



# Arctic terns from circumpolar breeding colonies share common migratory routes

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**ABSTRACT:** The Arctic tern is an iconic seabird, famous for its annual migrations between the Arctic and the Antarctic. Its wide geographical range has impeded knowledge of potential population bottlenecks during its annual bi-hemispheric movements. Although Arctic terns breed in the Pacific, Atlantic, and Arctic coasts of North America, few tracking studies have been conducted on North American Arctic terns, and none in Canada, which represents a significant proportion of their circumpolar breeding range. Using light-level geolocators, we tracked 53 Arctic terns from 5 breeding colonies across a wide latitudinal and longitudinal range within North America. We compared the routes taken by birds in our study and migration timing to those previously tracked from Greenland, Iceland, The Netherlands, Sweden, Norway, Maine (USA), and S. Alaska (USA). Most Arctic terns tracked globally used one of 3 southbound migration routes: (1) Atlantic West Africa; (2) Atlantic Brazil; and (3) Pacific coastal, and one of 2 northbound migration routes: (1) Mid-ocean Atlantic and (2) Mid-ocean Pacific. Some other trans-equatorial seabirds also used these migration routes, suggesting that Arctic tern routes may be important for other species. The migration timing for southbound and northbound migrations was generally different between tracked tern colonies worldwide but generally fell within a 1–2 mo window. Our research suggests that conservation management of Arctic terns during their migration should dynamically adapt with the times of the year that terns use parts of their route. Future identification of common multi-species seabird flyways could aid the international negotiations required to conserve pelagic seabirds such as Arctic terns.

**KEY WORDS:** Arctic tern · Migration · Timing · Geolocators · North America

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## 1. INTRODUCTION

The Arctic tern *Sterna paradisaea* is an iconic seabird, famous for its record-breaking pole-to-pole annual migration (Egevang et al. 2010, Fijn et al. 2013). Its breeding range extends across the Arctic and sub-Arctic regions of North America, Europe, and Asia (Russia), with the southernmost breeding limits recorded at Cape Cod, Massachusetts (US Fish & Wildlife Service 2013, Hatch et al. 2020). Despite

the Arctic tern's wide breeding range, its global breeding population has been declining (US Fish & Wildlife Service 2006, Burnham et al. 2017, BirdLife International 2020b). This decline has generated widespread concern among Inuit, who rely on Arctic tern eggs as a food resource and use Arctic terns as indicators of environmental conditions (e.g. seasonal weather changes) and wildlife presence (e.g. seal hunting spots, presence of predators) (Mallory & Akearok 2010, Henri et al. 2020). Arctic tern eggs (and

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sometimes chicks) are also important prey for gulls, jaegers, ravens, falcons, Arctic foxes, polar bears, and gray wolves, and thus, a decline in their population could negatively impact the Arctic food web (Henri et al. 2020). This recent decline in Arctic tern numbers has been evidenced by Inuit local ecological knowledge (Henri et al. 2020) and reduced survival rates of terns in Iceland (Petersen et al. 2020) and the Canadian High Arctic (Mallory et al. 2018). Causes for mortality in adult terns are still poorly understood and do not appear to be linked to the breeding period (Mallory et al. 2018). Consequently, there is speculation that mortality may be occurring during the tern's migratory and wintering periods. For seabirds, bycatch has been regarded as one of the largest threats faced at sea (Croxall et al. 2012). While Arctic terns have not been observed as bycatch, they migrate through the High Seas where reporting is rarely enforced. Similarly, common threats to pelagic seabirds such as overfishing of food sources and pollution (Croxall et al. 2012) likely affect Arctic terns, but due to the lack of documentation for this species, cannot be ascertained. Thus, investigating these nonbreeding periods could shed light on potential causes of decline and where conservation should be focused.

Understanding geographic distributions is commonly identified by experts as one of the top priority research actions for effective seabird conservation (Croxall et al. 2012). The wide geographic range of seabirds, such as Arctic terns, across different ecosystems, international boundaries, and exclusive economic zones (EEZs) requires internationally coordinated conservation action (Jodice & Suryan 2010, Harrison et al. 2018). Thus, developing effective management strategies for seabirds at an international scale first requires a thorough understanding of their migration ecology, including variation between populations. Variation in individuals' migration routes may influence how colonies respond to global environmental changes and affect the resilience of metapopulations (Sutherland 1998, Gilroy et al. 2016). Moreover, when conspecific individuals or colonies have shared migration routes, conservation attention can be directed to the routes used by the greatest number of birds.

Studying the migration routes of trans-equatorial seabirds can reveal important marine areas used by other long-distance migrants (e.g. Gilg et al. 2013), and Arctic terns appear to be a good model for understanding pelagic, offshore migration due to their wide geographic extent across different oceanic zones and remote environments. Studies to date sug-

gest that understanding Arctic tern migration could be useful to inform the timing of migration with shifting oceanic productivity (McKnight et al. 2013) and broader environmental drivers of pelagic migration (Hromádková et al. 2020). Most studies of migratory behaviour of Arctic terns have focused on those marked on breeding colonies in Europe (Fijn et al. 2013, Hromádková et al. 2020, Redfern & Bevan 2020), Greenland (Egevang et al. 2010), or the USA (McKnight et al. 2013, US Fish & Wildlife Service 2013, Duffy et al. 2014). No migration information existed to date from Arctic terns breeding in Canada, despite the importance of the Canadian Arctic to their widespread distribution (Gaston et al. 2012, Hatch et al. 2020) and observed declines in some Canadian breeding colonies (Gilchrist & Robertson 1999, Maftei et al. 2015, Mallory et al. 2018).

