BioOne COMPLETE

Migratory routes and wintering locations of declining inland North American Common Terns

Authors: Bracey, Annie, Lisovski, Simeon, Moore, David, McKellar, Ann, Craig, Elizabeth, et al.

Source: The Auk, 135(3) : 385-399

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-17-210.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

The Auk
Ornithological Advances

AmericanOrnithology.org

Volume 135, 2018, pp. 385–399
DOI: 10.1642/AUK-17-210.1

RESEARCH ARTICLE

Migratory routes and wintering locations of declining inland North American Common Terns

Annie Bracey,[1,2#*] Simeon Lisovski,[3,4#] David Moore,[5] Ann McKellar,[6] Elizabeth Craig,[7] Sumner Matteson,[8] Fred Strand,[9a] Jeffrey Costa,[5] Cynthia Pekarik,[10] Paul Curtis,[7] Gerald Niemi,[2] and Francesca Cuthbert[1]

[1] Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, Minnesota, USA
[2] Natural Resources Research Institute, University of Minnesota, Duluth, Minnesota, USA
[3] Swiss Ornithological Institute, Department of Bird Migration, Sempach, Switzerland
[4] Department of Neurobiology, Physiology and Behavior, University of California, Davis, California, USA
[5] Canadian Wildlife Service, Environment and Climate Change Canada, Burlington, Ontario, Canada
[6] Canadian Wildlife Service, Saskatoon, Saskatchewan, Canada
[7] Department of Natural Resources, Cornell University, Ithaca, New York, USA
[8] Wisconsin Department of Natural Resources, Madison, Wisconsin, USA
[9] Wisconsin Department of Natural Resources, Brule, Wisconsin, USA
[10] Canadian Wildlife Service, Gatineau, Quebec, Canada
[a] Retired.
[#] These authors contributed equally to the paper.
[*] Corresponding author: brace005@d.umn.edu

Submitted October 31, 2017; Accepted January 24, 2018; Published April 4, 2018

ABSTRACT

Common Terns (*Sterna hirundo*) breeding at inland lakes in North America have experienced significant population declines since the 1960s. Although management actions aimed at mitigating effects of habitat loss and predation have been largely effective, numbers continue to decline, which suggests that the population may be limited during the nonbreeding season. Between 2013 and 2015, we used light-level geolocators to track Common Terns nesting at 5 inland colonies—from Lake Winnipeg in Manitoba, Canada, to the eastern Great Lakes region of the United States and Canada—to identify migratory routes and stopover and wintering sites and to determine the strength of migratory connectivity among colonies. Within 46 recovered tracks, we found evidence of a longitudinal gradient in use of migration routes and stopover sites among colonies and identified major staging areas in the lower Great Lakes and at inland and coastal locations along the Atlantic coast, Florida, and the Gulf of Mexico. Low migratory connectivity across inland colonies illustrates high intermixing within wintering sites, with many birds spending the nonbreeding season in Peru (70%) and the remainder spread throughout the Gulf of Mexico, Central America, and northwestern South America. While the large spatial spread and intermixing of individuals during the nonbreeding season may buffer local effects of climate change and human disturbance, the aggregation of individuals along the coast of Peru could make them vulnerable to events or changes within this region, such as increased frequency and intensity of storms in the Pacific, that are predicted to negatively influence breeding productivity and survival of Common Terns. Identifying sources of mortality during the nonbreeding season, quantifying winter site fidelity, and reinforcing the importance of continued management of inland breeding colonies are vital priorities for effective conservation and management of this vulnerable population.

Keywords: ENSO, geolocation by light, migratory connectivity, seabirds, *Sterna hirundo*

Rutas migratorias y sitios de invernada de *Sterna hirundo*, especie en disminución en el interior de América del Norte

RESUMEN

Los individuos de *Sterna hirundo* que crían en los lagos del interior en América del Norte han experimentado disminuciones poblacionales significativas desde los 1960s. Aunque las acciones de manejo dirigidas a mitigar los efectos de la pérdida de hábitat y la depredación han sido enormemente efectivas, los números continúan disminuyendo, sugiriendo que la población puede estar limitada durante la estación no reproductiva. Entre 2013 y 2015, usamos geo-localizadores de nivel de luz para seguir a individuos de *S. hirundo* anidando en cinco colonias tierra adentro desde el Lago Winnipeg, Manitoba hacia el este en la región de los Grandes Lagos, para identificar las rutas migratorias y los sitios de parada e invernada, y para determinar la fortaleza de la conectividad migratoria entre las colonias. De los 46 recorridos recuperados, encontramos evidencia de un gradiente longitudinal en el uso de rutas migratorias y sitios de parada entre las colonias e identificamos las principales áreas de parada en la parte baja de los

© 2018 American Ornithological Society. ISSN 0004-8038, electronic ISSN 1938-4254
Direct all requests to reproduce journal content to the AOS Publications Office at pubs@americanornithology.org

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Grandes Lagos y en sitios tierra adentro y costeros a lo largo de la Costa Atlántica, Florida y el Golfo de México. Una baja conectividad migratoria de las colonias tierra adentro muestra una alta entremezcla adentro de los sitios de invernada, con muchas aves pasando la estación no reproductiva en Perú (70%) y el resto distribuidos a lo largo del Golfo de México, América Central y noroeste de Sud América. Mientras que la gran distribución espacial y la entremezcla de individuos durante la estación no reproductiva pueden amortiguar los efectos locales del cambio climático y los disturbios humanos, la agregación de individuos a lo largo de la costa de Perú podría hacerlos vulnerables a eventos o cambios dentro de esta región, como el aumento en la frecuencia e intensidad de tormentas en el Pacífico que se predice que influenciarán negativamente la productividad reproductiva y la supervivencia de *S. hirundo*. Identificar las causas de mortalidad durante la estación no reproductiva, cuantificar la fidelidad a los sitios de invernada y reforzar la importancia de un manejo continuo de las colonias reproductivas tierra adentro son prioridades vitales para la conservación y el manejo efectivo de esta población vulnerable.

Palabras clave: aves marinas, conectividad migratoria, ENSO, geo-localización por luz, *Sterna hirundo*

INTRODUCTION

The Common Tern (*Sterna hirundo*) is the most widespread tern in North America (Nisbet et al. 2017). However, as with many other colonial-nesting waterbirds, its populations are declining globally (Wendt et al. 2006, Wetlands International 2010). As a group, colonial waterbirds are considered especially sensitive to anthropogenic disturbances such as degradation, modification, and loss of habitat (Wetlands International 2010). These threats are most pronounced in coastal environments where human population growth and urbanization rates have greatly increased during recent decades, and these trends are expected to continue into the future (Neumann et al. 2015).

Inland freshwater habitats, including the Great Lakes region of the United States and Canada and large lakes of south-central Manitoba, are thought to be the ancestral population centers for North American Common Terns and are often considered ideal habitat for breeding terns from a historical perspective (Arnold et al. 2016, Szczys et al. 2017). Despite this view, long-term decreases in the numbers of nests and colony sites have been significant in the interior of North America since the 1960s (Cuthbert et al. 2003). For example, in the Great Lakes region, the estimated number of breeding pairs of Common Terns declined by 18% between 1976 and 2009 (Morris et al. 2010, 2012, Wires et al. 2010, Nisbet et al. 2017); in large lakes in southern Manitoba, nest numbers are estimated to have declined by 57–67% from the early 1990s to 2012 (Wilson et al. 2014). As a result, 6 of the U.S. states that border the Great Lakes have listed the Common Tern as threatened or endangered (Cuthbert et al. 2003). In the Canadian portion of the Great Lakes, the number of nesting pairs declined by ~41% between 1976 and 2009 (Morris et al. 2010), but the Common Tern has not been identified as a species at risk in Canada. Given the magnitude of these declines, management actions have been implemented in the Great Lakes region at some colony sites to conserve this species (Cuthbert et al. 2003); these efforts have included habitat restoration and protection, predator control, and construction of artificial nesting structures (Jones and Kress 2012). Similar actions have been effective in restoring Common Tern colonies on the Atlantic coast of North America, where populations are now generally thought to be stable (Jones and Kress 2012, Morris et al. 2012, Szczys et al. 2017). In the Great Lakes region, however, despite the success of these activities at some locations, the numbers of breeding pairs and colonies have continued to decline, which suggests that inland-nesting birds may be experiencing pronounced threats during the nonbreeding season.

To effectively conserve declining populations, such as inland-nesting, long-distance migratory Common Terns, it is crucial to determine where in the annual cycle they are being limited (Marra et al. 2015). Furthermore, identifying the strength of migratory connectivity—the geographic linking of individuals and populations between one life-cycle stage and another—may help in evaluating the vulnerability of populations to local environmental hazards and human influences (Webster et al. 2002, Trierweiler et al. 2014, Bauer et al. 2016) and explaining differences in population trends among populations. Determining how connected migratory individuals and populations are throughout the year requires knowledge of the seasonal distribution of a species and a corresponding measure of strength of co-occurrence between seasons (Cohen et al. 2017). Migratory connectivity is considered strong (positive) when populations remain together between seasons and weak (negative) when there is little or no co-occurrence between seasons (Cohen et al. 2017). Knowledge of connectivity is especially important for migratory species in decline (Fraser et al. 2012, Lyons et al. 2018). Thus, tracking individuals during their full annual cycle is crucial to identifying important locations used by these inland birds during the nonbreeding season, identifying potential risks, and developing strategies to target non-breeding-season actions.

