenile birds arrived almost three weeks after unrelated adults at Lake Erie, their departure dates and movement towards more southern sites did not appear to differ from the unrelated adult birds, although we did not have the sample size necessary to draw conclusions of significance in the southern regions. Among the Lake Superior colonies, individual interactions, i.e. presence of two individuals within a restricted region and window of time, indicate that a large proportion of individuals migrated together, notably during the initial parts of migration. However, even within the Gulf of Mexico and off the coast of Peru, individuals from the Lake Superior breeding colonies were linked in space and time, highlighting the strong migratory connectivity and the need to identify potential spatial and temporal bottlenecks for the species.

Effect of tracking devices

Return rates and tag integrity varied for each of the tracking devices. Return rates were highest for adults fitted with GPS tags (74%) followed by GLS (63%) and nanotags (50%). Overall, our results suggest that the impacts of deploying tracking devices on common terns appear to be minimal but may vary by tag type. Our criteria for assessing effects included comparing return rates of birds fit with transmitters to those that were not (i.e. control birds). We found that return rates were similar regardless of tag type, which is valuable for assessing potential impacts to survival. When comparing pre- and post-deployment weights, we only measured birds fit with transmitters and not control birds (which were often only resighted); therefore, it was not possible to compare fitness to control birds. However, based on pre- and post-weights for birds fit with transmitters, it appears that GLS and GPS tags did not influence body condition whereas the nanotags may have had negative effects. We did not have a large enough sample size to determine whether differences were statistically significant but the differences in weights of the few birds that were recaptured with nanotags were larger than the other tag types, especially for the two females.

Only a few birds fitted with GLS were observed but never recaptured, all others attempted to nest in the year following deployment, regardless of tag type. Therefore, attachment of transmitters does not appear to have influenced the likelihood of nesting. Additionally, there were no major signs of physical wear on birds for any tag type. This information, coupled with information on tag functionality suggests that GLS and GPS tags appear safe to deploy on common terns and have relatively low rates of failure compared to use of nanotags. Although return rates of control birds were similar to that of birds fit with nanotags, relative to the other tag types, return rates were lowest and transmitter failure was highest. Therefore, use of nanotags on common terns for

long-term deployment requires caution and at minimum, use of control measures should be included in any study to determine whether long-term deployment is advisable using the methods we used in this study.

Phenology and stopover region by sex, age class, and family group

Large staging flocks of common terns have commonly been reported during autumn migration in Lakes Michigan and Erie (Arnold et al. 2020). In our study, 53% of the nanotag detections from Lake Erie occurred at four Motus Stations located along the Long Point peninsula in Norfolk, ON, CA (stations: BSC HQ, Old Cut, Breakwater, and Long Point Tip). Arrival to Lake Erie occurred within a shorter timeframe than arrival to the southern Atlantic Coast and Florida, likely due to its proximity to the breeding colonies and to its size relative to other inland lakes. Although females were documented departing from the breeding colonies on average earlier than males (Bracey et al. 2018), which has been previously documented for this species (Nisbet et al. 2011a), arrival to and departure from Lake Erie was not variable by sex. This suggests that females likely spent time at other nearby locations before beginning southward migration. While not true for Lake Erie, females arrived earlier to and departed earlier from staging locations along the southern Atlantic Coast and Florida, suggesting that southward migration schedules may accelerate, particularly for females, after staging in Lake Erie.

On average, juvenile birds were first detected on Lake Erie ~ 3 weeks later than unrelated adults; however, last detection was similar for both adult and juvenile birds. Arrival to and departure from the southern Atlantic Coast and Florida occurred within a broader timeframe. Adult common terns are largely separated from related juvenile birds by December (Arnold et al. 2020). Based on band recovery and color-mark resight data, adult birds have primarily been recovered in South America whereas first year birds have primarily been recovered or observed in Florida, the Gulf of Mexico, and the western Caribbean (Haymes and Blokpoel 1978, Blokpoel et al. 1987, 1996, Hays et al. 1997).

First and last detection was much shorter for adult birds than for juvenile birds in Florida, with many individuals only being detected at a single station multiple times on the same day (i.e. first and last detection were the same day). This is likely because adult birds are continuing southward migration to South America whereas juvenile birds likely stay to winter in Florida, the Gulf of Mexico, and the western Caribbean (Blokpoel et al. 1987, 1996). Because first year birds typically stay on the wintering grounds during the first breeding season (Arnold et al. 2020), and because there were active Motus stations within their suspected wintering areas, we anticipated higher detection rates for juvenile birds. However, due to the extensive failure (e.g. loss of antennas and water ingress) of adult nanotags, the lack of detections may have been associated with tag failure rather than survival or movement.