Using light-level geolocators, we implemented a large-scale tracking study of 5 populations of Arctic terns breeding across North America. Our study aimed to identify migratory routes shared between populations to inform conservation strategies. We investigated patterns in the southbound and northbound migration routes used by Arctic terns, including the first recorded routes for Canadian Arctic terns and the first record of northbound migration routes for an Alaskan population of Arctic terns. We compared our findings to those from colonies on Svalbard (Norway; Hromádková et al. 2020), the Baltic Sea (Sweden; Alerstam et al. 2019), the Netherlands (Fijn et al. 2013), Greenland and Iceland (Egevang et al. 2010), Maine (USA; US Fish & Wildlife Service 2013), and southern Alaska (USA; McKnight et al. 2013) to identify shared migration corridors.

## 2. MATERIALS AND METHODS

### 2.1. Field methods

We initially tracked 123 Arctic terns from 6 geographically distinct breeding colonies in North America: Alpine, Alaska (70.35° N, 151.03° W, n = 23); Nasaruaalik Island, Nunavut (75.83° N, 96.30° W, n = 30); Igloodik, Nunavut (69.23° N, 81.48° W, n = 10); Karrak Lake, Nunavut (67.25° N, 100.25° W, n = 10); East Bay, Nunavut (64.01° N, 82.07° W, n = 25); and Country Island, Nova Scotia (45.06° N, 61.32° W, n = 25).

We used bownets to capture adult Arctic terns on their nests during June and July 2017, usually late in incubation to minimize the risk of abandonment, and we recaptured terns using the same method in June

and July 2018 and 2019. Upon capture, a US Geological Survey/Canadian Wildlife Service (USGS/CWS) metal leg band was attached. Intigeo archival light-level geolocators (Migrate Technology, model W65; mass 0.65 g) were wound around the center with self-amalgamating tape and attached to the legs of birds using a miniature UV-resistant zip-tie fastened around a plastic ('Darvic' PVC) ring (1 g total mass, <2% of tern's body mass) and then glued with super glue (avoiding the light sensor). Standard morphometrics (mass, wing and central tail feather length, bill and tarsus measurements) were recorded upon capture and recapture (data used for other studies). Our goal was to deploy the units for the tracking study, so in most cases we did not follow nests to assess nesting success. However, in previous years at Country and Nasaruaalik Islands we have had effectively no abandonment after banding, and many of the terns in this study were observed on their nests again shortly after transmitter deployment as we continued to trap other terns. All research was conducted under approved animal care (ACC 04-17 Acadia University; National Zoological Park ACUC Protocols 15-20, 18-06) and scientific (e.g. banding 10694; US Federal Bird Banding Permit 09700; Alaska Scientific Permit 17-162, 18-156) permits.

## 2.2. Analysis

Intigeo tags recorded light intensities (lux) once every 5 min, as well as temperature and conductivity every 4 h. Water immersion was assessed every 30 s (dry = 0, wet = 1), and the total number of wet readings was recorded by the tags every 4 h (up to a maximum of 480 wet readings). Wet readings correlated with a conductivity level >63 (range: 0–127; based on the approximate fresh–brackish water threshold recommended by Migrate Technology) indicated immersion in saltwater and could be used in conjunction with the recorded temperature to infer sea surface temperature (SST) for this period.

We processed the light and activity data collected by the geolocators in R v.3.6.0 (R Core Team 2019) using the package 'TwGeos' (Lisovski et al. 2016). First, sunrise and sunset times (i.e. twilight events) were identified using a light-level threshold of 1, following the approach of Bracey et al. (2018). We deleted false twilights (e.g. caused by complete shading of the logger or by artificial light during the night). We also deleted twilights during days with less than 2 h of darkness (approaching 24 h daylight periods during the Arctic and Antarctic summer, up

to a maximum of 2 wk for the Arctic colonies) in order to eliminate large errors in twilight detection caused by the very slow increase/decrease in light. Next, for each tag we performed an on-bird calibration based on light recordings at the known breeding location pre- and post-migration to estimate the reference median sun elevation angle and the twilight error distribution (Lisovski et al. 2020). Four of our study colonies (Alaska, East Bay, Karrak Lake, Nasaruaalik Island) were located in polar regions with close to 24 h daylight during the summer deployment and recapture periods. Therefore, tag calibration for these colonies was not possible and instead was based on the median calibration parameters from the tag calibration of the Nova Scotia colony (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m671p191\\_supp.pdf](http://www.int-res.com/articles/suppl/m671p191_supp.pdf)). Calibration periods were defined as consecutive days without any distinct changes in the length of night inferred from recorded light data, suggesting that birds had not yet left breeding locations.