One method used to track individual bird movement—and, more recently, to quantify migratory connectivity—is band re-encounter data. Over 1.5 million Common Terns have been banded in North America since the early 1900s

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

(Nisbet et al. 2017). On the basis of band recovery data, 3 broadly defined breeding populations of Common Terns have been proposed: the Atlantic, Central, and Northwest units (Nisbet et al. 2017). Birds associated with the Atlantic unit include individuals banded on the Atlantic coast of North America and Canada and recovered in the Bahamas, in the West Indies, and along the north and east coasts of South America (Nisbet et al. 2017). Birds associated with the Central unit include individuals banded in the Great Lakes region and observed or recovered in southern Florida, the Gulf of Mexico, Central America, and the west coast of South America (Haymes and Blokpoel 1978, Blokpoel et al. 1987, Nisbet et al. 2017). Common Terns nesting in Oneida Lake, New York, are also considered part of the Central unit based on band recoveries (Cuthbert and Wires 2002, Nisbet et al. 2017). Birds associated with the Northwest unit include individuals banded in Alberta and Saskatchewan and recovered on the Pacific coast from central Mexico to Costa Rica (Nisbet et al. 2017). Although recoveries of birds banded in Manitoba and North Dakota are sparse, the majority of these were reported along the Pacific coast, with one recovery from the north coast of South America (Nisbet et al. 2017). Therefore, it is still uncertain where the boundary between western Central colonies and birds breeding in the Northwest unit occurs.

When using band re-encounter data to quantify migratory connectivity, it is important to account for potential biases associated with spatial variation in banding efforts and re-encounter probabilities (Cohen et al. 2014, Thorup et al. 2014, Korner-Nievergelt et al. 2017). When accounting for spatial heterogeneity in re-encounter probabilities, Cohen et al. (2014) found regional migratory connectivity of Common Terns breeding in North America to be strong. Along with band re-encounter data, a recent study using light-level geolocators reinforced use of the east coast of South America by the Atlantic population during the nonbreeding season (Nisbet et al. 2011a). Although band re-encounter data have been useful in identifying discrete locations used during the nonbreeding season and in revealing potential geographic connections between populations, detailed annual movement patterns remain unknown for inland birds, and the degree to which these local (colonies) and regional populations are segregated can be better informed by tracking individuals over their full annual cycle.

The objectives of our study were to identify migratory routes, stopover locations, and overwintering hot spots for 5 inland colonies of Common Terns breeding in central North America with light-level geolocators and to use these data to quantify the strength of migratory connectivity among breeding colonies during winter. If all 5 breeding colonies are part of the Central population unit, we expected that (1) their nonbreeding distributions would mirror that of Central birds identified from band re-encounter studies (e.g., Cohen et al. 2014, Nisbet et al. 2017) and (2) migratory connectivity among colonies would be weak (i.e. mixing of individuals from all colonies on the wintering grounds would be high) while maintaining regional segregation (i.e. strong migratory connectivity among the 3 North American population units). We didn't expect geographic distribution to be associated with sex; however, we did predict that females would depart from the breeding colony earlier than males, independent of colony location, based on documented differences in postfledging care by sex (Nisbet et al. 2011b, 2017). With the exception of departure date, we expected no significant differences in migration schedules between sexes or among colony sites. Our results will provide important information about the geographic distribution and connectedness of inland-nesting Common Terns, which enable improved assessment of sensitivity to local threats and help identify conservation and management goals for the declining Central population of Common Terns breeding in North America.

METHODS

Study Sites

Our study sites consisted of 5 Common Tern breeding colonies located within the interior of North America. Colonies spanned a range of ~21° longitude and ~9° latitude and were located in 2 Canadian provinces and 3 U.S. states. Study sites from west to east included Egg Island, a ~15 ha sandy island located in central Lake Winnipeg near Princess Harbour, Manitoba (51.93°N, 97.08°W); Interstate Island, a ~1.9 ha dredge-spoil island situated in the Duluth-Superior Harbor on Lake Superior (46.75°N, 92.11°W); Ashland Island, a ~0.03 ha reconstructed pier remnant located in Ashland, Wisconsin, on Lake Superior (46.61°N, 90.87°W); Elm Island, a ~1.9 ha rocky island located in the northeastern portion of the North Channel, Lake Huron, Ontario (46.02°N, 82.13°W); and Little Island, a ~0.09 ha rocky island located in the western portion of Oneida Lake, New York (43.24°N, 76.00°W) (Figure 1 and Table 1). We will refer to the lake where each colony is located as the unit of study. Because of their proximity (~96 km apart), we considered the 2 Lake Superior colonies (Interstate and Ashland islands) as one unit (hereafter "Lake Superior").

Field Methods

We deployed 106 archival light-level geolocators on Common Terns across the 4 lakes during the breeding seasons of 2013, 2014, and 2015; the years in which the breeding colonies were visited post-deployment varied by breeding lake (Table 1). Intigeo geolocators (model W65A9; Migrate Technology, Cambridge, UK) were deployed on individuals breeding on lakes Winnipeg ($n =$

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

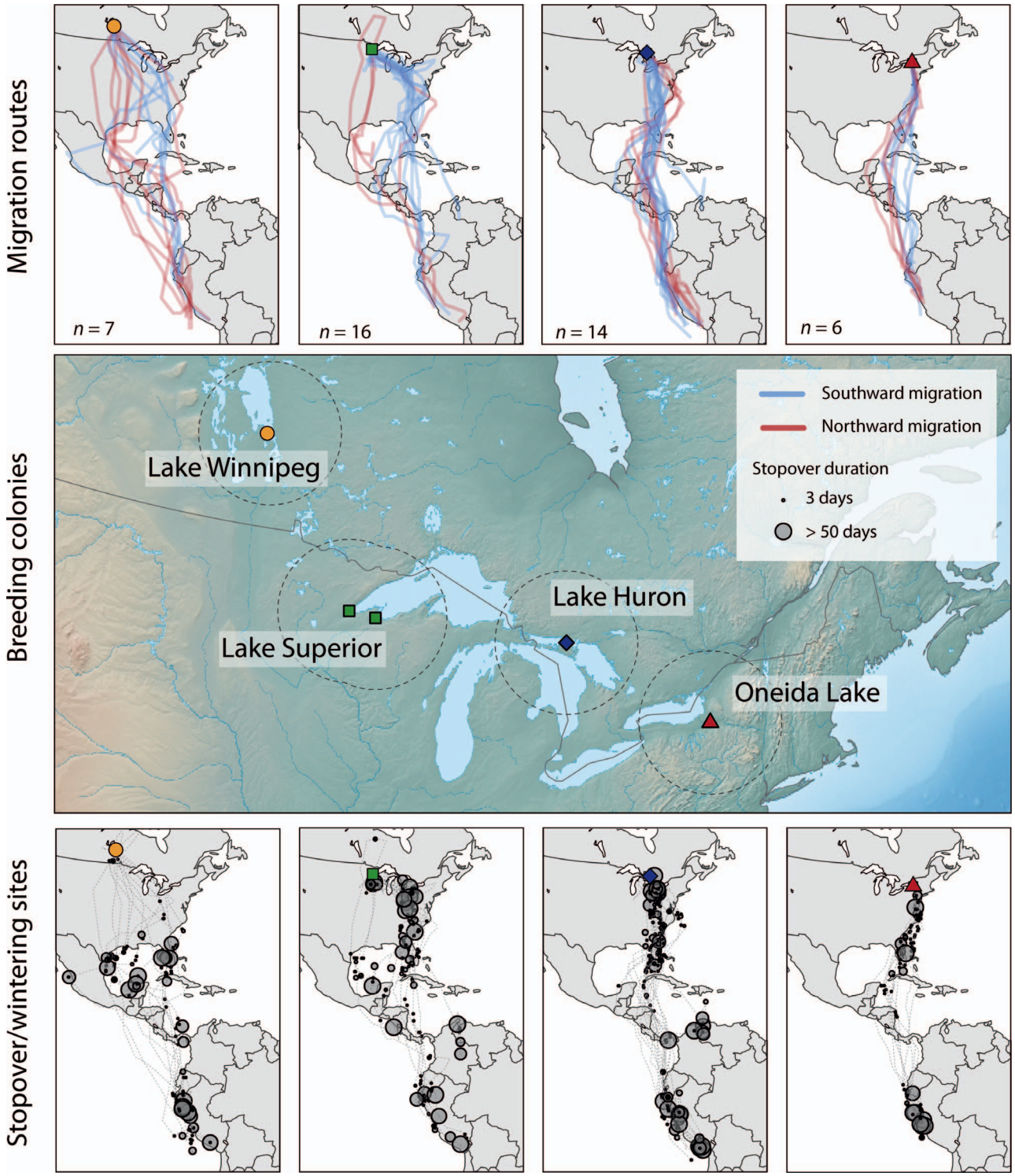

FIGURE 1. Locations of 5 inland breeding colonies where Common Terns were tracked using light-level geolocators: Egg Island, Lake Winnipeg (Manitoba, Canada); Interstate Island, Lake Superior (Minnesota and Wisconsin, USA); Ashland Island, Lake Superior (Wisconsin); Elm Island, Lake Huron (Ontario, Canada); and Little Island, Oneida Lake (New York, USA). Circles around each breeding colony, with a radius of 250 km, represent the zone outside of which we considered movements to be associated with migration. Individual migration routes, shown in the upper panel, represent median daily location estimates, which describe the general migration patterns of each colony. Error estimates associated with individual migration routes are provided in Supplemental Material Figure S1. Stopover and wintering sites are depicted by circles in the lower panel, with the size of the circle indicating the duration of stay at each location (minimum of 3 days). For dates of geolocator deployment and years of data collection, see Table 1.