Although the amount of post-fledging care provided by parents is largely unknown, it has been suggested that male

common terns likely provide more post-fledging care than females, including during the staging periods (Nisbet et al. 2011a). This has also been observed in other seabird species including Caspian terns *Hydroprogne caspia* (Byholm et al. 2022) and common murrelets *Uria aalge* (Burke et al. 2015). We could not determine whether this was the case with our dataset due to the low sample size. Anecdotally, the only family group that we were able to track (M1; Supporting information) indicated that both parents migrated south prior to their offspring reaching the first major stopover region (Lake Erie). This suggests that juvenile birds may not always migrate with relatives but may rely on social interactions with other non-related individuals (Aikens et al. 2022).

Strength of connectivity among individuals

Highly accurate location estimates from GPS tags can provide unparalleled information on interactions across the migratory season. Moreover, even though our sample size was relatively low, network analysis revealed spatiotemporal links across the major stopover regions as well as along the coastline of Peru, where the majority of birds fitted with geolocators were documented to spend the winter (Bracey et al. 2018). Given that links were found within regions that were also indicated as major aggregations by the geocator analysis, we can assume a fission-fusion dynamic with fewer interactions during active flight and regathering of individuals during stopovers, as is found in other taxa (Dhanjal-Adams et al. 2018, Aikens et al. 2022). Although the degree to which these social interactions influence spatial site fidelity is unknown, social interactions may play a more significant role than previously imagined (DeSimone and Cohen 2023). Indeed, genetic analyses suggest migratory routes and non-breeding areas may influence the dispersal of individuals and degree of genetic structure of common terns and black terns *Chlidonias niger* in North America (Szczyz et al. 2017, Shephard et al. 2022). Our results show the initial potential of network analysis for the identification of important sites but also for the investigation of social interactions and their consequences.

Conclusions

Migratory seabirds face a multitude of threats to their survival; leading causes include impacts from invasive species, fisheries bycatch, and climate change (Passuni et al. 2016, Dias et al. 2019, Phillips et al. 2022). Additional threats include loss and degradation of coastal habitat from development, including the impacts of offshore wind farms and pollution (Bertram et al. 2022, Phillips et al. 2022) and impacts of emerging pathogens such as Highly Pathogenic Avian Influenza (Gamarra-Toledo et al. 2023, Pohlmann et al. 2023, Roberts et al. 2023). Identifying key locations that seabirds depend upon throughout their annual cycle will help inform conservation actions for threatened and vulnerable species. Documenting age class- and sex-specific differences in movement can also help identify demographic-specific

vulnerabilities within a population. Social interactions additionally inform the strength of connectivity between individuals in a given population or among populations.

The spatial consistency of tracks documented, regardless of tracking method, and the large number of tagged individuals, suggest that the key stopover regions identified in this study are likely very important to common terns breeding at inland lakes in North America. We determined that juvenile birds were delayed in their southward migration by roughly three weeks relative to unrelated adults based on arrival to their first staging area in Lake Erie and that they utilized the same staging areas. Social interactions of adults within the Lake Superior colonies were maintained throughout the migratory and non-breeding season, which suggests social structure was maintained throughout the annual cycle and not seasonally dependent for this species. Our study provides important information about the movement ecology of common terns and highlights how use of multiple tracking technologies can reveal different aspects of migratory behavior that can help inform conservation actions for this vulnerable species.

List of abbreviations

DOP = Dilution of precision; GLS = Global location sensors; GMT =, greenwich mean time; GPS = Global positioning system; VHF = very high frequency.

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and Use Committee (proposal no. 2016-AB-01), the Cornell University Animal Care and Use Committee (protocol no. 2001-0091), the Animal Care Committee of the Wildlife and Landscape Science Directorate and the Canadian Wildlife Service Ontario, Environment Canada, with due regard for the Guidelines of the Canadian Council of Animal Care.

Author contributions

Annie Bracey: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – original draft (equal). **Fred Strand:** Data curation (equal); Methodology (equal); Writing – review and editing (equal). **Alexis Grinde:** Conceptualization (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – review and editing (equal). **Francesca Cuthbert:** Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Supervision (equal); Writing – review and editing (equal). **Ann E. McKellar:** Data curation (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **David Moore:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Methodology (equal); Writing – review and editing (equal). **Elizabeth Craig:** Data curation (equal); Funding acquisition (equal); Investigation (equal); Writing – review and editing (equal). **Simeon Lisovski:** Formal analysis (equal); Methodology (equal); Software (equal); Visualization (equal); Writing – original draft (equal).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/jav.03308>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/doi:10.5061/dryad.z34tmpgpx> (Bracey et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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