We estimated locations and their uncertainties using the R package SGAT (Wotherspoon et al. 2013, Lisovski et al. 2020). SGAT provides a Bayesian framework which combines prior information on (1) the twilight error distribution, (2) the flight speed distribution (defined using a gamma distribution of shape = 1.6 and rate = 0.27, reflecting the most likely flight speed of ~40 km h<sup>-1</sup>; Gudmundsson et al. 1992), and (3) a spatial probability including SST measurements over time. The SST mask was based on satellite-derived SST from NOAA (0.25° resolution; Reynolds et al. 2007). This mask assigned a low probability of occurrence to proposed locations where geocator-recorded SSTs did not match the satellite-derived SSTs. Except for the rare occurrences when the immersion and conductivity data indicated that the tag did not record saltwater readings for more than 3 d, the mask also assigned low probability to locations on land. Near equinoxes, when day and night lengths are equal, the solar declination angle is close to 0°, and latitude estimates become highly inaccurate. To account for this, we skipped over the equinox periods up to a maximum solar declination angle of 0.13° (~8.4 d before and after the equinoxes). We first ran a 'modifiedGamma' model (relaxed assumptions) for 500 iterations to initiate the model before tuning the model with final assumptions/priors (3 runs with 300 iterations). Finally, the model was run for 2000 iterations. Most likely tracks (median locations) were constructed using the location estimations from the final 2000 Markov chain Monte Carlo chains, and the uncertainty around estimated

tracks was displayed using the density of simulated/sampled locations in each  $1 \times 1^\circ$  grid cell. All subsequent analyses were conducted using only the median predicted locations.

To ensure our analysis included only periods of migration, we set a conservative 300 km buffer around each colony location (based on the estimated migration speed of Arctic terns of  $200 \text{ km d}^{-1}$ ; Alerstam 1991) and considered travel outside of this buffer (without return) to be associated with migration. We defined both the end of southbound migration and start of northbound migration as the birds' crossing of  $60^\circ \text{ S}$ .

We used 1-way ANOVA to test whether individuals from different breeding colonies differed in the timing of important migration milestones (start/end date; arrival/departure from North Atlantic staging site; crossing equator; crossing  $10^\circ \text{ S}$ ; duration of migration; time spent in wintering region). We included the North Atlantic staging site because previous studies identified it as an important site for Arctic terns migrating in the Atlantic (Egevang et al. 2010, Fijn et al. 2013, van Bemmelen et al. 2017). In line with these studies and our data (Fig. S1 in the Supplement), we defined arrival to this staging site as when Atlantic birds first crossed  $53^\circ \text{ N}$  and departure when they crossed  $40^\circ \text{ N}$ . We looked at the equator crossing as it is often reported (Alerstam et al. 2019, Hromádková et al. 2020) and the  $10^\circ \text{ S}$  crossing because our results (see Fig. 1) indicate that Atlantic routes become far apart around this latitude. We used the Shapiro-Wilk test for normality and Levene's test for homogeneity of variance. Outliers were detected using the R package 'rstatix' (Kassambara 2020). Tukey's HSD post hoc analyses were conducted to differentiate the colonies with significant differences in timing. A Bonferroni correction was made to account for multiple comparison testing.

We expanded our assessment of inter-colony differences in seasonal migratory routes of Arctic terns by visually comparing migration routes from our study to those described by Alerstam et al. (2019), Duffy et al. (2014), Egevang et al. (2010), Fijn et al. (2013), Hromádková et al. (2020), McKnight et al. (2013), and US Fish & Wildlife Service (2013). Arctic terns from the Farne Islands (UK) were excluded from comparison because Redfern & Bevan (2020) did not describe total migration.

### 3. RESULTS

We recovered 58 of 123 deployed tags in June and July 2018 (1 yr migration record), and July 2019 (2 yr

migration record). Of the 58 recovered tags, 53 contained usable light recordings for analysis, and the number of tags recovered ( $r$ ) and with usable ( $u$ ) data varied by breeding colony: Alaska ( $r = 9$ ,  $u = 8$ ), Nasaruaalik Island ( $r = 24$ ,  $u = 19$ ), Karrak Lake ( $r = 5$ ,  $u = 4$ ), East Bay ( $r = 9$ ,  $u = 7$ ), and Nova Scotia ( $r = 23$ ,  $u = 15$ ). One tag was recovered from the colony in Igloodik, but the data were not usable and are therefore excluded from this study. Of the 53 usable tags, 25 tags were recovered in the first year after deployment (June–July 2018; Alaska:  $n = 6$ ; East Bay:  $n = 2$ ; Karrak Lake:  $n = 4$ ; Nova Scotia:  $n = 13$ ), and 28 tags were recovered in the second year (July 2019; Alaska:  $n = 2$ ; East Bay:  $n = 5$ ; Nasaruaalik Island:  $n = 19$ ; Nova Scotia:  $n = 2$ ). All tags recovered in the first year were still recording upon retrieval, while tags recovered in the second year were battery-depleted by October–November 2018 and therefore documented a 1.5 yr migration record. Routes used by birds from Canada were remarkably similar in pattern, despite originating from different breeding colonies (see Figs. 1 & 3, and Fig. S2 in the Supplement). Alaskan birds had migration routes distinct from those from Canadian colonies (see Figs. 1 & 3). Southbound migration routes were generally similar between years (2017 and 2018) for all colonies (see Figs. 1 & 3, and Fig. S3).