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 1. Numbers of light-level geolocators deployed, retrieved, and missing (i.e. auxiliary marker present but geolocator absent), by year, at 5 inland breeding colonies on 4 breeding lakes where Common Terns were tracked. Also shown are dates of deployment and numbers of geolocator-tagged birds that were resighted but not recaptured. Numbers in parentheses indicate the sex of individuals (F = female, M = male, U = unknown).

				Geolocators (*n*)			
Breeding lake	Breeding colony	Year	Date	Deployed	Retrieved	Missing	Resighted
Lake Winnipeg, Manitoba, Canada	Egg Island	2015	June 24–30	30	–	–	–
		2016		–	7 (4F, 3M)	–	3
		2017		–	2 (2F)	–	–
Lake Superior, Minnesota and Wisconsin, USA	Interstate Island	2013	June 13	15	–	–	–
		2014		–	7 (4F, 3M)	3 (3F)	–
		2015	June 9	10	1 (M)	–	–
		2016		–	6 (4F, 2M)	–	–
		2017		–	–	–	2
Lake Superior, Wisconsin, USA	Ashland Island	2015	June 8	11	–	–	–
		2016		–	4 (3F, 1M)	1 (M)	–
		2017		–	–	–	–
Lake Huron, Ontario, Canada	Elm Island	2013	June 18–20	30	–	–	–
		2014		–	15 (10F, 4M, 1U)	1 (M)	–
		2015		–	3 (1F, 2M)	–	2
Oneida Lake, New York, USA	Little Island	2014	June 19	10	–	–	–
		2015		–	7 (3F, 4M)	–	–

30), Huron ($n = 30$), and Oneida ($n = 10$). British Antarctic Survey (BAS) geolocators (model MK5093; Biotrak, Wareham, UK) were deployed on Common Terns nesting at the 2 Lake Superior colonies (Interstate, $n = 25$; Ashland, $n = 11$). Fieldwork was conducted during favorable weather conditions (e.g., no extreme temperatures or rain) to minimize exposure-related adverse effects on eggs, chicks, and adults. All birds included in the study were adults (most $\geq$3 yr old; see below) that were trapped on a nest during incubation. Maximum handling time for each bird was approximately 15–20 min, which included the time necessary to attach the geolocator and weigh, measure, and sex the bird. The sex of individuals was determined by genetic analysis via a blood sample, with the exception of birds from Oneida Lake, where sex was determined using biometric measurements (i.e. tarsus length, head plus bill length, bill depth, and wing chord; Supplemental Material Table S1; Nisbet et al. 2007). Most birds returned to incubate eggs within 5–10 min of release. Birds were captured using either open-bottom walk-in traps made of polyvinyl pipe and nylon mesh or box traps made of welded rectangular mesh wire (approximately 43 × 51 × 23 cm).

A geolocator was attached to the leg of each bird using a darvic ring or flag, similar to the methods of Nisbet et al. (2011a). In addition to the U.S. Geological Survey band that each bird received, geolocator-tagged birds from Lake Huron ($n = 30$; Supplemental Material Table S1) and their mates ($n = 11$), as well as the mates of geolocator-tagged birds from Lake Winnipeg ($n = 30$), were fitted with field-readable color bands. Geolocator-tagged birds marked at the Lake Superior colonies in 2013 and 2015 were also fitted with an auxiliary flag (Supplemental Material Table S1). The combined mass of each attachment (geolocator + plastic ring or flag + adhesive + auxiliary band) was $\leq$2.0 g (<2% of Common Tern body weight). Birds were weighed prior to deployment of geolocators and again when geolocators were retrieved. Results are presented as means (± SE) and ranges. Birds fitted with geolocators at the Lake Superior colonies and Oneida Lake were adults of known age (Supplemental Material Table S1). We monitored all geolocator-tagged birds after deployment for signs of possible negative effects associated with the attachment of the geolocator (e.g., not incubating eggs, pecking or favoring a leg) by observing individuals from a distance, using 10 × 40 binoculars. Observations generally occurred for 1–2 hr after initial deployment and for ~30 min during repeat visits to the colony, if repeat visits were possible.

Analytical Methods

The Intigeo and BAS geolocators recorded light readings every minute, with the maximum light recorded every 5 min. In contrast to BAS geolocators, which record only low light levels, Intigeo geolocators record the entire light range. We used the R package TwGeos (Lisovski 2016) to import data and to identify sunrise and sunset (i.e. twilight times) using light-level thresholds of 1.0 (Intigeo) and 2.5 (BAS). Extreme outliers (e.g., >60 min different than adjacent twilight times, interpolating between the previous and subsequent twilight times) were adjusted manually. Twilight periods, the periods of increasing and decreasing light, were then automatically determined as the periods before and after sunrise and sunset. To calibrate geolocators, we chose recordings post-deployment, when the

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

bird was at the breeding colony (i.e. light recordings at known locations; Supplemental Material Table S1). For geolocators that were still recording data upon retrieval, we specified a second calibration period to account for potential changes in the sensor sensitivity due to wear. We chose on-bird calibration periods to be after incubation (period of high shading) but prior to migration, allowing for more realistic light-level readings, given a bird's behavior and habitat. Then we employed the R package "FLightR" (Rakhimberdiev et al. 2015b, Rakhimberdiev and Saveliev 2016), which uses a template fit, to derive location estimates (spatial likelihood surfaces) based on the shape and timing of the light transition during twilight periods. To refine estimates, a hidden Markov model was computed using a particle filter to weight locations based on the results of the template fit, a movement model, and spatial masks. Because Common Terns use both inland and coastal habitats, we didn't include spatial or behavioral constraints (e.g., flight distances/speeds or a land mask). The particle filter generates the probability of occurrence of an inferred location on a spatial grid and the probability of transition between nodes (i.e. movement from one location to another), with the distance between nodes equal to 50 km (Rakhimberdiev et al. 2015b). The particles are simulated locations, with each particle representing a possible location within a path that is developed using the rules of the movement model (Rakhimberdiev et al. 2015b). At each twilight, all generated particles are compared to data passed through the observation model, with unlikely particles being replaced by more likely ones based on the product of previous likelihoods (Rakhimberdiev et al. 2015b). Once all iterations are completed, a posterior probability distribution is approximated for each bird at each twilight (Rakhimberdiev et al. 2015b). Ultimately, a million particles were used to optimize the track of each bird and its uncertainty (Rakhimberdiev et al. 2015b).

To identify all locations used during the nonbreeding season, we summarized flight-path estimates and movement patterns for individual birds with both partial and complete annual tracks ($n = 46$). To summarize each track, we used the median of the posterior probability distribution of the million particles per twilight. Furthermore, we distinguished stationary behavior from movement using the "find.time.distribution" function in FLightR. If estimated track locations occurred within a radius of 150 km for a minimum of 3 days (6 twilights), we considered the bird stationary. Stationary periods identified during migration were considered "stopover" locations. When estimating the number and duration of stopovers and the duration of the nonbreeding, nonmigratory stationary periods, we summarized data only for individuals with complete information. Results are presented as means ($\pm$ SE) and ranges.

As noted previously, we buffered each colony by 250 km (Figure 1) to account for potential movements within the breeding period, including foraging trips, travel to nearby locations used after breeding, and loafing (i.e. local movement after breeding failure but before migration). We used median date to estimate arrival at and departure from breeding colonies based on the proportion of particles that arrived within the 250 km radius surrounding each colony. Defining arrival and departure as occurring outside of this buffer zone likely reflects the true start of autumn migration and the end of spring migration for most birds. We calculated the total distance of migration for each bird by summing daily estimates of movement to and from the breeding colony outside of the defined stationary periods. There is inherent error associated with measuring distances traveled on the basis of successive daily estimates of location, due either to assuming straight-line travel (underestimate) or to compounding errors (overestimate). However, we were able to reduce error during preprocessing removal of extreme outliers and by excluding movement occurring within stationary periods. Migration schedules were summarized using mean values and ranges for estimates of duration of stay and number of stopovers, and mean values and 95% credible intervals for estimates involving dates (e.g., dates of departure and arrival).

We used generalized linear models to determine differences in migration schedules between sexes, breeding lakes, and years of deployment for each event (e.g., beginning autumn and spring migration); we present chi-square and P values for each explanatory variable. We excluded 2 birds from this particular analysis; the first (Lake Superior, COTE_4) departed on June 16, indicating a failed breeding attempt, not typical of a normal annual schedule for a breeding adult. This bird also arrived on the breeding grounds on July 11, the year following deployment, and didn't breed, so its arrival didn't reflect the end of a normal migration. The second bird (Lake Huron, D851) was of unknown sex and therefore also excluded. A paired t-test was used to determine whether there were differences in body weight between year of deployment and year of geolocator recovery.

