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**Research Article**

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# Weak genetic structure, shared nonbreeding areas, and extensive movement in a declining waterbird

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## ABSTRACT

Understanding population mixing, movements, and connectivity of populations is an important first step towards effective conservation, particularly for long distance migrants that are suffering the greatest population declines, as this allows researchers to recognize how populations may face different risks throughout the annual cycle. We combined population genetic and individual tracking data to quantify the genetic structure and full-cycle movements of the declining North American Black Tern (*Chlidonias niger surinamensis*). A total of 147 genetic samples were collected from 9 breeding colonies across the range (Maine, Ontario, Michigan, Iowa, Wisconsin, Nebraska, Saskatchewan, and Oregon), and 19 light-level geolocators were recovered from 3 colonies (Ontario, Michigan, and Saskatchewan). Our results demonstrated weak genetic structure, and tracking data demonstrated the use of shared nonbreeding areas between central (Saskatchewan) and eastern (Ontario and Michigan) breeding populations. Our tracking data also provide novel evidence of long-distance breeding dispersal (~1,400 km between breeding locations across years) based on an individual tracked across multiple years, as well as short distance dispersal (~2.5–57 km) based on new recovery locations of 6 tracked individuals. Our results are consistent with the hypothesis that the shared use of nonbreeding areas influences physical condition, timing of departure, and subsequent reproductive timing in such a way as to facilitate dispersal across the breeding range and contribute to weak genetic structure among breeding populations. This study is the first to explore population genetics and migration of North American Black Terns. Extensive movement of individuals may pose a challenge from a conservation perspective as important areas and habitats throughout the annual cycle may be difficult to predict, and future studies should build on our work via extensive mark-resight effort using color bands, tracking individuals from more breeding sites, and examining carry-over effects to further investigate when in the annual cycle populations are most limited.

**Keywords:** annual cycle, Black Tern, dispersal, genetic structure, movement tracking

### How to Cite

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## LAY SUMMARY

- Conserving migratory birds is challenging, as they often travel thousands of kilometers throughout the year and, for most species, we lack information on connections between breeding and wintering populations as well as movements of individuals on the breeding grounds from one year to the next (breeding dispersal). Yet understanding these movements is crucial as they shape the patterns of genetic variability within a species—information that directly impacts conservation management strategies.
- In studying North American Black Terns (*Chlidonias niger surinamensis*), a waterbird species in decline, we found small differences in genetic variability across the range, suggesting substantial mixing of individuals among breeding populations.
- Movement tracking of 19 individuals from Ontario, Michigan, and Saskatchewan revealed variation in migratory routes coupled with substantial mixing on the wintering grounds, as well as one case of long-distance (~1,400km) breeding dispersal.
- Together, these findings indicate breeding dispersal and population mixing as mechanisms that limit genetic differentiation across the range, and suggest a potential challenge for conservation managers given that important locations and habitats for the species may be difficult to predict across years.

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## Faible structure génétique, zones de non-reproduction partagées et déplacements importants chez un oiseau aquatique en déclin


### RÉSUMÉ

Comprendre le mélange, les mouvements et la connectivité des populations est une première étape importante vers une conservation efficace, en particulier pour les migrateurs de longue distance qui subissent les plus grands déclins de population, car cela permet aux chercheurs de reconnaître comment les populations peuvent être confrontées à différents risques tout au long du cycle annuel. Nous avons combiné des données de génétique des populations et de suivi des individus pour quantifier la structure génétique et les mouvements sur l'ensemble du cycle de *Chlidonias niger surinamensis*, une espèce en déclin. Un total de 147 échantillons génétiques a été recueilli dans 9 colonies nicheuses à travers l'aire de répartition (Maine, Ontario, Michigan, Iowa, Wisconsin, Nebraska, Saskatchewan et Oregon), et 19 géolocalisateurs légers ont été récupérés dans 3 colonies (Ontario, Michigan et Saskatchewan). Nos résultats ont démontré une faible structure génétique, et les données de suivi ont démontré l'utilisation de zones de non-reproduction partagées entre les populations nicheuses du centre (Saskatchewan) et de l'est (Ontario et Michigan). Nos données de suivi fournissent également de nouvelles preuves de dispersion sur de longues distances (~1 400 km entre les lieux de reproduction d'une année à l'autre), d'après un individu suivi sur plusieurs années, ainsi que de dispersion sur de courtes distances (~2,5-57 km), d'après les nouveaux lieux de récupération de six individus suivis. Nos résultats sont cohérents avec l'hypothèse selon laquelle l'utilisation partagée des zones de non-reproduction influence la condition physique, le moment du départ et le moment subséquent de reproduction de manière à faciliter la dispersion dans l'aire de reproduction et à contribuer à une faible structure génétique parmi les populations reproductrices. Cette étude est la première à explorer la génétique des populations et la migration de *C. niger surinamensis*. Les mouvements importants d'individus peuvent poser un défi du point de vue de la conservation, car les zones et les habitats importants tout au long du cycle annuel peuvent être difficiles à prévoir. Les études futures devraient s'appuyer sur nos travaux en déployant un effort important de marquage et de réobservation à l'aide de bagues de couleur, en suivant les individus à partir d'un plus grand nombre de sites de reproduction et en examinant les effets différés afin d'étudier plus en détail le moment du cycle annuel où les populations sont plus limitées.


**Mots-clés:** cycle annuel, *Chlidonias niger*, dispersion, structure génétique, suivi des mouvements

## INTRODUCTION

Understanding full annual cycle movement and population structure is crucial for effective protection and conservation of migratory bird species as this may provide insights into the use of important habitats and the probability of local extinction, and may ultimately allow for the development of strategies to address the causes of population declines (Harrison et al. 2011, Marra et al. 2015). Recent advances in both tracking technology and analytical techniques are allowing researchers to understand patterns and processes throughout the annual cycle and effectively measure the degree of spatial and genetic connectedness and associated risks among populations of a species (Ambrosini et al. 2009, Larison et al. 2021). Low migratory connectivity occurs when there is extensive mixing of individuals from different breeding populations during the nonbreeding season (Webster et al. 2002), as is observed in some waterbird species (Bracey et al. 2018, Scarpignato et al. 2021). In this scenario, different breeding populations may share the same risks during the nonbreeding season but experience different risks on the breeding grounds. In contrast, high migratory connectivity implies spatial segregation of populations across different phases of the annual cycle, which may be linked to shared risks and associated population trends among different breeding populations (Kramer et al. 2018). The degree of genetic differentiation and spatial segregation across breeding and nonbreeding ranges can influence whether there are adaptive differences among individuals occupying these sites (Ruegg et al. 2021), and ultimately determine whether different conservation strategies may be required across a species' range (Moussy et al. 2018).

Migratory waterbirds can travel long distances throughout their migrations and generally experience few physical barriers to dispersal. Nevertheless, strong population genetic structure is documented in some species and migratory behavior is posited to contribute to differentiation among breeding colonies (Friesen et al. 2007, Lombal et al. 2020). Segregation occurring in the nonbreeding areas can influence physical condition, timing of northward departure, social group formation, and subsequent reproductive timing and pair formation (Marra et al. 1998, Lombal et al. 2020): all important aspects of survival and population dynamics such as dispersal (Webster et al. 2002, Fromant et al. 2021). Genetic differentiation can also be the result of historical colonizations during post-glacial expansion (Hewitt 2000). The pattern of genetic structure associated with degree of segregation in the nonbreeding distribution is documented in studies of both coastal and inland tern (Sternidae) species. When breeding populations of Common Tern (*Sterna hirundo*) overlap significantly in the nonbreeding season (corroborated with tracking data: Nisbet et al. 2011, Bracey et al. 2018), differentiation among them is weaker than when segregation occurs in the nonbreeding distribution, where strong differentiation is documented (Szczys et al. 2012, 2017a, Arnold et al. 2022).