#### 3.1. Southbound migration

During migration, all birds from Canadian colonies (East Bay, Karrak Lake, Nasaruaalik Island, Nova Scotia) used Atlantic routes to reach waters near the Antarctic (major non-breeding grounds). All Canadian birds also stopped at a North Atlantic staging site (approximately  $41^\circ$ – $53^\circ \text{ N}$  and  $27^\circ$ – $41^\circ \text{ W}$ ) known to be used by other migratory seabirds (Boertmann 2011, Gilg et al. 2013, van Bemmelen et al. 2017), including Arctic terns (Egevang et al. 2010, Fijn et al. 2013; Fig. S1). Although Atlantic routes were relatively similar in the Northern Hemisphere, birds from Canadian colonies consistently used 2 distinct routes in the Southern Hemisphere, diverging in the South Atlantic (at  $\sim 10^\circ \text{ S}$ ) toward either the Brazilian or West African coast (Fig. 1). Birds from the same breeding colony did not necessarily use the same route, and birds from each of the Canadian colonies were observed in both Brazilian ( $n = 23$ ) and West African ( $n = 22$ ) routes. Birds breeding in northern Alaska were the only group in our study that used a Pacific migration route. All Alaskan birds followed a coastal path along western North America before

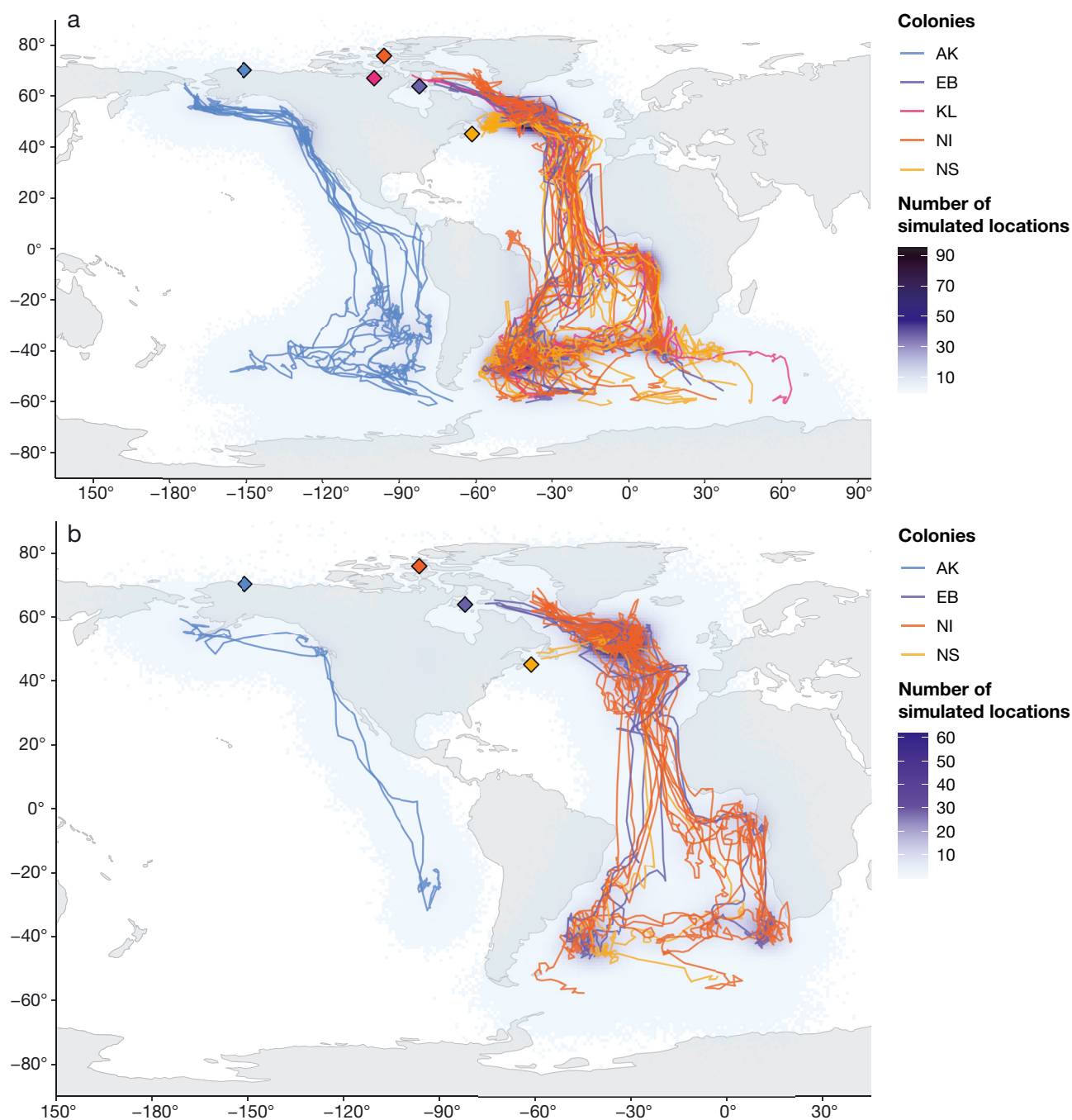


Fig. 1. Most likely individual southbound migration routes used by Arctic terns during (a) Year 1 (August–December 2017) from each breeding colony (denoted by corresponding coloured diamond; AK = Alaska: 70.35°N, 151.03°W,  $n = 8$ ; EB = East Bay: 64.01°N, 82.07°W,  $n = 7$ ; KL = Karrak Lake: 67.25°N, 100.25°W,  $n = 4$ ; NI = Nasaruvaalik Island: 75.83°N, 96.30°W,  $n = 19$ ; NS = Nova Scotia: 45.06°N, 61.32°W,  $n = 15$ ), and (b) Year 2 (August–November 2018; AK:  $n = 2$ ; EB:  $n = 5$ ; NI:  $n = 19$ ; NS:  $n = 2$ ). The uncertainty is displayed with the density of simulated/sampled locations by the model (purple shading; see also Fig. S2). All Canadian colonies used a known North Atlantic staging site (between 41°–53°N and 27°–41°W; Egevang et al. 2010). The tracks shown do not extend to the breeding colonies or to Antarctic non-breeding grounds, and it is likely that the birds travelled farther north or south, respectively. However, due to 24 h daylight or battery depletion in the second year, tracks for this period could not be interpreted reliably from the geolocator data. Background map source: Natural Earth (<https://www.naturalearthdata.com/downloads/110m-physical-vectors/110m-land/>)

splitting into diverse offshore paths south of the equator (Fig. 1). While our model created a few tracks that briefly crossed land, the large level of uncertainty associated with these tracks indicates that the location estimates on land may be attributed to geolocation inaccuracy. Birds tagged in Canadian breeding colonies appeared to spend their major

Antarctic non-breeding season between 60° W and 70° E, while birds tagged in the North Alaskan breeding colony appeared to spend the Antarctic period between 160° and 60° W (Fig. 1).

Arctic terns from Canada and Alaska showed similarities in route patterns used between years. Of the 28 birds that were tracked for 1.5 yr, 25 used