We defined the nonbreeding, nonmigratory stationary period for each bird as the interval between the end of fall migration and the start of spring migration. Birds often moved to multiple locations within this period, so we also summarize the distances traveled and number of movements during this period. To calculate the strength of migratory connectivity (MC) among breeding colonies, we used the method described by Cohen et al. (2017), which uses transition probabilities from discreet regions, while also accounting for the relative abundance of populations and estimates of uncertainty due to geolocation error. To determine the main wintering site, we used all particles

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

that were generated for the period between December 15 and March 31 for each individual and calculated a density map with a resolution of 50 × 50 km. Although some birds reached their wintering grounds much sooner than December 15, others didn't; therefore, dates used in calculating connectivity vary among individual birds (Supplemental Material Table S4). We then defined the major wintering site by the coordinate of the grid cell that had the most particles for that period. For birds carrying geolocators that failed during this interval, we included estimates of wintering location but excluded these individuals from estimates of duration of stay. Although individuals may have moved after the geolocators failed, we still summarized wintering locations for failed geolocators if locations occurred during the specified "wintering" months, but we state which individuals had complete annual tracks and which did not. The quantification of MC based on Cohen et al. (2017) requires spatial polygons that characterize the breeding (origin) as well as the wintering (target) sites. For the breeding sites, we drew circles with a 250 km radius around each colony. Similarly, we drew circles with a 250 km radius around the major wintering location of each individual. Overlapping circles were merged, resulting in 6 distinct target polygons. Using these spatial polygons, the coordinates for the breeding colonies as well as the major wintering sites, we estimated the strength of MC using the "estMC" function for 3 scenarios: (1) using equal population size among breeding lakes, (2) using nest counts from each of the 5 breeding colonies to determine "mean nesting pairs/colony" to calculate relative abundance, and (3) using lake-specific estimates of nesting pairs of Common Terns to estimate relative abundance (Supplemental Material Table S5). All data were analyzed using R 3.3.1 (R Core Team 2015).

RESULTS

Geolocator Recovery Rates

We recaptured 57 of 106 birds fitted with geolocators. Five were missing geolocators (4 from Lake Superior and 1 from Lake Huron). Of the 52 recovered geolocators, we were unable to extract data from 4, including 2 from Lake Winnipeg, 1 from Lake Superior, and 1 from Lake Huron. Two geolocators (Lake Superior, Lake Huron) failed on the breeding grounds, prior to first migration. Of the remaining 46 geolocators, 19 recorded data for a full year (41%), one recorded data for 2 yr, and the remaining 27 stopped recording data during the course of the year in which they were deployed. Of the 46 geolocators with usable data, 25 were from females, 20 from males, and 1 from an individual of unknown sex. Birds of known age ($n = 25$) ranged from 4 to 14 yr with a median age of 7 yr (Supplemental Material Table S1). The overall return rate of geolocators (2014–2017), including birds observed but not recaptured ($n = 7$), was 60% (64/106). The percentage of birds wearing geolocators that were recaptured or resighted from the year of deployment to the subsequent breeding season ranged from 33% (Lake Winnipeg) to 70% (Oneida Lake) (Table 1). At lakes Winnipeg and Huron, where mates of birds with geolocators were color banded, return rates were 33% (10/30) for both geolocator and color-banded mates (Lake Winnipeg) and 50% (15/30) for geolocator-tagged birds and 64% (7/11) for color-banded mates (Lake Huron).

There was no significant difference in pre-deployment and recovery weight for female or male birds fitted with geolocators (female, paired-sample t-test: $t = -1.4$, $P = 0.17$, $n = 25$; male, paired-sample t-test: $t = 0.9$, $P = 0.37$, $n = 16$). The mean pre-deployment weight for females was 128 ± 1.4 g (range: 115–143 g); for males it was 125 ± 2.1 g (range: 112–140 g). The mean recovery weight for females was 130 ± 1.5 g (range: 112–145 g); for males it was 123 ± 1.6 g (range: 107–132 g).

Overall Migration Patterns

Flight paths, duration of stay at stopover and wintering locations, and total distance traveled varied among individual birds within and among breeding colonies (Figure 1; Supplemental Material Table S2, Table S3, Supplemental Figure S1). There were prebreeding and postbreeding movements observed near each breeding colony but located outside the defined breeding site (i.e. >250 km from breeding colony); therefore, observations occurring near this boundary were included as stopover locations in our summaries. The duration of autumn migration was greater than that of spring migration. Based on estimated departure from breeding grounds and arrival at wintering grounds, the mean duration of autumn migration was 88 ± 5.0 days (range: 19–170 days; $n = 32$). The mean number of stopover locations used during autumn migration was 4.6 ± 0.4 (range: 1–11), and the mean duration at stopover locations was ~21 ± 2.2 days (range: 3–71 days). For spring migration, the mean duration was 32 ± 3.6 days (range: 19–86 days; $n = 19$). The mean number of stopover locations used during spring migration was 2.4 ± 0.2 (range: 1–4), and the mean duration at stopover locations was 12 ± 1.7 days (range: 3–29 days).

We identified several stopover locations used by individuals from all inland-breeding lakes during autumn migration. These include inland locations in states south of the Great Lakes, as far south as Florida; and locations along the Atlantic coast of the United States to Florida, Cuba, and the Caribbean Sea (Table 2). With the exception of Oneida Lake, at least one individual from all other breeding lakes also staged in the Great Lakes region during autumn migration (Table 2). The Gulf of Mexico was identified as another important staging location for

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 2. Mean duration of stay (days; with range in parentheses) at migratory stopover sites for Common Terns from 4 North American breeding lakes, and number of individuals tracked using light-level geolocators on which this is based (*n*; numbers in parentheses are total numbers of individuals observed where some individuals were excluded from the calculation because geolocator failure made their duration of stay unknown; when a bird with a failed geolocator was the only individual observed at a given location, a plus sign is placed after the mean duration of stay to indicate that this is a minimum estimate). Major staging locations were identified on the basis of estimates from movement models for the 4 lakes. For dates of geolocator deployment and years of data collection, see Table 1.

	Lake Winnipeg		Lake Superior		Lake Huron		Oneida Lake	
	Mean duration	*n*	Mean duration	*n*	Mean duration	*n*	Mean duration	*n*
Autumn stopover sites								
Southern Manitoba	7 (3–15)	3	–	–	–	–	–	–
Southeast Minnesota	–	–	30 (10–50)	5	–	–	–	–
Great Lakes region [a]	3 (3–3)	2	32 (3–64)	11 (15)	36 (4–66)	14 (15)	–	–
Ohio	–	–	–	–	25 (20–34)	3	–	–
Inland states [b]	5 (4–6)	2	21 (8–34)	5 (7)	11 (3–31)	11	8	1
Atlantic coast [c]	4 (3–6)	2	16 (3–44)	4	30 (3–55)	6 (7)	32 (15–71)	6
Florida	50 (39–57)	3	16 (4–54)	6	15 (5–36)	9	32	1
Cuba [d]	75	1	18 (14–21)	2	25 (3–47)	2	37 (28–50)	3
Gulf of Mexico	53 (32–71)	3	21+	1	3	1	–	–
Yucatán Peninsula	–		8 (5–11)	2	–		–	
Pacific coast of Mexico	42	1	–	–	–	–	–	–
Gulf of Tehuantepec	3	1	–	–	–	–	–	–
Caribbean Sea	4	1	4 (4–4)	2	5 (3–8)	4	5 (5–6)	3
Panama	5	1	5	1	8 (6–10)	2	–	–
Columbia–Ecuador	4 (3–5)	2	12	1 (3)	3	1	–	–
Peru	–	–	–	–	3 (3–6)	3	8 (5–11)	2
Spring stopover sites								
Northwest Peru	3	1	–	–	–	–	–	–
Panama–Nicaragua	3 (3–4)	2	–	–	–	–	–	–
Cuba [d]	–	–	11	1	14	1 (2)	–	–
Florida	–	–	–	–	7 (3–9)	3	3	1
Gulf of Mexico	21(13–30)	6	11 (7–15)	3	3 (3–3)	2	–	–
Coastal Yucatán	24	1	–	–	–	–	–	–
Atlantic coast [c]	10	1	3	1	8 (4–14)	4	11 (8–14)	4
Inland states [b]	–	–	6	1	3+	1	–	–
Great Lakes region [a]	–	–	–	–	4 (3–8)	4	–	–
Eastern Pennsylvania	–	–	–	–	–	–	28	1
Southeast Minnesota	–	–	37 (21–63)	3	–	–	–	–
Northwest Ontario	–	–	13+	1	–	–	–	–

[a] "Great Lakes region" refers primarily to the lower Great Lakes region, including Lake Erie and northern Ohio.
[b] Inland states include Kentucky, West Virginia, Virginia, North Carolina, South Carolina, Georgia, and Florida.
[c] Atlantic coast states include Virginia, North Carolina, South Carolina, and Georgia.
[d] Cuba includes Straits of Florida and Yucatán Channel.

Common Terns during both autumn and spring migration. The percentages of individuals that used the Gulf of Mexico were as follows (during autumn and spring, respectively): Lake Winnipeg (43%, 86%); Lake Superior (8%, 60%); Lake Huron (7%, 33%); and Oneida Lake (0%, 0%) (Table 2). Birds also staged along the U.S. Atlantic coast in the following percentages (during autumn and spring, respectively): Lake Winnipeg (29%, 14%); Lake Superior (25%, 20%); Lake Huron (41%, 67%); and Oneida Lake (100%, 100%) (Table 2). The mean distance traveled during autumn migration ($n = 32$) was ~7,553 ± 337.0 km (range: 4,004–11,270 km). During spring migration, the mean distance traveled ($n = 19$) was ~7,640 ± 452.3 km (range: 4,474–12,062 km). Estimated total distance traveled during migration (both autumn and spring) by birds with complete annual tracks ($n = 19$) averaged 15,141 ± 695.0 km (range: 9,511–19,639 km).