Tern species that breed exclusively inland at continuously distributed freshwater sites (i.e., "marsh" terns) also exhibit this pattern of association between genetic structure and nonbreeding area use. Black Tern (*Chlidonias niger niger*) populations across Eurasia were genetically differentiated by migratory route and staging area use (van der Winden et al. 2014, Szczys et al. 2017b), and Whiskered Terns (*C. hybrida hybrida*) within Europe were genetically differentiated according to migratory route and nonbreeding distribution (Dayton et al. 2017). The Black-fronted Tern (*C. albostriatus*) showed little differentiation across New Zealand, but the association with nonbreeding distribution in Black-fronted Terns remains unknown as connectivity between nonbreeding and breeding sites has not been quantified (Schlesselmann et al. 2020). Because these "marsh" terns tend to breed in dynamic and unpredictable habitats, one may expect high levels of gene flow across the breeding distribution, except where individuals from different breeding regions stick to strict migratory routes and nonbreeding distributions. This is supported by above examples and in line with the concept of using nonbreeding site and route use for predicting patterns of population genetic structure for species that have not been studied using molecular markers (Friesen et al. 2007).

Advances in technology have allowed for precise tracking of animal movements (i.e., migration and/or dispersal) across

long distances using devices and methods such as satellite trackers, radio transmitters, and light-level geolocators, many of which have only recently been refined and miniaturized enough for application on small birds (Marra et al. 2015). Similarly, incorporation of environmental tracers (e.g., stable isotope analysis) and genetic/genomic techniques have increased our understanding of avian migration and dispersal (Larison et al. 2021). The combined use of external tracking devices and genetic analysis is a potentially powerful approach to concurrently examine movement patterns and spatial connections of a species at multiple temporal scales.

Genetic studies can reveal historic (post-glacial/thousands of years) and recent (last 30 years) patterns of dispersal and may support theoretical expectations with respect to factors maintaining structure (Friesen et al. 2007), while tracking devices can provide information on current (2–3 year) movement patterns. However, these complimentary tools are seldom used within the same study. Nonetheless, this two-pronged method of tracking is a powerful approach that can confirm that the genetic structure fits the actual movements documented by tracking devices (Quillfeldt et al. 2017, Hipfner et al. 2020). In this study, we use combined genetic analysis and light-level geolocators to quantify genetic structure and full-cycle movement patterns of North American Black Terns (*C. niger surinamensis*).

Understanding population genetic structure, and the factors that influence it, are critical for conservation planning for North American Black Terns, a species that has experienced long-term declines across its breeding range (North American Breeding Bird Survey [NABBS], 1970–2019: –2.96% year$^{-1}$; Smith et al. 2020; –67% since 1960s, Stephens et al. 2015). The severity of population declines appears to vary across the breeding range, with steeper declines on the periphery (e.g., Oregon, Stephens et al. 2015; jurisdictions surrounding the Laurentian Great Lakes, NABBS; Wisconsin, Matteson and Mossman 2000, Matteson et al. 2012; Maine, MDIFW 2016) than those located in the core of the breeding range–generally considered to be the Prairie Pothole Region (Heath et al. 2020; NABBS). The causes of population declines remain unclear, with some studies attributing declines to the loss of nesting and foraging habitat due to the destruction of wetland environments, and others suggesting that mortality may be occurring primarily during the nonbreeding season (Heath et al. 2020). Despite intense banding efforts in some regions (Shealer 2003), little band re-sighting data exist for the Black Tern. Furthermore, no information exists on annual movements or nonbreeding distributions of individual terns. As a result, it is not known whether Black Terns, both within and among populations, and across the breeding range, overlap in nonbreeding site use (and potentially experience similar threats) or whether they use different sites with different threats. Similarly, gene flow and population genetic structure in North American Black Terns have not been quantified. A greater understanding of population structure and movement patterns is thus a critical first step in understanding when and where populations are most limited, as well as informing species conservation plans (Chabot et al. 2018, Moussy et al. 2018, Dayton and Szczys 2021).

Our study is based on genetic samples collected from 9 breeding colonies across the Black Tern range and tracking of individuals from 3 colonies. Given predicted patterns of association between nonbreeding site use and genetic structure across bird species, we aimed to document these patterns in this marsh-breeding tern. This is the first examination of population genetics and full annual cycle tracking data for the North American subspecies of Black Tern, and a first step in elucidating potential causes of long-term population declines by revealing connections across breeding and nonbreeding seasons.

## METHODS

### Study Sites

Black Terns were captured for genetic sampling at 9 breeding colonies across the North American breeding range, spanning a range of 12.3° latitude and 53.7° longitude, and including 6 U.S. states and 2 Canadian provinces (Figure 1). From west to east, samples were collected at colonies in Oregon (44.328°N, 123.165°W, $n$ = 16 individuals), Saskatchewan (53.132°N, 108.426°W, and 51.552°N, 102.629°W, $n$ = 24), Nebraska (41.434°N, 102.203°W, $n$ = 24), Iowa (43.171°N, 93.461°W, $n$ = 11), Wisconsin (43.331°N, 88.382°W, $n$ = 24), Michigan (42.582°N, 82.641°W, $n$ = 17), Ontario (44.607°N, 79.935°W, $n$ = 20), and Maine (44.270°N, 69.420°W, $n$ = 11). Light-level geolocators were deployed on individuals at a subset of these colonies in Michigan ($n$ = 9 individuals) and Ontario ($n$ = 31). In addition, geolocators were deployed at 3 colonies in Saskatchewan ($n$ = 48) including the 2 indicated above, and a third (53.762°N, 103.573°W) where genetic sampling did not occur (Table 1).

### Field Methods

Black Tern adults were trapped on the nest during the late-incubation period from mid-late June through mid-late July (Heath et al. 2020), depending on the colony. Genetic sampling took place in 2005–2006, 2015–2016, and 2019, and geolocator tracking took place from 2016–2021 (Table 1). Fieldwork only occurred during favorable weather conditions (i.e., no extreme temperatures or precipitation) to minimize adverse effects on adults, chicks, and eggs. We followed protocols of Shealer and Haverland (2000) for the trapping and banding of Black Terns, as they have been found to not have detrimental effects on reproductive success. Adults were trapped on the nest when they returned to incubate using wire mesh remote-controlled and manual treadle traps, remote-controlled bow traps, drop-in traps, or noose traps, all of which were placed over the eggs. At the 9 colonies included in the genetic analysis, we collected small (<50 µg) blood samples from 11–24 unrelated individuals (adults and chicks sampled from different nests; Table 1) by pricking the femoral or tarsal vein with a hypodermic needle and collecting blood in capillary tubes and stored in lysis buffer or by collecting breast feathers (Szczys et al. 2017b). For birds not included in the genetic analysis, a drop of blood was taken from the metatarsal vein for molecular sex determination. At all sites, adults received an aluminum or stainless steel United States Fish and Wildlife Service (USFWS) band and were weighed and measured (mass and tarsus, bill, head-bill, tail, and wing length). At the 5 colonies where tracking occurred, we deployed 88 geolocators (Intigeo model W65A9; Migrate Technology, Cambridge, UK), each attached to a darvic band and placed on the opposite leg to that receiving an aluminum band, similar to the methods of Nisbet et al. (2011) and Bracey et al. (2018). The combined mass of all attachments

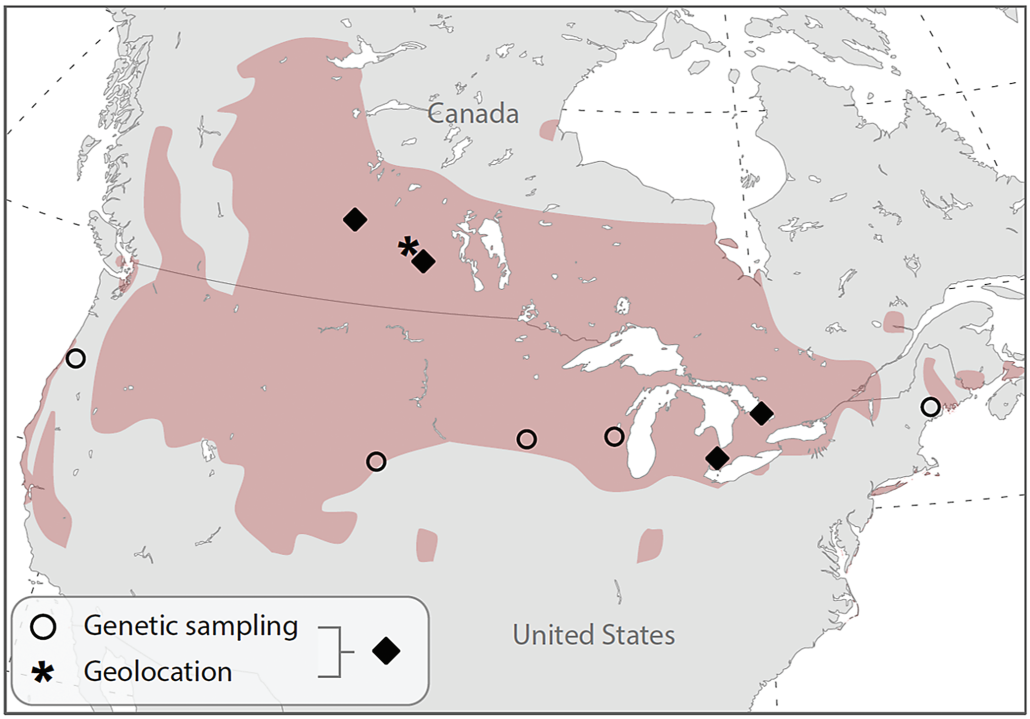


**FIGURE 1.** Locations where Black Terns were sampled and tagged. The North American Black Tern breeding range is shown in purple (source: BirdLife International). Map data from Natural Earth (naturalearthdata.com).