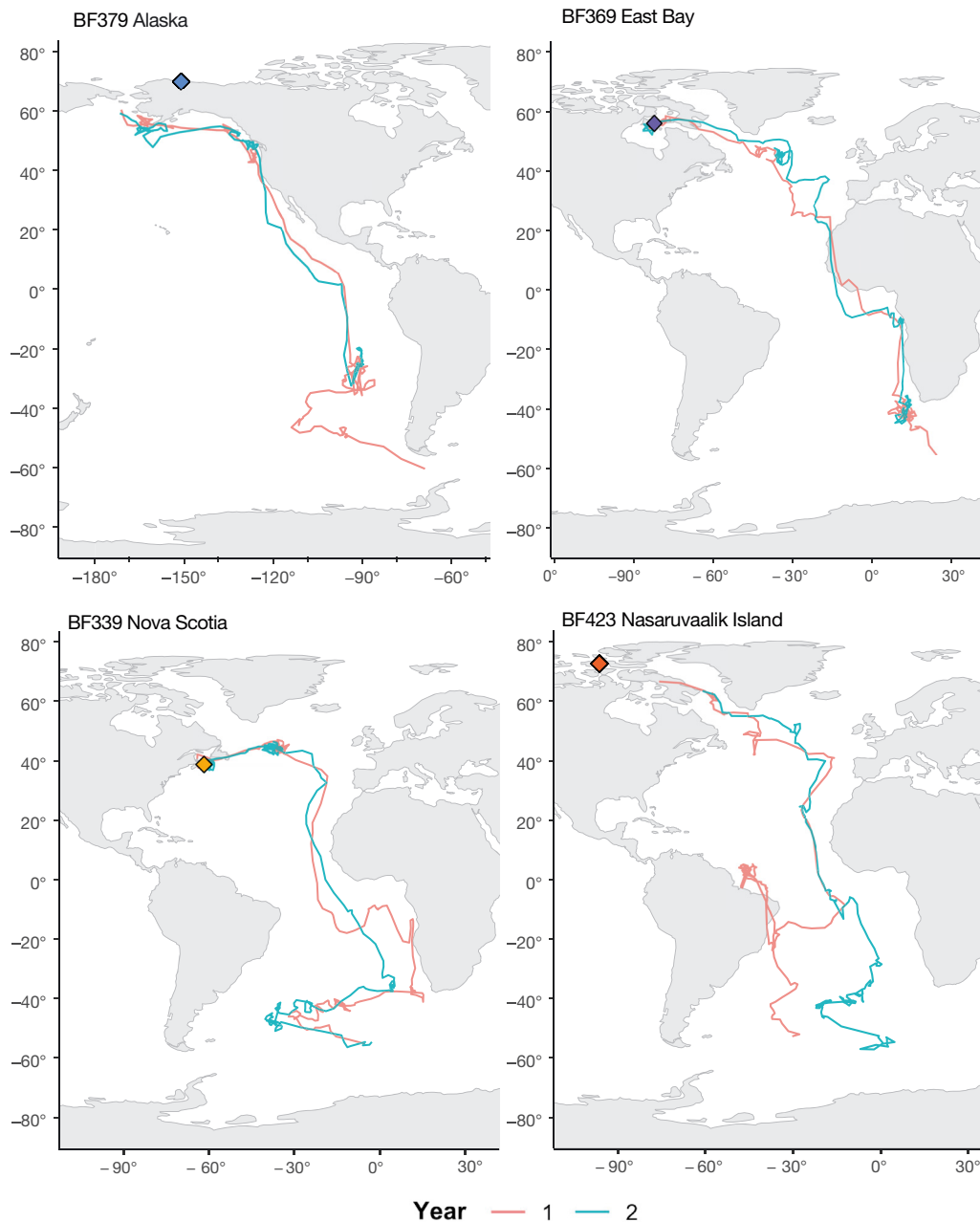


Fig. 2. Comparison of southbound migration routes for 4 individual Arctic terns from Alaska (70.35° N, 151.03° W), East Bay (64.01° N, 82.07° W), Nova Scotia (45.06° N, 61.32° W), and Nasaruaalik Island (75.83° N, 96.30° W), for which Year 1 (orange; August–December 2017) and Year 2 (turquoise; August–November 2018) migration data are available. Original breeding locations are denoted by coloured diamonds. The individual from each colony with the longest migration time (before battery depletion) is shown here; all individual tracks (n = 28) by year can be found in Fig. S3

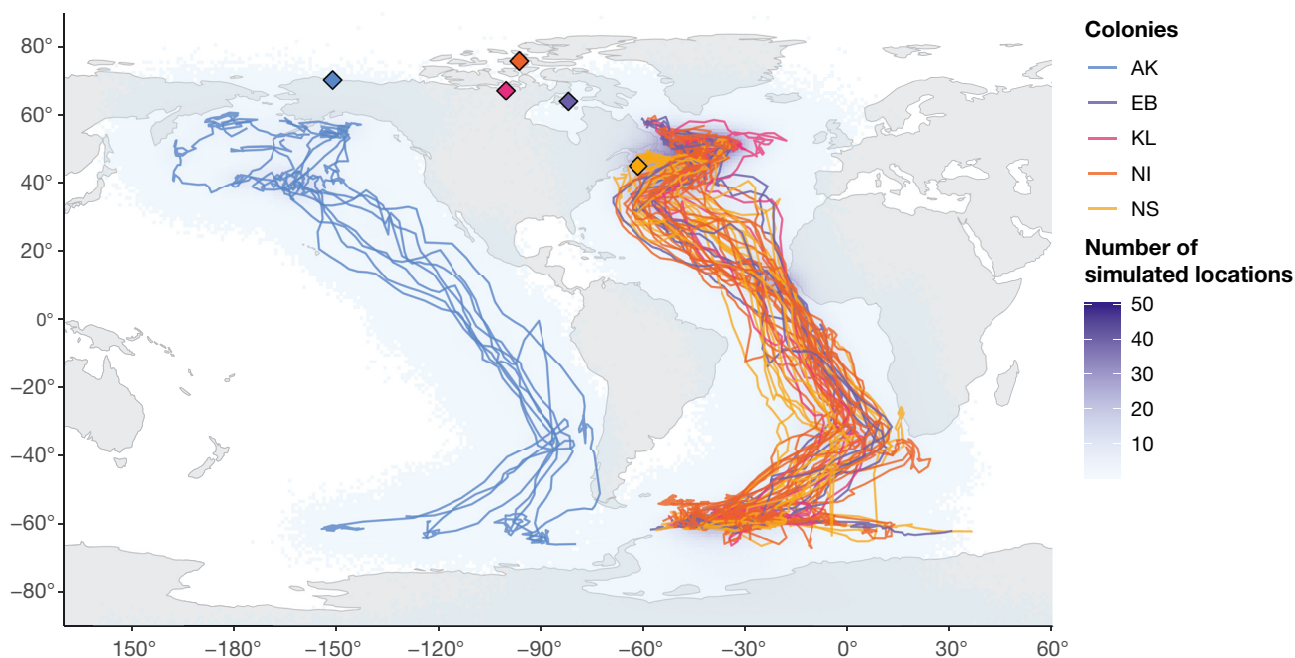


Fig. 3. Most likely individual northbound migration routes used by Arctic terns during Year 1 (February–June 2018) from each breeding colony (denoted by corresponding coloured diamond; AK = Alaska: 70.35° N, 151.03° W,  $n = 8$ ; EB = East Bay: 64.01° N, 82.07° W,  $n = 7$ ; KL = Karrak Lake: 67.25° N, 100.25° W,  $n = 4$ ; NI = Nasaruaalik Island: 75.83° N, 96.30° W,  $n = 19$ ; NS = Nova Scotia: 45.06° N, 61.32° W,  $n = 15$ ). The uncertainty is displayed with the density of simulated/sampled locations by the model (purple shading; see also Fig. S2). The tracks shown do not originate from Antarctica or extend to the original breeding grounds, and it is likely that the birds travelled farther north. However, due to 24 h daylight, tracks for these periods could not be interpreted reliably from the geolocator data. Background map source: Natural Earth (<https://www.naturalearthdata.com/downloads/110m-physical-vectors/110m-land/>)

the same general southbound migration routes as the previous year (Figs. 2 & S2). Only 3 individuals, including two from Nasaruaalik Island (BF423, BF455) and one from East Bay (BF334), used spatially different routes between years, with differences starting at  $\sim 50^\circ$  N (BF334),  $\sim 20^\circ$  N (BF455), and  $\sim 20^\circ$  S (BF423) (Fig. S3). The batteries in 5 tags were exhausted before crossing the Equator in the second year (Fig. S3).