The mean duration of stay during the nonbreeding, nonmigratory stationary period ($n = 21$) was 151 ± 3.4 days (range: 130–183 days), although the duration is longer if considering data from failed units (e.g., ≥238 days for one bird from Lake Superior; Supplemental Material Table S3). The mean number of nonbreeding, nonmigratory movements associated with the time spent on the wintering grounds was 3.7 ± 0.5 (range: 0–9). The mean distance moved within this period was 1,322 ± 177 km

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

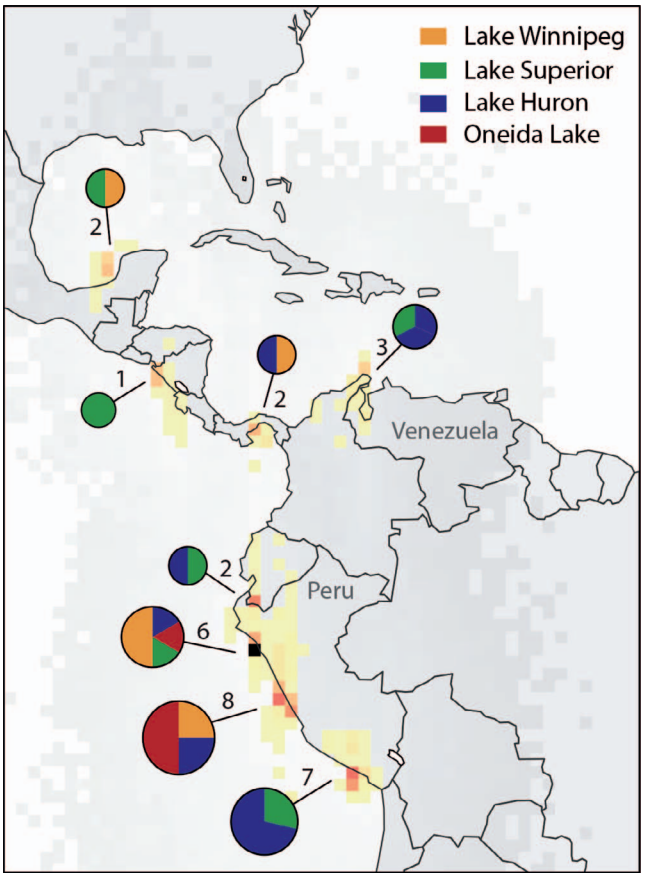

FIGURE 2. Median "wintering" locations identified for geolocator-tagged Common Terns ($n = 31$) breeding at 4 inland lakes in North America. Median latitude and longitude were quantified on the basis of location estimates occurring between December 15 and March 31. Shaded areas indicate 95% credible interval (estimated error around median location). For dates of geolocator deployment and years of data collection, see Table 1.

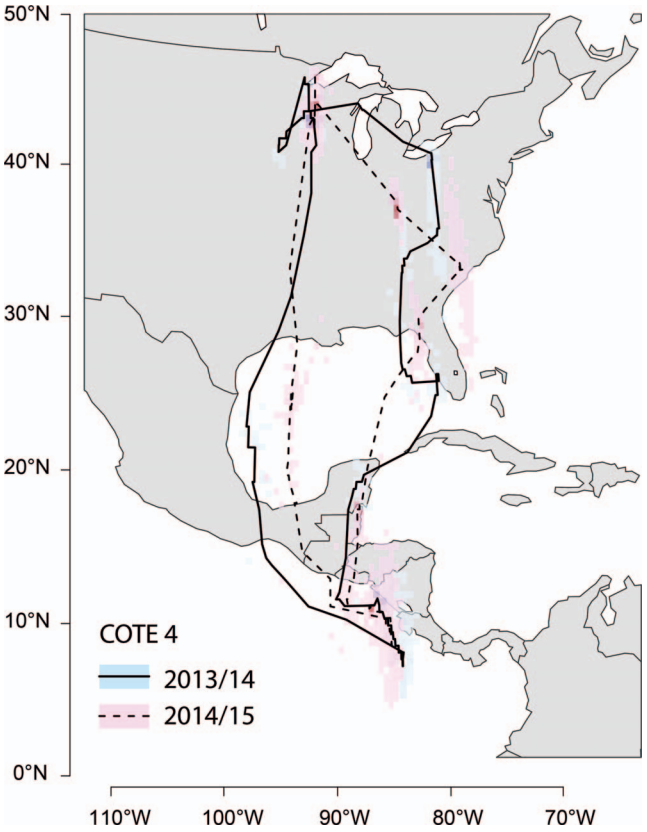

FIGURE 3. Two consecutive migratory journeys of one individual Common Tern (COTE_4) breeding at a Lake Superior colony (Interstate Island). Lines represent the median estimated track; shaded area indicates 95% credible interval, blue for 2013–2014 and pink for 2014–2015. For detailed migration schedules, see Supplemental Material Table S6.

(range: 0–2,678 km; $n = 20$) (Supplemental Material Table S3). Of all "wintering" sites identified, including those from partial tracks ($n = 30$), 70% of birds spent the majority of the defined wintering period in Peru, and the remaining 30% wintered in the Gulf of Mexico, Central America, Venezuela, and Ecuador (Figure 2, Table 3, and Supplemental Material Table S4). For the 3 relative abundance scenarios, the estimated strength of MC (with corresponding estimates of sampling error in parentheses) was as follows: –0.03 (0.08) for scenario 1 (equal size/lake); 0.05 (0.10) for scenario 2 (colony nest counts); and 0.19 (0.15) for scenario 3 (lake estimates of breeding pairs). These results suggest high inter-colony mixing during the "wintering" period and weak migratory connectivity for the Central population unit (strong MC would result in an estimate close to 1).

Two years of data were collected from a geolocator retrieved from a bird on one of the Lake Superior colonies (Interstate Island) in 2015. The bird, a male hatched on Interstate Island in 2004, was 9 yr old at the time of deployment (2013). The number and location of stopover sites identified were similar for both autumn and spring migration, although timing of migration and length of stopovers varied slightly between years (Figure 3 and Supplemental Material Table S6).

Timing of Migration

Date of departure from the breeding lake varied significantly by sex and lake; on average, females departed earlier (August 9) than males (August 24) and birds from Lake Winnipeg and Oneida Lake departed later (August 28 and August 26, respectively) than birds from Lake Superior and Lake Huron (August 2 and August 15, respectively) (Table 4). Arrival at wintering grounds also varied by sex, but not by lake or year; on average, females arrived earlier than males (November 2 and November 20, respectively) (Table 4). Finally, date of arrival at the breeding colony in spring was significantly different

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 3. Mean duration of stay (days; with range in parentheses) at nonbreeding, nonmigratory stationary ("wintering") locations of Common Terns ($N = 31$; total shown is >31 because some individuals moved during the study period) from 4 North American breeding lakes, and the number of individuals tracked using light-level geolocators on which this is based (*n*; numbers in parentheses are total numbers of individuals observed where some individuals were excluded from the calculation because geolocator failure made their duration of stay unknown; when a bird with a failed geolocator was the only individual observed at a given location, a plus sign is placed after the mean duration of stay to indicate that this is a minimum estimate). Wintering locations were identified on the basis of estimates from movement models for the 4 lakes. For dates of geolocator deployment and years of data collection, see Table 1.

	Lake Winnipeg		Lake Superior		Lake Huron		Oneida Lake	
Wintering locations	Mean duration	*n*	Mean duration	*n*	Mean duration	*n*	Mean duration	*n*
Gulf of Mexico	122 (60–183)	2	175	1	–	–	–	–
Straits of Florida–Gulf of Mexico	–	–	–	–	46	1	–	–
Caribbean Sea–Honduras–Nicaragua	–	–	–	–	12	1	–	–
Nicaragua–Costa Rica	–	–	131	1	–		–	–
Panama	71	1	–	–	110+	1	–	–
Northwest Venezuela	–	–	238+	1	129+ (114–143)	2	–	–
Ecuador	–	–	12 (8–15)	2	14	1	–	–
Peru	152 (130–171)	5	132 (124–139)	2 (4)	147 (140–151)	6 (9)	147 (130–162)	4 (5)

between sexes; on average, males arrived 1 wk earlier than females (Table 4).

DISCUSSION

Tracking Common Terns throughout their annual cycle allowed us to document important routes, migration schedules, and wintering locations of individuals from the declining North American inland-breeding population. The nonbreeding distributions identified in our study suggest that Common Terns nesting in southern Manitoba (Lake Winnipeg) are part of the Central population unit, providing additional insight into where Central and Northwestern population units potentially diverge. We also documented a high degree of intermixing among the inland colonies during the nonbreeding season, with many birds wintering in coastal Peru, a location where large concentrations of waterbirds are known to depend on adequate food and habitat for survival (Blokpoel et al. 1989, Pulido et al. 1996).