**TABLE 1.** Sample sizes and year for individuals genotyped via blood or feathers and light-level geolocator deployments and retrievals from 8 states/provinces across the North American Black Tern breeding range. M = male, F = female, U = unknown sex.

| Site | Year | Genetic samples | Geolocators deployed | Geolocators retrieved |
|---|---|---|---|---|
| Maine | 2015 | 11 | – | – |
| Ontario | 2016 | 20 | 31 | – |
| | 2017 | – | – | 5 (2F, 3M) |
| | 2018 | – | – | 4 (4F) |
| | 2019 | – | – | 1 (M) |
| | 2021 | – | – | 1 (U) |
| Michigan | 2015 | 17 | – | – |
| | 2017 | – | 9 | 2 (2F) |
| | 2018 | – | – | 3 (2M, 1U) |
| Iowa | 2016 | 11 | – | – |
| Wisconsin | 2005 | 24 | – | – |
| Nebraska | 2006 | 24 | – | – |
| Saskatchewan | 2018 | – | 23 (11F, 12M) | – |
| | 2019 | 24 | 25 (13F, 8M, 3U) | – |
| | 2020 | – | – | 1 (1F) |
| | 2021 | – | – | 2 (1F, 1M) |
| Oregon | 2016 | 16 | – | – |
| Total | – | 147 | 88 | 19 |

for birds receiving a geolocator was 0.9 g, less than 2% of an adult Black Tern's body mass (~50–60 g). We assumed that movement of individuals carrying geolocators was similar to non-equipped individuals, although some effect might be expected even at this device mass (Brlík et al. 2020). We subsequently returned to these colonies 1–5 years post-deployment to recapture tagged birds. Procedures for the recapture of geolocator-tagged birds were the same as initial capture, except that we removed the geolocator, and did not take a blood sample. If we failed to locate tagged birds at their original colony of capture, we attempted to search nearby breeding areas (≤60 km) for suitable habitat and potential colonies and tagged individuals, as capacity allowed. Thus, device recovery was biased to individuals that returned to sites nearby the original capture and tagging site. Indeed, the primary drawback with using archival logging devices such as geolocators is that they must be retrieved in order for the data to be downloaded, generally restricting data to individuals that return to or near the breeding site. Unfortunately, at the time of this study, there were no alternative devices that would have been able to transmit data throughout a full annual cycle while remaining below 2–3% body mass (a requirement for Animal Care permits). Geolocators were thus the most appropriate device for our study given that our primary objective from the tracking work was to examine patterns of nonbreeding site use.

## Molecular Analyses

High-quality DNA was extracted from whole red blood cells or breast feathers with noticeable tissue in the shaft from adults or non-sibling chicks using a Qiagen DNEasy Kit (Qiagen, Valencia, California, USA). We obtained multilocus microsatellite genotypes for 147 individuals at 8 nuclear microsatellite markers: RBG 27 and 29 (Given et al. 2002), AAT27 (Szczys et al. 2005), MsSh 20 and 23 (Janowski et al. 2016), and Calbo 2, 35, and 40 (Schlesselmann and Robertson 2017). Polymerase-chain reactions (PCR) were carried out in 10 µL reactions containing 2x Promega GoTaq PCR MasterMix. Standard thermocycling conditions included an initial denaturation step of 94.0°C for 5 min, followed by 30 cycles of 94°C for 30 s, 50–55°C for 30 s, 72°C for 1 min,

and a final 72°C extension for 10 min. PCR products were resolved on a 4300 DNA Analyzer with IRDye infrared dye size standard (LiCOR) and alleles identified using SAGA G2 software (LiCOR).

Diversity indices, $F_{ST}$, $D_{est}$, and tests for deviations from Hardy–Weinberg equilibrium (HWE) were conducted in GenAnIEx (Peakall and Smouse 2012). We implemented Microchecker (van Oosterhout et al. 2004) to detect possible allele scoring errors and estimate the frequency of null alleles. FreeNA (Chapuis and Estoup 2007) was used to assess the impact of potential null alleles on population structure. To control for uneven sampling across sites, allelic richness was calculated in FSTAT 2.9.3 (Goudet 1995).

Genetic structure was identified in STRUCTURE (Pritchard et al. 2000) using the admixture model with correlated allele frequencies (Falush et al. 2003, Falush et al. 2007). We conducted these analyses with an initial alpha of 0.25 (i.e., 1/*K*; Wang 2017) for each prior: $K$ = 1–8, where $K$ = number of genetic clusters. These included 25,000 burn-in steps followed by 250,000 MCMC (Markov chain Monte Carlo) iterations for 15 replications. Genetic clusters were visualized for all values of $K$ through the multiple methods of Structure Harvester (Earl and von Holt 2012) and CLUMPAK (Kopelman et al. 2015) performed in STRUCTURE SELECTOR (Li and Liu 2018). To assess the robustness of clustering results to uneven sampling, we conducted identical analyses with a random subset of individuals from each site ($n$ = 11; Puechmaille 2016). We investigated contemporary gene flow among sites using BayesAss 3.0 (Wilson and Rannala 2003) to estimate migration rates among sites. Ten replicates of $3 \times 10^6$ MCMC iterations were run following a burn-in of $10^6$ with $m$ = 1.0, $a$ = 0.55, and $f$ = 1.0. Replicates were not substantively different ($m < 0.06$).

We obtained mitochondrial sequences from the cytochrome-*b* region for 124 individuals for primers b5 and b6 published by Boutilier et al. (2014) and sanger sequencing was implemented by CDGenomics (Shirley, NY). Sequences were aligned and trimmed to 484 base pairs (bp) in Geneious 7.1.9 (Kearse et al. 2012). Mitochondrial diversity analysis was conducted in ARLEQUIN 3.5 (Excoffier and Lischer 2010) to describe the number of unique haplotypes, haplotype diversity (H), nucleotide diversity ($\pi$; Nei 1987), the degree of selective neutrality ($D$, Tajima 1989; $F_S$, Fu 1997), and a measure of differentiation, $Phi_{ST}$. We used a minimum spanning network to visualize the relationship between haplotypes, which was implemented in PopArt 1.0 (Leigh and Bryant 2015).

### Geolocator Analysis

Intigeo geolocators use a light sensor to record light intensities over time. Light readings are taken every minute and the maximum light reading in a 5-min period is recorded. We used the package *TwGeos* in program R v. 4.0.3 (R Core Team 2020) to import data and define twilight times (when sunrise and sunset occur) with a light-level threshold of 10 (Lisovski et al. 2020). For each tag, sunrise and sunset times were calibrated using "on-bird" data during after deployment and before retrieval when the bird was stationary at the breeding colony. Next, we estimated locations using the *thresholdPath* function from the R package *SGAT* (Wotherspoon et al. 2013, Lisovski et al. 2021). To identify migration schedules and periods of movements, we analyzed the changes in sunrise, sunset, noon, and moon across the tracking period using the R package *invMovement* (Lisovski et al. 2021), that has previously been described by Meier et al. (2022). In short, abrupt changes in the twilight events that are outside the tag specific twilight error (estimated in a calibration process), indicate periods of movements with associated likelihood. We applied a starting threshold of 0.7 that was refined slightly for each tag to ensure that clear shifts in longitude resulted in different stopover sites (while this method is partly subjective, we chose a conservative and relatively high threshold that results in more stopover sites rather than in single sites that may contain different locations). Based on the results, we summarised the location estimates and calcualted the median location per stationary period with credibility intervals (95 percentile of latitude/longitude estimates).