### 3.2. Northbound migration

During the northbound migration, all birds returned to their original breeding grounds through the same ocean (Pacific or Atlantic) used for southbound migration. Canadian and Alaskan birds returned on 2 predominant routes and exhibited similar directional movements at similar latitudes. Following departure from Antarctica, all birds showed initial eastward movement towards the South African (East Bay, Karrak Lake, Nasaruaalik Island, Nova Scotia) or Chilean (Alaska) coast. Movement shifted westward at  $\sim 40^\circ$  S for all colonies, as birds transi-

tioned to more dispersed, mid-ocean routes back to their breeding grounds (Fig. 3). Overall, northbound migration routes were at least  $10^\circ$ – $40^\circ$  farther offshore (west or east) than their original coastal southbound migration routes.

### 3.3. Shared routes with other Arctic tern colonies

Routes recorded by our study had similarities and differences with those reported in previous studies of other Arctic tern colonies. Canadian birds (East Bay, Karrak Lake, Nasaruaalik Island, and Nova Scotia) followed the same 2 southbound routes (coastal West Africa and Brazil) and a single northbound route (mid-Atlantic) used by Arctic terns from Greenland and Iceland (Egevang et al. 2010), Maine (US Fish & Wildlife Service 2013), and Svalbard (Hromádková et al. 2020) (Fig. 4). However, Canadian birds exhibited differences compared to terns from the Netherlands and the Baltic Sea (Fig. 4). Although terns from the Netherlands and Baltic Sea followed a similar coastal West African route during southbound migration, those terns continued