Migration Routes and Stopover Locations

Some evidence exists for a longitudinal gradient in the use of migration routes and stopover sites among the colonies. Birds from the western breeding colonies (lakes Winnipeg and Superior) followed a pattern similar to a clockwise loop migration (e.g., Berthold 2001, Trierweiler et al. 2014), with many birds traveling southeast during autumn migration but using a route farther west during spring migration. By contrast, individuals from Lake Huron used migratory routes that followed a more direct north–south route, and Common Terns from Oneida Lake showed a pattern of counterclockwise loop migration. It is noteworthy that we documented substantial use of inland locations during autumn migration, when it was previously thought that most inland populations of Common Terns migrated from the lower Great Lakes to the U.S. Atlantic coast before continuing south (Haymes and Blokpoel 1978, Blokpoel et al. 1987, Szczys et al. 2017). Not only did birds appear to be using inland sites, but many remained for several weeks to (in a few cases) months and didn't stop along the U.S. Atlantic coast at all. During spring migration, birds used fewer stopover locations and stayed for shorter periods than during autumn migration, which is typical of many migratory birds (Horton et al. 2016) and consistent with observations of Common Terns from the North American Atlantic population unit (Nisbet et al. 2011b).

On average, females departed from the breeding colonies and arrived on the wintering grounds earlier than males; this behavior is consistent with observations by Nisbet et al. (2010, 2011b) and lends further evidence that males perform more postfledging care than females. In general, departure dates were more variable than arrival dates, which were likely determined by local postbreeding conditions (e.g., food availability) within the defined breeding areas and may be why we observed differences in departure dates among colonies that didn't appear to be strictly associated with latitude. Although we expected females to depart the breeding colony earlier than males, based on observations of Nisbet et al. (2011a), there was no evidence to suggest differences in timing and duration of migration between sexes of Common Terns in North America. The observed differences in arrival dates at wintering grounds between males and females suggest that, in general, when females leave the breeding colony they don't extend the postbreeding period elsewhere, leading to earlier female arrival dates. However, the amount of overlap in arrival date at wintering grounds between sexes could also potentially reflect variation in the

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

TABLE 4. Timing and duration of migration, timing of arrival at wintering grounds, median wintering location, and time spent on wintering grounds for male and female Common Terns from 4 North American breeding lakes: Lake Winnipeg, Lake Superior, Lake Huron, and Oneida Lake. *P* values represent significance levels from generalized linear models, which included sex + lake (location of breeding lake) + year in which geolocators were deployed. Significant values ($P \leq 0.05$) are in bold. For dates of geolocator deployment and years of data collection, see Table 1.

	Females			Males			Sex		Lake		Year	
	n	Mean	Range	*n*	Mean	Range	χ^2	*P*	χ^2	*P*	χ^2	*P*
Begin autumn migration	25	August 9	July 1–August 29	19	August 24	August 4–September 10	13.85	**0.00**	16.61	**0.00**	0.15	0.70
Duration of autumn migration	14	82 days	19–135 days	16	86 days	55–126 days	0.47	0.49	3.45	0.33	2.56	0.11
Arrive at wintering grounds	14	November 2	August 26–December 3	16	November 20	October 24–December 27	4.32	**0.04**	1.85	0.60	2.24	0.13
Median wintering location (latitude)	13	9.64°S	17.05°S–19.87°N	15	7.81°S	17.97°S–20.76°N	0.12	0.73	3.91	0.27	1.37	0.24
Duration on wintering grounds	9	153 days	130–183 days	11	149 days	130–183 days	0.00	0.96	0.80	0.67	–	–
Begin spring migration	9	April 16	April 9–May 1	11	April 16	March 30–April 28	0.00	0.95	0.30	0.86	–	–
Duration of spring migration	8	32 days	23–48 days	10	24 days	19–54 days	0.75	0.39	0.05	0.98	–	–
Arrive at breeding colony	8	May 19	May 6–30	10	May 12	May 1–22	4.43	**0.04**	1.60	0.45	–	–

extent of male postfledging care or juvenile survival. We didn't observe differences in median wintering locations (latitudes) between sexes, although this has been observed in Common Terns nesting in the German North Sea, where females wintered farther north than males (Becker et al. 2016). Adult Common Terns returning to breed in the spring typically look for previous mates, or for a new partner, within a few days of arrival at the breeding colony (Ludwig and Becker 2006, Nisbet et al. 2017), with 53% of pairs estimated to arrive within 3 days of each other (Ludwig and Becker 2006). In our study, males were estimated to return to the breeding area approximately a week earlier than females, which contradicts reports that males and females arrive at the same time. However, because we buffered each breeding colony by 250 km, to more accurately identify true departure dates, it is possible that earlier-arriving males staged somewhere within the buffered zone without actually returning directly to the breeding colony. Therefore, males and females may still have returned to their respective breeding colonies more synchronously.

Wintering Locations and Migratory Connectivity

Many birds moved throughout the nonbreeding, nonmigratory period, often spending a few weeks to a few months in one location before moving to another. Median "wintering" locations, defined as December 15–March 31, were spread throughout the Gulf of Mexico and Central America and along the northwest coast of South America. However, most birds in our study spent the majority of the nonbreeding season along the coast of Peru, which was previously identified as an important wintering location for Great Lakes Common Terns, based on observations of color-banded birds (Austin 1953, Blokpoel et al. 1987).

The high degree of intermixing of birds from each of the 4 inland lakes suggests high population spread and weak connectivity among inland colonies; high intermixing was also proposed recently, based on band encounter data, at least for birds from the Great Lakes region (Culp et al. 2017). It is suggested that under weak connectivity, a localized catastrophic event on the wintering grounds would have a diffuse effect across multiple breeding populations (Webster and Marra 2005). However, given that 70% of the birds in our study spent the winter months in coastal Peru, a large portion of these inland colonies appear to be dependent on a relatively small geographic range, making them vulnerable to events or changes within this region that could have strong negative effects on multiple inland-breeding colonies. This observation reinforces the need to consider scale when examining levels of migratory connectivity (Finch et al. 2017). Because there is a high rate of dispersal among Great Lakes breeding colonies (Cuthbert et al. 2003, Szczys et al. 2017), we suggest that it is more appropriate to consider connectivity

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

at a broader scale. The degree of segregation between inland and Atlantic populations was estimated to be high, based on band re-encounters (Cohen et al. 2014, Nisbet et al. 2017) and light-level geolocators (Nisbet et al. 2011a). Together, these results suggest that at a continental scale, Common Terns breeding in North America show strong connectivity (i.e. segregation), with little overlap on the wintering grounds among breeding units, at least when Atlantic and Central populations are compared. Results from our study support the inclusion of the Oneida Lake colony as part of the Central unit, which was previously suggested on the basis of band re-encounter data (Cuthbert and Wires 2002, Nisbet et al. 2017). Birds nesting in Lake Winnipeg also appear to be part of the Central unit, based on nonbreeding distributions identified in our study. However, several Common Terns banded in Manitoba, including one from Lake Winnipeg, were recovered on the Pacific coast between Mexico and El Salvador, where Northwest-unit birds are known to winter, which suggests that Manitoba could be the boundary where Northwest and Central populations diverge (Nisbet et al. 2017). Increasing banding efforts and using tracking technologies to identify the migration routes and wintering areas used by Common Terns breeding in the Northwest unit (i.e. Saskatchewan and Alberta), Manitoba and North Dakota, and the St. Lawrence River and Quebec is an important next step in determining where migratory patterns diverge at the edges of the 3 broadly defined population units.

Although little is known about winter site fidelity of Common Terns, evidence from banding records reported by Nisbet et al. (2017) suggests that it may be high. Common Terns from the Great Lakes region, including birds from our study, have been observed in coastal Peru during consecutive years, based on mark–resighting data (e.g., Blokpoel et al. 1987). The Common Tern in our study for which we have 2 yr of tracking data used similar migration routes and wintering locations in successive years. Because of the small number of multiyear observations in our study and in previous studies (Haymes and Blokpoel 1978, Becker et al. 2016), it is not possible to determine the degree of winter site fidelity in Common Terns. However, based on these collective observations, this species appears to display moderate to high levels of winter site fidelity. This information is important from a conservation perspective, because it will be difficult to determine the effects of localized events or to predict future threats without confirmation that birds are returning to the same wintering sites. The degree of fidelity is likely associated with changes in food availability, which is directly linked to biotic and abiotic conditions on the wintering grounds (Becker et al. 2016).

Conservation Implications

A recent genetic study, aimed at identifying the population structure of inland and eastern North American Common Tern colonies, found evidence of asymmetrical dispersal from inland to coastal colonies thought to be associated with nonbreeding distributions (Szczys et al. 2017). Dispersal rates from inland colonies to the Atlantic coast have increased tenfold since the 1960s, which may partly explain the apparent population decline of inland colonies during this period. Although similar management strategies have been implemented at inland and coastal colonies, the Atlantic coast population is considered stable, whereas the Central population continues to decline. Because these populations don't overlap on their wintering grounds, a focus on nonbreeding habitat use and juvenile dispersal will be important for understanding metapopulation dynamics (Szczys et al. 2017). Additional genetic analyses of Common Terns breeding in the western portion of the Central unit and Northwest unit, as well as use of stable isotopes, are needed to further identify and quantify dispersal among units. Weak migratory connectivity among the 4 inland lakes and consistent declines in nest numbers throughout the Central unit make it difficult to identify bottlenecks using data loggers alone, because birds must survive and return to the same site for data to be retrieved. To identify threats, other methods, such as satellite tracking and analysis of mark–recapture data, will be needed to estimate seasonal apparent survival (e.g., Lok et al. 2015, Rakhimberdiev et al. 2015a, Huang et al. 2017).