We buffered each colony location by 250 km and used median dates to estimate departure from and arrival to breeding colonies. Multiple departure dates are provided for birds with more than one year of geolocation data available. This is also true for arrival dates for a few tags that lasted for more than two years (Supplementary Material Table 1). We provide mean (range) and sample size for estimated arrival to and departure from breeding colonies. To identify major stopover and overwintering locations from the geolocation movement data, we merged all output from the individual tracks and filtered it to include only nonbreeding season movements (i.e., all data occurring >250 km from each colony). We then filtered data by season using dates defined by experts, based on distribution and abundance maps from Black Terns provided by eBird (Fink et al. 2021). Using this criteria, seasons were defined as follows; breeding season (June 7–21); southward migration (June 28 to November 9); nonbreeding (wintering) season (November 16 to March 1), and northward migration (March 8 to May 31). All stationary periods identified from geolocation analyses were summarized by breeding colony. We provide mean (range) and sample size for estimated stationary periods by general geographic region (Supplementary Material Table 2).

## RESULTS

### Molecular Analysis

We used 8 polymorphic microsatellite loci to assess genetic diversity. Loci represented a total of 117 alleles ranging from 6 to 21 per locus (mean = 14.6). Only 5 of 64 sites by locus comparisons deviated from HWE expectations after Bonferroni adjustment ($P < 0.00078$) and 8 of 64 with B-Y adjustment ($P < 0.01$) per Narum (2006), with no pattern by site or locus observed. Similarly, homozygous excess was identified by Microchecker (van Oosterhout et al. 2004) for 7 of 64 tests without site or locus correlation and no evidence of allelic dropout was indicated. Estimates of genetic diversity ($H_E$) by site ranged from 0.706 to 0.797 with low $F$ values except within the Oregon population (Table 2). Mitochondrial diversity was high as evidenced by number of haplotypes, gene diversity, and nucleotide diversity (Table 2). Negative values of $F_S$ (mean = –0.68) resulted from an excess of haplotypes, and together with the negative (though non-significant) $D$ values (mean = –0.70), are evidence of recent (post-glacial maximum) population expansion (Table 2).

Both $F_{ST}$ and $D_{EST}$ indicated through pairwise comparisons that sites are not well-differentiated from one another,

**TABLE 2.** Genetic diversity indices by sampling site and origin of individual. Eight microsatellite loci were genotyped for 147 birds. $N_a$, mean number of alleles; $A_R$, mean alleles based on a theoretical idealized population; $H_O$, mean observed heterozygosity; $H_E$, mean expected heterozygosity, also called "genetic diversity"; $F_{IS}$, inbreeding coefficient. $N_{MT}$, number of individuals sequenced for cytochrome-*b* region; *A* = number haplotypes; *H* = gene diversity; π = nucleotide diversity; *F* = Fu's *F*; *D* = Tajima's *D*.

| Site | $N_a$ | $A_R$ | $H_O$ | $H_E$ | $F_{IS}$ | $N_{MT}$ | *A* | *H* | π | *F* | *D* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ME | 7.4 | 7.2 | 0.83 | 0.80 | –0.04 | 12 | 3 | 0.44 | 0.002 | 0.18 | –0.73 |
| ON | 8.8 | 7.2 | 0.76 | 0.77 | 0.02 | 10 | 1 | 0.00 | 0.000 | 0.00 | 0.00 |
| MI | 9.5 | 7.9 | 0.78 | 0.80 | 0.05 | 11 | 5 | 0.62 | 0.002 | 0.70 | –0.93 |
| IA | 8.1 | 7.8 | 0.70 | 0.71 | 0.02 | 11 | 3 | 0.35 | 0.001 | –0.54 | –1.60 |
| WI | 9.0 | 7.3 | 0.75 | 0.80 | 0.06 | 22 | 3 | 0.57 | 0.003 | 1.64 | 0.99 |
| NE | 9.3 | 7.2 | 0.68 | 0.75 | 0.09 | 24 | 7 | 0.61 | 0.002 | –1.91 | –1.10 |
| SK | 9.5 | 7.4 | 0.73 | 0.78 | 0.07 | 24 | 7 | 0.61 | 0.002 | –3.17* | –1.46 |
| OR | 8.9 | 7.5 | 0.66 | 0.74 | 0.13 | 10 | 6 | 0.84 | 0.004 | –0.93 | –0.76 |

*$P$ = 0.009; all other values non-significant.

**TABLE 3.** Population differentiation based on (A) microsatellite data. $F_{ST}$ values below the diagonal and Jost's $D_{est}$ above the diagonal; (B) mitochondrial data. $Phi_{ST}$ values below the diagonal and *P* values above. Bold values indicate low levels of differentiation that differ significantly from zero where $0.001 < P < 0.01$.

| | ME | ON | MI | IA | WI | NE | SK | OR |
|---|---|---|---|---|---|---|---|---|
| (A) | | | | | | | | |
| ME | – | 0.03 | 0.04 | 0.08 | 0.11 | 0.08 | 0.05 | 0.08 |
| ON | 0.02 | – | 0.06 | 0.02 | 0.08 | **0.09** | **0.07** | 0.04 |
| MI | 0.02 | 0.02 | – | 0.07 | 0.06 | **0.12** | **0.07** | 0.08 |
| IA | 0.04 | 0.02 | 0.03 | – | **0.15** | 0.04 | 0.05 | 0.01 |
| WI | 0.03 | **0.02** | 0.02 | **0.04** | – | **0.14** | **0.16** | **0.14** |
| NE | 0.03 | **0.03** | **0.03** | 0.03 | **0.03** | – | **0.12** | **0.14** |
| SK | 0.02 | **0.02** | **0.02** | 0.03 | **0.03** | **0.03** | – | **0.07** |
| OR | 0.03 | **0.02** | **0.03** | 0.02 | **0.03** | **0.04** | 0.03 | – |
| (B) | | | | | | | | |
| ME | – | 0.22 | 0.84 | 0.59 | 0.10 | 0.89 | 0.33 | 0.20 |
| ON | 0.10 | – | 0.09 | 0.47 | **0.00** | 0.04 | 0.05 | **0.01** |
| MI | –0.05 | 0.16 | – | 0.37 | 0.15 | 1.00 | 0.33 | 0.52 |
| IA | –0.02 | 0.04 | 0.01 | – | 0.02 | 0.22 | 0.21 | 0.04 |
| WI | 0.12 | **0.38** | 0.06 | 0.25 | – | 0.10 | **0.00** | 0.36 |
| NE | –0.04 | 0.14 | –0.05 | 0.03 | 0.06 | – | 0.17 | 0.39 |
| SK | 0.01 | 0.12 | 0.01 | 0.02 | **0.19** | 0.03 | – | 0.07 |
| OR | 0.05 | **0.33** | –0.03 | 0.15 | –0.01 | –0.00 | 0.07 | – |

even at continental scales (all $F_{ST}$ < 0.04; Table 3). The global $F_{ST}$ value (0.0226) was not different when corrected for null allele frequencies ($F_{ST}$ = 0.0219; FreeNA). These indices suggest high levels of gene flow among sites that were further evidenced by the analysis in STRUCTURE (Pritchard et al. 2000). Two genetic clusters were represented in the data. Although STRUCTURE detected 2 clusters (Delta *K*; mean LnP(K) = –4864.14; Evanno et al. 2005) or 4 clusters (mean, median, and maximum; Puechmaille 2016) when sampling location was included as a prior (Figure 2), no clustering was detected in the absence of sampling location data. Further, when sites were subsampled for 11 individuals to even sample size across sites, no clusters were detectable even when site was given as a prior (Figure 2).

BayesAss provided further evidence from microsatellite data that gene flow among sites was substantial. All sites exhibited low affinity ($m$ = 0.68–0.78) except for Ontario, where $m$ = 0.80. Ontario exhibited strong outward migration to all other sites an order of magnitude greater than migration into Ontario (Table 4).

Of 15 haplotypes detected, 1 was very frequent (66%) and detected across all sites while 8 were detected at low frequency and at only 1 site each (Supplementary Material Tables 1 and 2). Though not strictly a star-like pattern as described for Eurasian Black Terns (Szczys et al. 2017b), the haplotype network suggests post-glacial demographic expansion (Figure 3A). Interestingly, haplotype 4 (Supplementary Material Tables 3 and 4) detected in a single individual sampled in Oregon, is also the most common haplotype documented in Eurasia (Szczys et al. 2017b) (Figure 3B) which suggests recent dispersal among the continents. Further, only 2 single-base mutations distinguish the most common haplotypes on each continent, which could indicate recent (post-glacial maximum) ancestry.

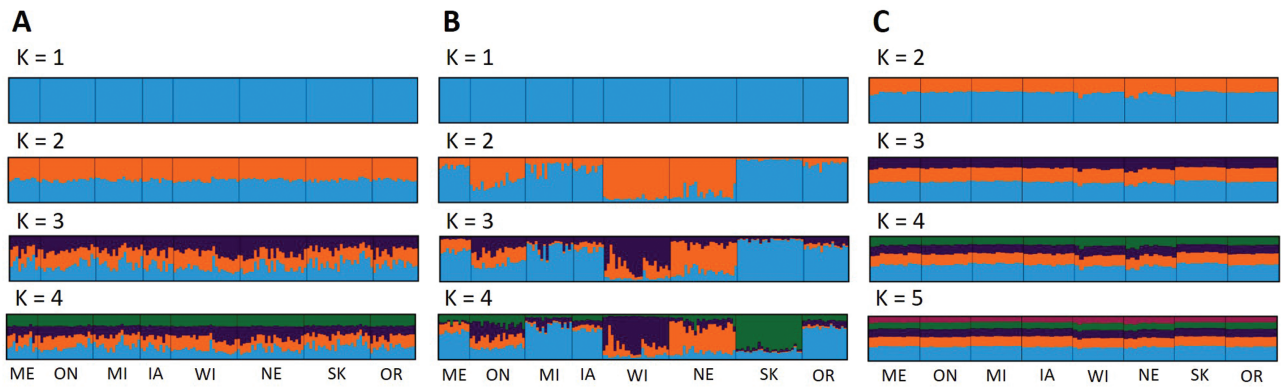


**FIGURE 2.** STRUCTURE estimates the number of genetic clusters (*K*). Each column represents an individual and the colors represent genetic clusters. Individuals have proportional identities with each cluster. (**A**) In absence of prior sample location information, no clusters could be detected when sampling among sites was uneven (*K* = 1–4 a priori). (**B**) When sample site is a priori, the Puechmaille method identified 4 clusters and the Evanno method identified 2 (*K* = 1–4 a priori). (**C**) When sample sizes are standardized (*n* = 11) across 8 sites, no clusters are identified (*K* = 2–5 a priori). Sites: (left to right) Maine, Ontario, Michigan, Iowa, Wisconsin, Nebraska, Saskatchewan, Oregon.

## Geolocator Analysis

Between 2016 and 2021, we retrieved 19 of the 88 (22%) geolocators deployed (Table 1). Geolocator recaptures varied between colonies. Geolocator recoveries were lowest in Saskatchewan (13%) and were reasonable in Michigan (56%) and Ontario (35%). In general, tagged birds were not recaptured because they were not seen, either as a result of permanent dispersal or mortality, although there were a few instances of a returning tagged individuals being re-sighted but not captured until a subsequent year. Interestingly, all 3 individuals (1 in 2020, 2 in 2021) from Saskatchewan bred at a different colony site on the same lake, ~2.5 km from their original 2019 breeding colony, where they were resighted and recaptured. Similar to what was found in Saskatchewan, 3 of the individuals from Ontario were recaptured at a different breeding colony from where they were initially tagged, in this case ~57 km away. There were no recaptures elsewhere in Saskatchewan due to the abandonment of the 2 other colonies in the years following deployment in 2018 and 2019. This was likely due to extreme drought in spring 2019 and 2020, leading to drying of the marshes and apparently unsuitable breeding habitat (Shephard et al. personal observation). Of the above recaptures, one geolocator deployed in Ontario in 2016 and recaptured in 2017 failed after 48 days. Of the remaining geolocators, 8 recorded data for a full year, 9 recorded data for >1 year, and 1 recorded data for >2 years (3 southward migrations, 2 northward migrations).

Individual migration maps with credibility intervals for each of the estimated stopover sites are shown in the Supplementary Material (Figure 1). Departure from breeding colonies varied by location, with a mean (range) departure date of August 8 (July 29 to September 13) in Michigan (*n* = 7); July 24 (June 3 to September 6) in Ontario (*n* = 18); and July 26 (July 16 to August 8) in Saskatchewan (*n* = 5) (Supplementary Material Table 1). Generally, birds from the eastern breeding colonies (Ontario and Michigan) showed a southward migration along the Atlantic coast (Figure 4). Florida and the Carolinas stood out as the key stopover sites for individuals from the eastern breeding colonies (Supplementary Material Table 2). Two individuals from the central breeding colony (Saskatchewan) migrated through the Midwestern states (North Dakota, South Dakota, Minnesota) during southward migration, travelling through the Gulf of Mexico and spending over a month along the western coast of Mexico (Figure 4).

Individuals moved during the nonbreeding (wintering) season, with many using multiple stationary sites during the defined nonbreeding season (Supplementary Material Table 2). Wintering sites ranged from Mexico to Peru with the majority of birds overwintering near Panama (Figure 4). The estimated mean duration of stay at nonbreeding locations for all birds was 70 (range: 29–176) days (Supplementary Material Table 2). Although sample size for birds breeding in Saskatchewan was small, there were notable differences in movement patterns with birds spending time on the Pacific coast of Mexico. However, these birds also wintered in Panama.

Generally, individuals from the eastern colonies showed a northward migration through the Gulf of Mexico (*n* = 16), Mississippi Flyway (*n* = 2), and along the Atlantic coast (*n* = 3) (Figure 4 and Supplementary Material Table 3). Individuals from the western colony migrated north through the Central Flyway (Figure 4). Staging occurred on the western coast of Mexico (*n* = 1) and along the Gulf of Mexico (*n* = 2). Arrival to breeding colonies was less variable than southward migration, with a mean arrival date of May 17 (range: May 11–22) in Michigan (*n* = 5); May 16 (range: May 10–27) in Ontario (*n* = 12); and May 19 (range: May 18–22) in Saskatchewan (*n* = 3).

Data obtained from light-level geolocators can be used to effectively document breeding behavior and to estimate incubation periods in birds (Schaub et al. 2019, Verhoeven et al. 2020). We found evidence of long-distance breeding dispersal (~1,400 km), with 1 individual switching breeding sites across years. This individual was tagged in Ontario (2016) and was re-captured (2019) with multiple years of migration data (3 southward and 2 northward migrations). Plotting the light image (Figure 5), allows for visualization of the entire dataset and is useful for identifying extreme deviations in light to dark transitions (outliers) and for approximating departure from and arrival to breeding/deployment locations (Lisovski et al. 2020). Patterns of consistent and extreme transition between light and dark periods during the day are indicative of breeding behavior (i.e., adults incubating eggs) that obscures the logger (Lisovski et al. 2020). This individual nested

**TABLE 4.** Migration estimates from BayesAss, with dispersal from sites across the columns and dispersal to sites across the rows. Ontario exhibited the highest individual affinity (*m* for self-affinity in bold) and high outward migration to all other sites. All other migration rates overlapped 0 (lower confidence intervals are negative) representing undetectable migration rates among those sites.