Climate change is currently identified as one of the greatest threats to Common Terns worldwide (Cabot and Nisbet 2013, Palestis 2014, Nisbet et al. 2017). Issues related to climate change—including increased severity of storms, changes in food availability, and rising water levels—are important factors that may negatively affect Common Terns throughout their annual cycle (Cuthbert et al. 2003, Cabot and Nisbet 2013). A recent climate-change vulnerability assessment suggests that migratory distance and degree of habitat specialization during breeding and nonbreeding seasons will likely pose the greatest direct challenges to this species, due to predicted sea-level rise (Culp et al. 2017). The greatest perceived indirect effect was related to vulnerability of aquatic prey and their habitats in response to climate change (Culp et al. 2017).

Predicted increases in the strength and frequency of storms will be detrimental to Common Terns nesting at inland colonies in North America (Cuthbert et al. 2003) and to individuals wintering in coastal Peru, where El Niño–Southern Oscillation (ENSO) events are also likely to intensify and occur more often (Wang et al. 2017). At inland breeding colonies, high water levels and severe storm events can erode or inundate island nesting habitats; when these events occur at peak nesting, total nest failure often results (Cuthbert et al. 2003). Additionally, during

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

years of high water, competition with gulls often increases as a result of reduced availability of nesting habitat (Cuthbert et al. 2003). Throughout the nonbreeding season, Common Terns follow the distribution and abundance of prey fish (Cabot and Nisbet 2013), and the northwest coast of South America is a hot spot for productivity (Jahncke et al. 2004, Capone and Hutchins 2013, Passuni et al. 2016). The Peruvian upwelling ecosystem, part of the Humboldt Current System, is one of the most biologically productive marine environments globally (Jahncke et al. 2004, Capone and Hutchins 2013). The cold, nutrient-rich water in this system is important to piscivorous birds that rely on the abundance of pelagic fish for survival (Pulido et al. 1996, Jahncke et al. 2004). The Peruvian anchovy (*Engraulis ringens*), which is the most abundant pelagic fish in this system, is not only an important species for foraging seabirds but also supports the largest single species fishery on Earth (Pulido et al. 1996, Jahncke et al. 2004). Though highly productive, this system is influenced by regional climatic fluctuations that can dramatically alter productivity (Jahncke et al. 2004, Capone and Hutchins 2013). In the late 1960s to early 1970s, the combination of heavy fishing pressure and 2 ENSO events (1965 and 1972) resulted in the collapse of the anchovy population, which led to major declines in seabird populations (Jahncke et al. 2004). In addition to pressures from commercial fishing, changes in sea surface temperatures caused by ENSO events further reduced prey availability by altering the distribution and abundance of fish along the Peruvian coast (Jahncke et al. 2004, Devney et al. 2009, Passuni et al. 2016). Declines in seabird and shorebird populations have been documented in years of extreme ENSO events such as 1982–1983, when populations of Red-necked Phalaropes (*Phalaropus lobatus*) assumed to be wintering in the region crashed (Nisbet and Veit 2015) and numbers of Common Terns wintering along the southern coast of Peru were substantially below normal (Hughes 1985). Although potential impacts of climate change on both breeding productivity and adult survival currently appear to be serious, it is difficult to predict how Common Terns will adapt to future environmental conditions.

In long-lived seabirds such as Common Terns, survival rates are more likely to influence population trends than annual changes in productivity (Cabot and Nisbet 2013, Palestis 2014); therefore, identifying potential causes of adult mortality during the nonbreeding season will be key to effectively targeting conservation efforts. Because we have identified Peru as a location where many Common Terns from inland populations concentrate during the nonbreeding season, research on habitat use (e.g., identification of feeding areas, prey species, and food availability) will help isolate local threats and potential risks to Common Tern survival. If survival during the nonbreeding season is primarily influenced by environmental factors, such as changing ocean temperatures and fluctuating food supplies, it will be important to better quantify winter site fidelity, monitor where birds are moving, and identify conditions associated with movements. This knowledge will also reinforce the importance of continued management of inland North American breeding colonies, as well as emphasizing the need for restoration and creation of additional breeding habitats.

ACKNOWLEDGMENTS

We thank the many people involved in forming this collaborative effort—most especially I. Nisbet, for his advice, guidance, and review of the manuscript; and S. Lewis, for his long-term dedication to conservation of Common Terns in the Great Lakes region. We are grateful to members of the AOU-COS 2015 light-level geolocation workshop in Norman, Oklahoma, and the 2016 NAOC workshop in Washington, D.C., specifically to E. Rakhimberdiev, E. Bridge, N. Seavy, and M. Hallworth for their assistance to A.B. during these workshops. We are also thankful for project advice and training from J. Arnold, S. Oswald, M. Mallory, R. Porter, G. Kramer, N. Walton, and J. Bednar as well as field assistance from R. Rodriguez, E. Hannan, N. Barlow, C. Dale, A. Foran, J. Galloway, B. Moray, N. Shephard, A. Stupich, R. Weeber, K. Rewinkel, and M. Minchak; and for logistical support from S. Vanneste, J. Hughes, L. Kress, P. Martin, B. Magnusson, S. Surprenant, and S. Song. DNA analysis was conducted in part by A. Idrissi, L. Gauthier, A. Lekorchi, C. Robert, and G. Savard. F.C. is grateful to the University of Michigan Biological Station for decades of logistical support for Common Tern research in the Great Lakes.

Funding statement: Funding was provided by the U.S. Fish and Wildlife Service (USFWS; agreement nos. F11AP00081 and F11AP00515); the USFWS Great Lakes Fish and Wildlife Restoration Act (agreement no. F16AP01000); the Coastal Zone Management Act of 1972, as amended, administered by the Office for Coastal Management, National Oceanic and Atmospheric Administration, under award no. NA16NOS4190119 provided to the Minnesota Department of Natural Resources for Minnesota's Lake Superior Coastal Program; the Minnesota and Wisconsin departments of natural resources; and various internal grants from the University of Minnesota, the Natural Resources Research Institute, and the University of Minnesota Conservation Sciences graduate program to A.B. to fund fieldwork and purchase geolocators. New York State Department of Environmental Conservation and Cornell Lab of Ornithology funded the purchase of geolocators and management of the Oneida Lake colony. F.C.'s contribution to this research was supported by the USDA National Institute of Food and Agriculture, Hatch project no. 1007020. Funding for the Canadian portion of the study was through Canadian Wildlife Service, Environment and Climate Change Canada.

Ethics statement: We acquired all necessary permitting for handling and marking Common Terns in the United States and Canada (2013–2016). This project was approved by the

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

USGS Bird Banding Laboratory (permit nos. 05322 and 08781) and the Canadian Wildlife Service Bird Banding Office (permit no. 10431), the Wisconsin Department of Natural Resources Animal Care and Use Committee, the Cornell University Animal Care and Use Committee (protocol no. 2001-0091), and 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: D.M., A.M., E.C., S.M., F.S., F.C., G.N., and P.C. conceived the idea and supervised research. D.M., C.P., J.C., A.M., E.C., P.C., A.B., and F.S. collected data. S.L. and A.B. analyzed the data. A.B., S.L., and A.M. wrote the paper, with all authors contributing substantially to revisions.

LITERATURE CITED

Arnold, J. M., I. C. T. Nisbet, and S. A. Oswald (2016). Energetic constraint of non-monotonic mass change during offspring growth: A general hypothesis and application of a new tool. Journal of Animal Ecology 85:476–486.

Austin, O. L. (1953). The migration of the Common Tern (*Sterna hirundo*) in the Western Hemisphere. Bird-Banding 24:39–55.

Bauer, S., S. Lisovski, and S. Hahn (2016). Timing is crucial for consequences of migratory connectivity. Oikos 125:605–612.

Becker, P. H., H. Schmaljohann, J. Riechert, G. Wagenknecht, Z. Zajková, and J. González-Solís (2016). Common Terns on the east Atlantic flyway: Temporal-spatial distribution during the non-breeding period. Journal of Ornithology 157:927–940.

Berthold, P. (2001). Bird Migration: A General Survey, second edition. Oxford University Press, Oxford, UK.

Blokpoel, H., D. C. Boersma, R. A. Hughes, and G. D. Tessier (1989). Field observations of the biology of Common Terns and Elegant Terns wintering in Peru. Colonial Waterbirds 12: 90–97.

Blokpoel, H., G. D. Tessier, and A. Harfenist (1987). Distribution during post-breeding dispersal, migration, and overwintering of Common Terns color-marked on the lower Great Lakes. Journal of Field Ornithology 58:206–217.

Cabot, D., and I. Nisbet (2013). Terns. HarperCollins, London, UK.

Capone, D. G., and D. A. Hutchins (2013). Microbial biogeochemistry of coastal upwelling regimes in a changing ocean. Nature Geoscience 6:711–717.

Cohen, E. B., J. A. Hostetler, M. T. Hallworth, C. S. Rushing, T. S. Sillett, and P. P. Marra (2017). Quantifying the strength of migratory connectivity. Methods in Ecology and Evolution 9. In press.

Cohen, E. B., J. A. Hostetler, J. A. Royle, and P. P. Marra (2014). Estimating migratory connectivity of birds when re-encounter probabilities are heterogeneous. Ecology and Evolution 4: 1659–1670.