| | ME | | ON | | MI | | WI | | IA | | NE | | SK | | OR | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | m | 95% CI | m | 95% CI | m | 95% CI | m | 95% CI | m | 95% CI | m | 95% CI | m | 95% CI | m | 95% CI |
| ME | **0.685** | **0.721** | **0.649** | 0.134 0.221 | 0.047 | 0.018 0.052 | –0.016 | 0.018 0.050 | –0.014 | 0.027 0.074 | –0.021 | 0.079 0.162 | –0.003 | 0.019 0.053 | –0.016 | 0.020 0.057 |
| ON | 0.015 | 0.043 | –0.013 | **0.795** **0.889** | **0.702** | 0.015 0.043 | –0.014 | 0.013 0.036 | –0.011 | 0.062 0.130 | –0.006 | 0.071 0.167 | –0.025 | 0.016 0.047 | –0.015 | 0.014 0.040 |
| MI | 0.014 | 0.042 | –0.014 | 0.128 0.204 | 0.051 | **0.680** **0.705** | **0.655** | 0.014 0.041 | –0.012 | 0.111 0.185 | 0.036 | 0.025 0.070 | –0.019 | 0.014 0.040 | –0.012 | 0.014 0.039 |
| WI | 0.017 | 0.050 | –0.016 | 0.187 0.271 | 0.103 | 0.018 0.049 | –0.012 | **0.684** **0.715** | **0.653** | 0.027 0.074 | –0.019 | 0.031 0.086 | –0.025 | 0.018 0.051 | –0.015 | 0.018 0.052 |
| IA | 0.014 | 0.044 | –0.015 | 0.107 0.204 | 0.010 | 0.013 0.036 | –0.011 | 0.013 0.038 | –0.012 | **0.777** **0.862** | **0.691** | 0.052 0.130 | –0.026 | 0.013 0.037 | –0.012 | 0.011 0.032 |
| NE | 0.011 | 0.033 | –0.010 | 0.111 0.200 | 0.021 | 0.012 0.035 | –0.011 | 0.011 0.031 | –0.009 | 0.049 0.106 | –0.009 | **0.783** **0.872** | **0.695** | 0.012 0.033 | –0.009 | 0.011 0.033 |
| SK | 0.011 | 0.032 | –0.009 | 0.241 0.299 | 0.182 | 0.012 0.034 | –0.010 | 0.011 0.034 | –0.012 | 0.015 0.043 | –0.014 | 0.017 0.048 | –0.014 | **0.682** **0.713** | **0.650** | 0.012 0.033 |
| OR | 0.013 | 0.038 | –0.012 | 0.172 0.254 | 0.089 | 0.014 0.040 | –0.012 | 0.014 0.040 | –0.013 | 0.026 0.070 | –0.018 | 0.065 0.135 | –0.005 | 0.014 0.042 | –0.014 | **0.683** **0.714** |

in Ontario in 2016 where it was first captured, and light/dark patterns indicate such (Figure 5). It then migrated along the Atlantic Flyway, staged in the Carolinas, and wintered around Panama. During the 2017 northward migration, it staged in the Gulf of Mexico, then returned to Ontario for a few weeks before continuing to Manitoba, Canada, ~1,400 km to the west. Its stationary period indicated that it was there during the breeding season and light data indicated that it bred there (Figure 5). The 2017 southward migration showed a direct flight path from Manitoba to staging grounds along the southern Atlantic coast to nonbreeding grounds around Panama. The 2018 northward migration track was typical of other eastern breeding birds, with staging in the Gulf of Mexico and migration up the Central Flyway to Ontario. Here the stationary period is consistent with the individual being in Ontario during the breeding period (May 21 to July 17), although the light/dark pattern is not as clear as in previous years, and could be an indication of failed breeding or no breeding attempt that year. A lack of breeding or an early failed nest would be consistent with the fact that we did not re-sight the bird at the colony that year. This individual then migrated south along the Atlantic Flyway to Central America near the Caribbean Sea, before the geolocator stopped working in the winter of 2018. This individual was subsequently recaptured on a nest at the original Ontario breeding site in 2019. This suggests the individual used very similar stopover and wintering locations between the two years but had low breeding site fidelity between years. As far as we are aware, this is the very first documentation of long-distance breeding dispersal in North American Black Terns.

## DISCUSSION

Using a combination of population genetic and individual tracking data, we found evidence of contemporary (post-glacial) demographic expansion along with high levels of recent movement and gene flow in North American Black Terns. Patterns of nonbreeding area use among different breeding populations have been suggested to correlate with genetic structure in waterbirds (Friesen et al. 2007). Our results are consistent with this pattern, in that we found weak genetic structure and our tracking results demonstrate shared use of nonbreeding areas between central (Saskatchewan) and eastern (Ontario and Michigan) breeding populations. This finding contrasts with Eurasian Black Terns, which show strong genetic structure associated with use of different staging areas among populations following distinct migratory flyways. Despite a small sample size, our tracking data also provide evidence of long-distance breeding dispersal, providing further support for high levels of gene flow across the North American distribution. Although 7 of 8 breeding sites sampled in the genetic analysis exhibited low affinity (fidelity) based on microsatellite data, the one site exhibiting higher affinity showed evidence for strong outward migration to all other sites; this site (Ontario) is one of the areas that is also showing the steepest population declines, suggesting breeding dispersal, instead of or in addition to low survival, may be driving population trends in the east.

Microsatellite analysis revealed a lack of genetic structure at breeding sites across the Black Tern breeding range in North America. Studies of other waterbird species have noted a similar lack of genetic structure. American White

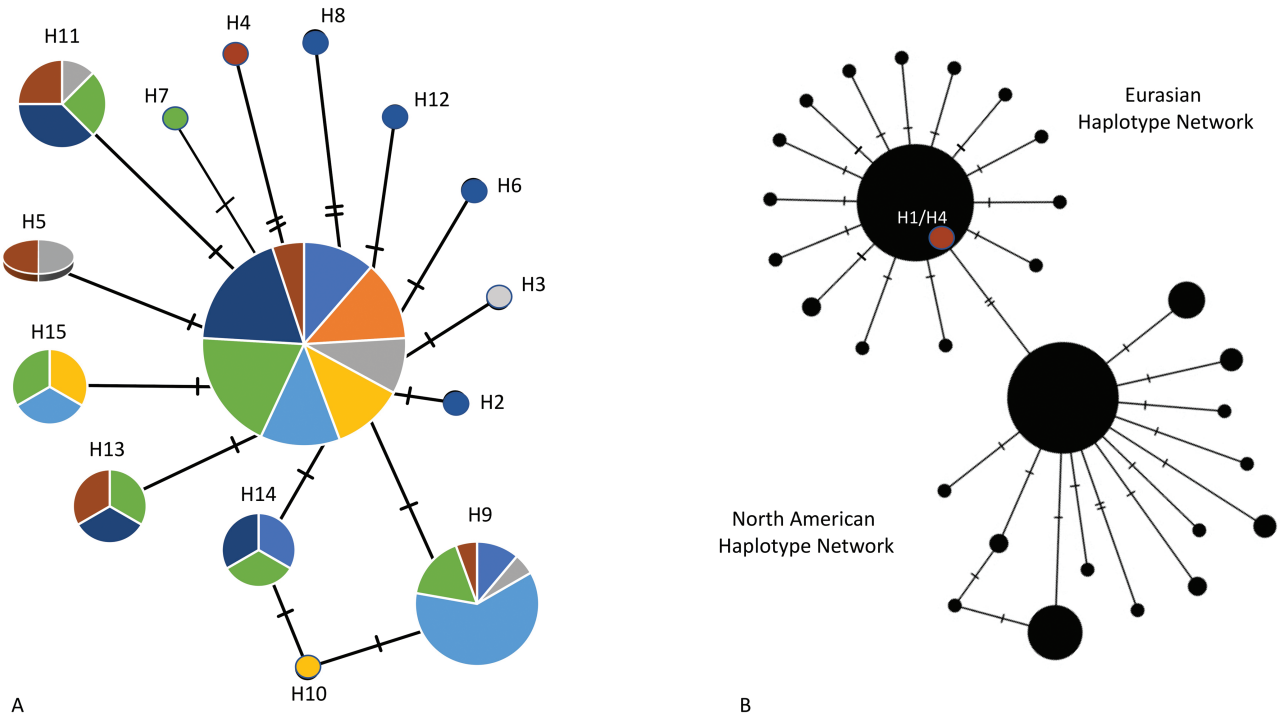


**FIGURE 3.** Minimum spanning network for North American Black Tern cytochrome-*b* haplotypes. (**A**) North American haplotypes for 124 Black Terns where circle size represents frequency and color represents site (red = Oregon, dark blue = Saskatchewan, green = Nebraska, yellow = Iowa, light blue = Wisconsin, grey = Michigan, orange = Ontario, blue = Maine; Supplementary Material Table S4). (**B**) Globally distributed Black Tern haplotypes. 124 North American haplotypes and 94 previously published Eurasian haplotypes (Szczys et al. 2017b). North American Haplotype 4 was identified in 1 individual sampled in Oregon and matches the sequence of Haplotype 1 in Europe (**B**; maroon inset).

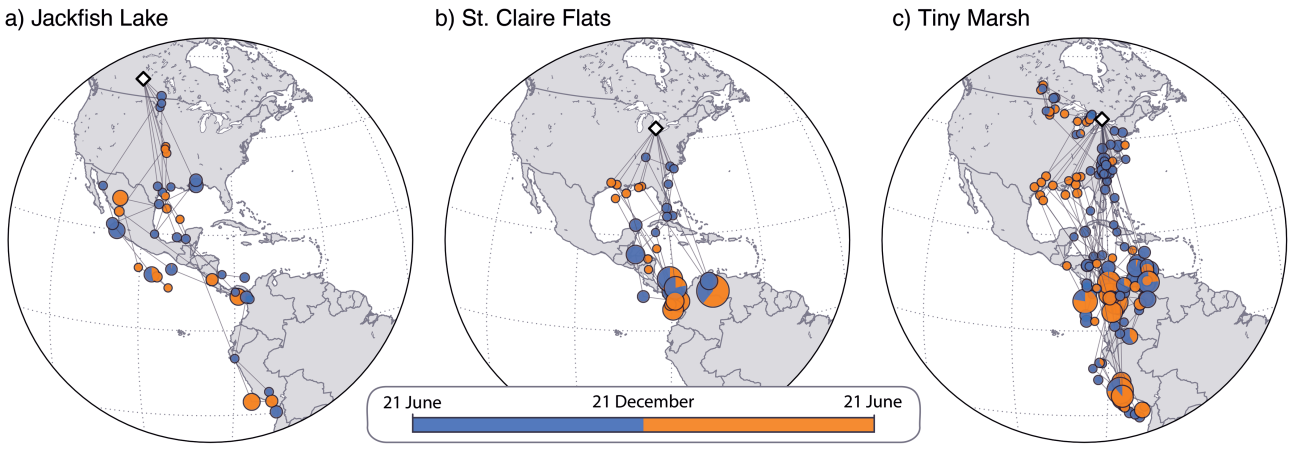


**FIGURE 4.** Southward migration (blue dots), northward migration (orange dots), and breeding/nonbreeding locations (blue and orange dots) of Black Terns recaptured from 3 breeding locations, $n = 19$ (Jackfish Lake, Saskatchewan; St. Claire Flats, Michigan; and Tiny Marsh, Ontario). Map data from Natural Earth (naturalearthdata.com).

Pelicans (*Pelecanus erythrorhynchos*) display complete panmixia across the continent (Oomen et al. 2011, Reudink et al. 2011) with high rates of colony abandonment, high stable isotope variation among individuals at breeding colonies (Reudink et al. 2016), and the propensity to move long distances for foraging (Oomen et al. 2011, Reudink et al. 2011, 2016). The unpredictability of North American Black Tern occurrence and lack of occupancy at seemingly suitable breeding sites (Naugle et al. 2000, Shealer and Alexander 2013, Wyman and Cuthbert 2016), a tendency towards low site fidelity (Shealer 2003, Heath et al. 2020, this study), and shared nonbreeding sites among individuals from across the range (i.e., low migratory connectivity) similarly suggest high rates of movement and gene flow contributing to the weak genetic structure that we uncovered. Genetic diversity of Black Terns across sample sites was high, with little evidence to suggest genetic structuring or differentiation on a continental scale. Signals of differentiation could be separated into 2 or 4 distinct clusters, likely influenced by differences in sampling years (differentiation of 2005–2006 samples from 2015–2019 samples), and strongly driven by unequal sampling among sites. When sample size was

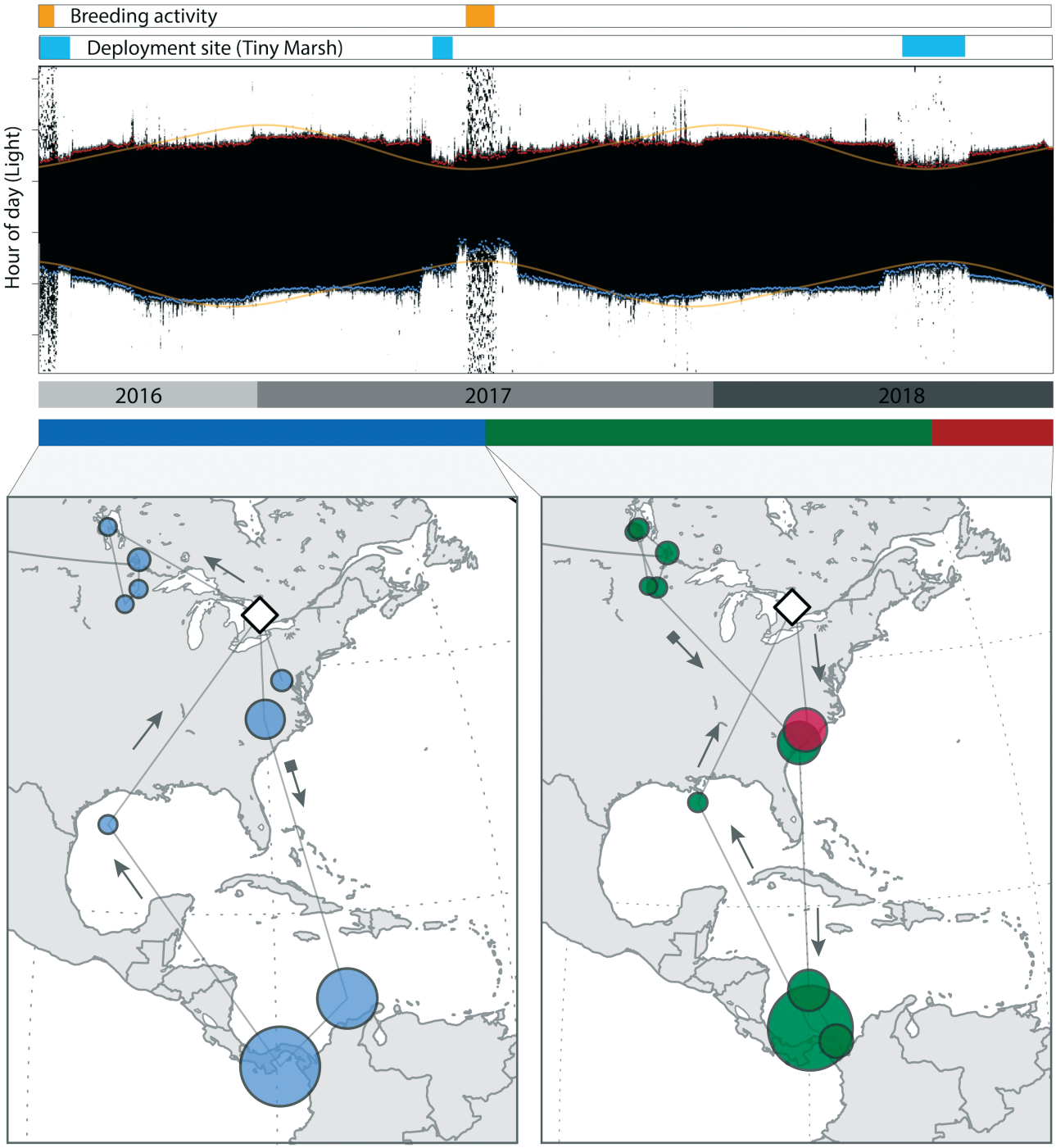


**FIGURE 5.** Migration routes over 2 consecutive annual cycles of 1 individual Black Tern. Upper panel shows the raw light recordings from the geolocator with one column per day and calculated sunrise (red dots) and sunset (blue dots) events. The yellow line shows the predicted sunrise and sunset of the deployment site (e.g., sunrise and sunsets close to the lines indicates that the individuals was at the deployment site; light blue periods shown above the panel). Alternating light/dark periods during the day provide evidence of breeding activity since the bird is obscuring the logger while sitting on the nest for incubation (shown by orange periods on the top panel). The maps show the migration journeys (stopover sites with larger circles for longer times spent), of the individual for the 2016/2017 season (left) and the 2017/2018 season (right). Map data from Natural Earth (naturalearthdata.com).

evened, all signals of potential clustering were lost and were analogous to not using sample location as a prior information. Taken together, these results support the notion that gene flow among colonies across North America is on-going across at least 2 generations (6 year generations; sampled sites across ~10 years). These results contrast what has been found in some other tern species (Dayton et al. 2017, Arnold et al. 2022), including Eurasian Black Terns (Szczys et al. 2017b), and further reinforces the idea that tern species breeding in dynamic wetland habitats are likely to display high rates of movement and gene flow, perhaps due to unpredictability of wetland presence/location from year to year, except where separation among breeding populations exists during some phase of the annual cycle.