Culp, L. A., E. B. Cohen, A. L. Scarpignato, W. E. Thogmartin, and P. P. Marra (2017). Full annual cycle climate change vulnerability assessment for migratory birds. Ecosphere 8: e01565.

Cuthbert, F. J., and L. R. Wires (2002). Common Tern breeding populations: A review of Common Tern band recovery data 1922–2000. Final report to Minnesota Cooperative Fish and Wildlife Research Unit. University of Minnesota, St. Paul, MN, USA.

Cuthbert, F. J., L. R. Wires, and K. Timmerman (2003). Status assessment and conservation recommendations for the Common Tern (*Sterna hirundo*) in the Great Lakes Region. U.S. Department of the Interior, Fish and Wildlife Service, Ft. Snelling, MN, USA.

Devney, C. A., M. Short, and B. C. Congdon (2009). Sensitivity of tropical seabirds to El Niño precursors. Ecology 90:1175–1183.

Finch, T., S. J. Butler, A. M. A. Franco, and W. Cresswell (2017). Low migratory connectivity is common in long-distance migrant birds. Journal of Animal Ecology 86:662–673.

Fraser, K. C., B. J. M. Stutchbury, C. Silverio, P. M. Kramer, J. Barrow, D. Newstead, N. Mickle, B. F. Cousens, J. C. Lee, D. M. Morrison, T. Shaheen, et al. (2012). Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. Proceedings of the Royal Society B 279:4901–4906.

Haymes, G. T., and H. Blokpoel (1978). Seasonal distribution and site tenacity of the Great Lakes Common Tern. Bird-Banding 49:142–151.

Horton, K. G., B. M. Van Doren, P. M. Stepanian, A. Farnsworth, and J. F. Kelly (2016). Seasonal differences in landbird migration strategies. The Auk: Ornithological Advances 133: 761–769.

Huang, R. M., O. L. Bass, Jr., and S. L. Pimm (2017). Sooty tern (*Onychoprion fuscatus*) survival, oil spills, shrimp fisheries, and hurricanes. PeerJ 5:e3287.

Hughes, R. A. (1985). Notes on the effects of El Niño on the seabirds of the Mollendo district, southwest Peru, in 1983. Ibis 127:385–388.

Jahncke, J., D. M. Checkley, Jr., and G. L. Hunt, Jr. (2004). Trends in carbon flux to seabirds in the Peruvian upwelling system: Effects of wind and fisheries on population regulation. Fisheries Oceanography 13:208–223.

Jones, H. P., and S. W. Kress (2012). A review of the world's active seabird restoration projects. Journal of Wildlife Management 76:2–9.

Korner-Nievergelt, F., C. Prévot, S. Hahn, L. Jenni, and F. Liechti (2017). The integration of mark re-encounter and tracking data to quantify migratory connectivity. Ecological Modelling 344:87–94.

Lisovski, S. (2016). R Package TwGeos: Basic data processing for light based geolocation archival tags. https://github.com/slisovski/TwGeos

Lok, T., O. Overdijk, and T. Piersma (2015). The cost of migration: Spoonbills suffer higher mortality during trans-Saharan spring migrations only. Biology Letters 11:20140944.

Ludwig, S. C., and P. H. Becker (2006). Waiting for the mate? Spatial behaviour of Common Terns, *Sterna hirundo*, during courtship. Animal Behavior 72:1093–1102.

Lyons, J. E., B. Winn, T. Keyes, and K. S. Kalasz (2018). Post-breeding migration and connectivity of Red Knots in the Western Atlantic. The Journal of Wildlife Management 82: 383–396.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra (2015). A call for full annual cycle research in animal ecology. Biology Letters 11:20150552.

Morris, R. D., C. Pekarik, and D. J. Moore (2012). Current status and abundance trends of Common Terns breeding at known coastal and inland nesting regions in Canada. Waterbirds 35: 194–207.

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Morris, R. D., D. V. Weseloh, F. J. Cuthbert, C. Pekarik, L. R. Wires, and L. Harper (2010). Distribution and abundance of nesting Common and Caspian terns on the North American Great Lakes, 1976 to 1999. Journal of Great Lakes Research 36:44–56.

Neumann, B., A. T. Vafeidis, J. Zimmermann, and R. J. Nicholls (2015). Future coastal population growth and exposure to sea-level rise and coastal flooding—a global assessment. PLOS One 10:e0118571.

Nisbet, I. C. T., and R. R. Veit (2015). An explanation for the population crash of Red-necked Phalaropes *Phalaropus lobatus* staging in the Bay of Fundy in the 1980s. Marine Ornithology 43:119–121.

Nisbet, I. C. T., J. M. Arnold, S. A. Oswald, P. Pyle, and M. A. Patten (2017). Common Tern (*Sterna hirundo*), version 3.0. In Birds of North America Online (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://birdsna.org/Species-Account/bna/species/comter/introduction

Nisbet, I. C. T., E. S. Bridge, P. Szczys, and B. J. Heidinger (2007). Sexual dimorphism, female–female pairs, and a test for assortative mating in Common Terns. Waterbirds 30:169–179.

Nisbet, I. C. T., C. S. Mostello, R. R. Veit, J. W. Fox, and V. Afanasyev (2011a). Migrations and winter quarters of five Common Terns tracked using geolocators. Waterbirds 34:32–39.

Nisbet, I. C. T., P. Szczys, C. S. Mostello, and J. W. Fox (2011b). Female Common Terns *Sterna hirundo* start autumn migration earlier than males. Seabird 24:103–106.

Nisbet, I. C. T., D. B. Wingate, and P. Szczys (2010). Demographic consequences of a catastrophic event in the isolated population of Common Terns at Bermuda. Waterbirds 33: 405–410.

Palestis, B. G. (2014). The role of behavior in tern conservation. Current Zoology 60:500–514.

Passuni, G., C. Barbraud, A. Chaigneau, H. Demarcq, J. Ledesma, A. Bertrand, R. Castillo, A. Perea, J. Mori, V. A. Viblanc, J. Torres-Maita, and S. Bertrand (2016). Seasonality in marine ecosystems: Peruvian seabirds, anchovy, and oceanographic conditions. Ecology 97:182–193.

Pulido, V., J. Jahncke, P. Makamatsu, and C. Flores (1996). Conservation of Charadriiformes on the Peruvian coast. International Wader Studies 8:55–61.

Rakhimberdiev, E., and A. Saveliev (2016). R Package FLightR: SSM for solar geolocation. http://github.com/eldarrak/FLightR

Rakhimberdiev, E., P. J. van den Hout, M. Brugge, B. Spaans, and T. Piersma (2015a). Seasonal mortality and sequential density dependence in a migratory bird. Journal of Avian Biology 46: 332–341.

Rakhimberdiev, E., D. W. Winkler, E. Bridge, N. E. Seavy, D. Sheldon, T. Piersma, and A. Saveliev (2015b). A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. Movement Ecology 3:25.

R Core Team (2015). R: A Language and Environment for Statistical Computing. http://www.r-project.org/

Szczys, P., S. A. Oswald, and J. M. Arnold (2017). Conservation implications of long-distance migration routes: Regional metapopulation structure, asymmetrical dispersal, and population declines. Biological Conservation 209:263–272.

Thorup, K., F. Korner-Nievergelt, E. B. Cohen, and S. R. Baillie (2014). Large-scale spatial analysis of ringing and re-encounter data to infer movement patterns: A review including methodological perspectives. Methods in Ecology and Evolution 5:1337–1350.

Trierweiler, C., R. H. G. Klaassen, R. H. Drent, K.-M. Exo, J. Komdeur, F. Bairlein, and B. J. Koks (2014). Migratory connectivity and population-specific migration routes in a long-distance migratory bird. Proceedings of the Royal Society B 281:20132897.

Wang G., W. Cai, B. Gan, L. Wu, A. Santoso, X. Lin, Z Chen, and M. J. McPhaden (2017). Continued increase of extreme El Niño frequency long after 1.5°C warming stabilization. Nature Climate Change 7:568–572.

Webster, M. S., and P. P. Marra (2005). The Importance of understanding migratory connectivity and seasonal interactions. In Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA. pp. 199–209.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes (2002). Links between worlds: Unraveling migratory connectivity. Trends in Ecology & Evolution 17:76–83.

Wendt, S., P. Schmidt, and G. Donaldson (2006). Issues and challenges facing migratory bird conservation programs in North America. In Waterbirds around the World (G. C. Boere, C. A. Galbraith, and D. A. Stroud, Editors). Stationery Office, Edinburgh, UK. pp. 214–216.

Wetlands International (2010). State of the World's Waterbirds 2010. Wetlands International, Ede, The Netherlands.

Wilson, S., R. Bazin, W. Calvert, T. J. Doyle, S. D. Earsom, S. A. Oswald, and J. M. Arnold (2014). Abundance and trends of colonial waterbirds on the large lakes of southern Manitoba. Waterbirds 37:233–244.

Wires, L. R., S. J. Lewis, G. J. Soulliere, S. W. Matteson, D. V. "Chip" Weseloh, R. P. Russell, and F. J. Cuthbert (2010). Upper Mississippi Valley / Great Lakes Waterbird Conservation Plan. Final report submitted to the U.S. Fish and Wildlife Service, Fort Snelling, MN, USA.

Downloaded From: https://bioone.org/journals/The-Auk on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use