Our combined use of genetics and movement tracking has allowed us to uncover insights not only into movement patterns over larger spatial and longer temporal scales, but also into smaller-scale contemporary movements on the breeding grounds. One tagged individual Black Tern showed the first evidence of long-distance breeding dispersal between central and eastern breeding locations. This individual was originally captured and banded in Tiny Marsh, near Georgian Bay in southwestern Ontario during the 2016 breeding season, and was recaptured at the same site during the 2019 breeding season. During the 2017 breeding season, rather than breed in Ontario, this individual apparently stopped at or somewhere near the Ontario site, then flew directly to a different breeding location ~1,400 km to the northwest in Manitoba, Canada. Although only from a single bird, this behavior shows evidence of long-distance breeding dispersal. This type information is novel and rarely obtained from studies that use archival tags such as geolocators, which must be retrieved from individuals, usually at the site of deployment. Further evidence for extensive inter-annual breeding movement in this species comes from the complete abandonment of 2 colonies in Saskatchewan, and generally low return rates of birds at all sites, but especially in Saskatchewan. Specifically, the 69 geolocators we were not able to re-sight or retrieve strongly suggest frequent and permanent dispersal of at least some individuals across years, with associated implications for gene flow. While we believe any tag effects to be minimal, some reduction in return rate is also possible (Brlík et al. 2020). Finally, short-distance breeding dispersal was confirmed by 6 tagged individuals which were recaptured on different breeding colonies from where they initially bred and were captured (3 in Saskatchewan, ~2.5 km from the original colony, and 3 in Ontario, ~57 km away). Thus, in addition to individuals from different breeding populations mixing at common locations during the nonbreeding period, we have evidence of mixing during the breeding period across years.

Study of annual survival and breeding recruitment of Black Terns in Wisconsin showed that vital rates at this location were far below those required to maintain a stable population. Adult apparent survival (true survival minus permanent dispersal) was lower than 70% and pre-breeding survival was ~2%, yet breeding populations increased between 1999 and 2003 (Shealer 2003). These results suggest that high adult breeding dispersal was the norm and that immigration was necessary to maintain the population. Given that Wisconsin could be considered as part of the eastern portion of the breeding range (although is further west than our 2 eastern study sites), one possibility is that eastern populations may be ecological traps acting as population sinks—an idea that is supported by stronger population declines in eastern populations versus in the core of the range. In this sense, the prairie core may represent a population source, while the edges act as population sinks (Pulliam 1988). However, this hypothesis does not explain the lower return rates documented at our central site compared to eastern sites, unless movements at central sites occur on a more local scale, which is indeed supported by the small-scale breeding dispersal of the 3 recaptured birds in Saskatchewan. Although specific drivers of breeding dispersal for Black Terns are unknown, many bird species show adaptations to seasonal changes through short distance movement (Hornell-Willebrand et al. 2014). Dispersal can also occur to avoid inbreeding, to locate a more desirable mate, to find a more suitable breeding area, or to avoid intra-specific competition (Daniels and Walters 2000). Research in Ukraine has recently found that breeding site fidelity was high among some local Black Tern populations and low at others, as terns easily re-nested in new nearby locations when faced with unfavourable conditions (Atamas and Tomchenko 2020). This situation may mirror what is occurring in central populations of North American Black Terns, where prairie wet–dry cycles and unpredictable suitability of habitat due to large annual fluctuations in water levels drive extensive small-scale movements between years. In eastern portions of the range, habitat degradation as a result of water control (artificially dampened fluctuations) leading to dense phragmites (*Phragmites australis*) and loss of hemi-marsh conditions may also result in movement between years (Wyman and Cuthbert 2017).

The genetic results and movement patterns revealed through our study have important implications for the conservation of the Black Tern in the Americas, both on the breeding and nonbreeding grounds. High gene flow and movement among populations of a species are generally good for species persistence, as these processes can facilitate the maintenance of small peripheral populations. For example, high gene flow and movement in Roseate Terns (*Sterna dougallii*) was critical for the redistribution of genetic variation across populations, therefore permitting the persistence of smaller more isolated tern colonies (Szczys et al. 2005, Dayton and Szczys 2021). However, dispersal away from Ontario could be contributing to the Great Lakes region showing some of the largest declines for the Black Tern across North America (Smith et al. 2020). These results are similar to those from Common Terns in the Great Lakes region, where gene flow displays a bias of movement out of the region (Szczys et al. 2017a) and populations have suffered long-term declines (Morris et al. 2012). Both low survival and biased movement could thus be impacting Common and Black terns in the Great Lakes Region.

Despite our small sample size of western breeding birds, our results are consistent with a pattern of low migratory connectivity, which may have implications for the effect of threats across the annual cycle. On the nonbreeding grounds, use of shared areas and high mixing of individuals from central and eastern colonies of Black Terns could make multiple breeding populations susceptible to severe localized events during the nonbreeding period. For example, almost all individuals spent some or most of the nonbreeding period in the seas surrounding Panama. Similarly, tracking data from Common Terns across their breeding range revealed large congregations of individuals in Peru, and the authors noted that this accumulation of individuals may make large portions of the continental breeding population vulnerable to threats such as storm events that could impact this region (Bracey et al. 2018). The coastal regions of Panama have been noted as important locations for many species of waterbirds, seabirds, and shorebirds (Butler et al. 1997, Kushlan et al. 2017). In particular, the Panama Bight, an area of the Pacific Ocean that extends westwards from the coasts of Panama, Columbia, and Ecuador, hosts especially high numbers of seabirds over the continental shelf (Spear and Ainley 1999). Despite heavy use of the Panama region, tracked Black Terns also made use of various other areas for shorter periods during the nonbreeding season, such as other off-shore and coastal areas of Central and northern South America.

Black Terns likely face a multitude of stressors while occupying a variety of different areas, in both coastal and marine habitats. Negative effects of climate change may be compounded due to this reliance on a network of spatially dispersed sites (Maclean et al. 2007). Availability of food resources, variations in water levels, and changing habitat conditions may pose the greatest challenges to the Black Tern during the nonbreeding period. On the other hand, the high mobility of Black Terns during the nonbreeding season may indicate that they are able to move to track resources, which could buffer them against negative effects of habitat change in particular areas, at least to some extent. Indeed, the Eurasian Black Tern nonbreeding distribution is thought to be related to marine food resources off the coast of Africa (van der Winden et al. 2014), and the same is likely true for North American Black Terns as they move to track schools of smaller fish driven to the surface by larger predators (Larson et al. 2007, Heath et al. 2020). The effects of threats on the nonbreeding grounds and those on breeding grounds such as land conversion for agriculture use, wetland drainage, and agrochemical runoff (Rashford et al. 2011, Matteson et al. 2012), in combination with potential carry-over effects between seasons (Marra et al. 2015) warrant further study in order to determine when in the annual cycle populations of Black Terns are most limited and where to target management actions (Harrison et al. 2011). To further investigate adult and natal philopatry and the causes and consequences of breeding dispersal, as well as how shared winter areas might be mechanistically linked to gene flow (e.g., social interactions leading to individuals following others back to their breeding sites), future studies could make use of satellite tracking (although device weight remains a limiting factor), extensive mark-resighting, or possibly long-lasting radio-tags and automated or manual tracking on the breeding grounds.

## Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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## Ethics statement

Work was conducted under CWS Banding Permit 10431 (D. Moore) and USFWS 23492 (P. Szczys), animal care protocols from Canadian Council on Animal Care (1633DM02, D. Moore and 18AM02, A. McKellar), and samples collected in Canada were imported under USDA 107951 and USFWSMB184899 (P. Szczys).

## Author contributions

N.G.S., P.S., D.J.M., M.W.R., and A.E.M. conceived the idea and formulated the questions; N.G.S., P.S., D.J.M., and A.E.M. collected data; M.W.R. and A.E.M. supervised research; N.G.S., P.S., J.N.C., A.M.B., and S.L. analyzed the data; and N.G.S., P.S., and A.E.M. wrote the paper.

## Data availability

Geolocator tracking data, including raw light recordings, annotated twilight times, estimated locations of stopover sites, and associated R code are available in Movebank (www.movebank.org, study id 2447006254), and microsatellite genotype data and cytochrome-b sequences are available in Dryad (https://doi.org/10.5061/dryad.m63xsj460).

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