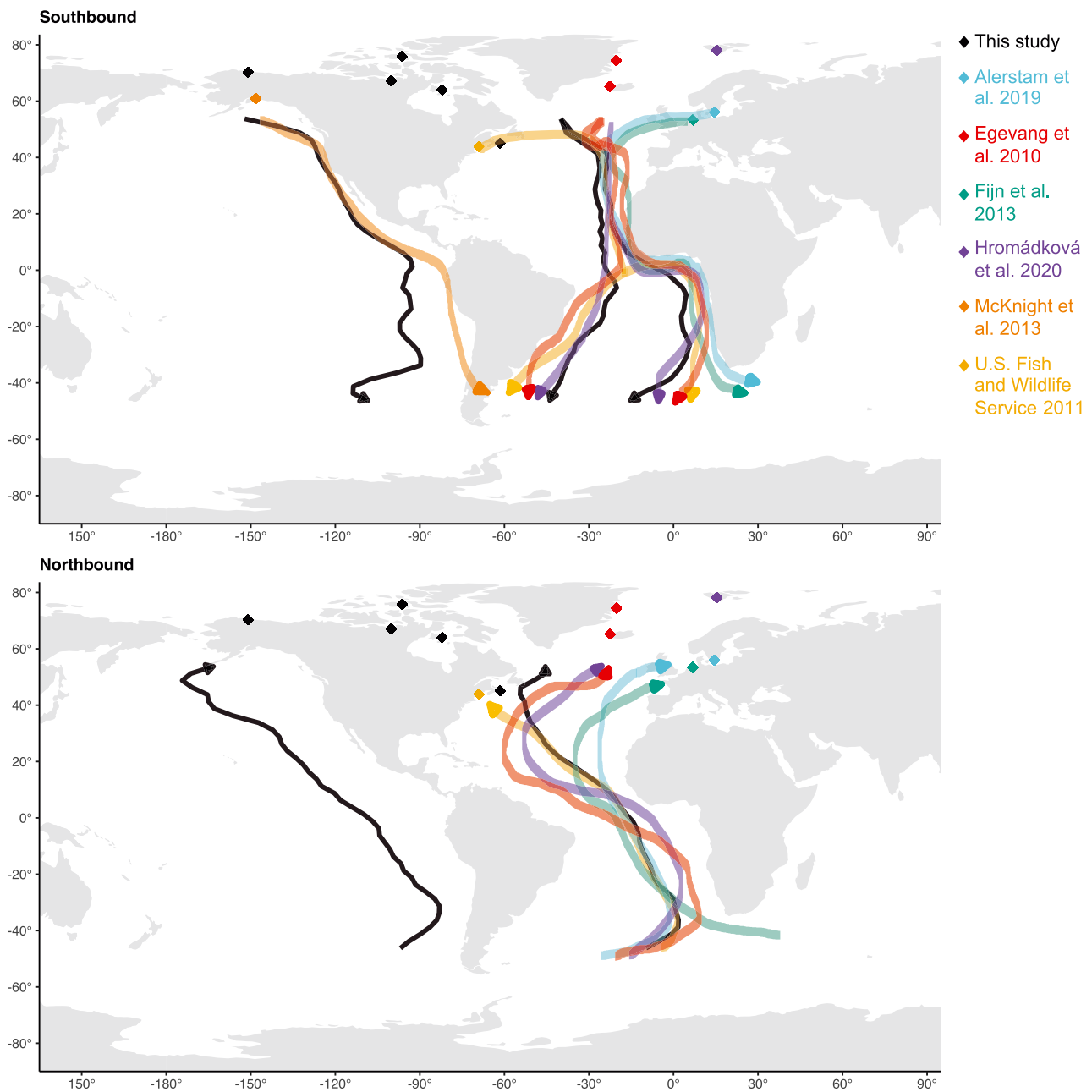


Fig. 4. Schematic comparison of the general southbound and northbound migration patterns used by Arctic terns tracked in previous studies. The mean tracks from this study are plotted, while tracks of previous studies are based on an interpretation of the mean as first shown in Fijn et al. (2013). Only migratory tracks between ca. 57.5° N to 50° S are plotted due to light-level limitation in polar regions and to allow more uniform comparison of all studies which reported location estimates within this latitudinal range. The breeding location where Arctic terns were tagged in each study is denoted by the corresponding coloured diamonds. Note McKnight et al. (2013) did not record a northbound migration

farther east (up to 150° and 167° E, respectively) from the South African coast (Fijn et al. 2013, Alerstam et al. 2019) (Fig. 4). In comparison, Canadian terns in our study (and all other tern colonies using Atlantic routes) remained west of ~70° E throughout their annual cycle (Figs. 1 & 3).

Arctic terns from northern Alaska (this study) followed a strict route along the Pacific coast of the USA (Fig. 4), similar to the southbound coastal route used by the southern Alaska breeding terns (McKnight et al. 2013, Duffy et al. 2014). However, in contrast to previously tracked Alaskan Arctic terns, the terns in our



study did not take overland trans-Andean migration routes into the Atlantic Ocean but instead maintained oceanic routes to winter west of the Weddell Sea.

### 3.4. Migration timing

In general, Nova Scotian terns (i.e. the terns breeding at the southernmost colony we tracked) crossed each latitudinal point significantly earlier than all other tern colonies tracked in this study (Fig. 5, Table S2). During southbound migration, colonies from the Canadian Arctic (East Bay, Karrak Lake, Nasaruaalik Island) arrived at a known North Atlantic staging site (Fig. S1; Egevang et al. 2010, Boertmann 2011, Gilg et al. 2013, van Bemmelen et al. 2017) at similar times, and only differed significantly in time from Nova Scotian birds (Fig. 5, Table S2). However, there were significant differences between colony departure times from the staging site, arrival time at the Equator, and time crossing 10° S (Fig. 5, Table S2). Date of southbound migration end (last date crossing 60° S) and duration of stay in Antarctic non-breeding grounds did not differ significantly across colonies (Fig. 5, Table S2). During the northbound migration, Alaskan and Nova Scotian Arctic terns headed west (40° S) and crossed the Equator at significantly earlier times than those from Canadian Arctic colonies (Fig. 5, Table S2). Northbound migration was also shorter than southbound migration by at least 29 d for all colonies (Table S2). Assumptions about homogeneity of variance were confirmed for all ANOVAs, and assumptions of normality were met in all but 2 cases (crossing 10° S, crossing 40° S) due to the presence of an outlier. All ANOVA results remained the same with and without the outlier (Table S2).

The timing of southbound and northbound migration for Arctic terns in this study and previous studies fell within a 1–2 mo window. Mean start dates of southbound migration were between mid-July and early September, and mean arrival dates to Antarctic wintering grounds were between October and early November. Mean start dates of northbound migration were between March and mid-April, and arrival back at the original breeding grounds was between April and May (Fig. 5, Tables S2 & S3). Overall, Arctic terns from the Baltic Sea (Alerstam et al. 2019) and the Netherlands (Fijn et al. 2013) seemed to have an earlier migration schedule than all other tracked tern colonies during both southbound and northbound migrations and crossed important latitudinal points almost 1 mo earlier than most other tern colonies

(Fig. 5). Arctic terns from Greenland and Iceland (Egevang et al. 2010) migrated at most similar times to the Canadian colonies during the southbound migration, while terns from Greenland, Iceland (Egevang et al. 2010), and the Netherlands (Fijn et al. 2013) demonstrated the closest similarities to Canadian terns in the northbound migration (Fig. 5). Comparison of migratory timing between Alaskan terns using the Pacific Ocean showed that previously tracked Alaskan terns (McKnight et al. 2013) started and ended southbound migration within a 2 wk window of the Alaskan Arctic terns tracked in this study (Fig. 5).

Comparison of migratory timing between Arctic terns using the Atlantic southbound West Africa route ( $n = 22$ ) or the Brazil route ( $n = 23$ ) showed minor differences in mean crossing times at each migration event (Fig. 6). Arctic terns using the West African route started southbound migration slightly earlier (mean difference = 4 d) than terns using the Brazilian route, but arrived slightly later at the wintering grounds (mean difference = 3 d; Fig. 6). Arctic terns using the Brazilian route also spent longer at the North Atlantic staging site than terns using the West African route but spent less time travelling between the staging site, the Equator, and 10° S (Fig. 6). However, the extensive overlap between the ranges of dates from both routes indicates that these differences are unlikely to be biologically important (Fig. 6).

## 4. DISCUSSION

Geolocator-tagged Arctic terns in our study were the first to document the full migration routes for Canadian Arctic terns, the first northbound migration routes in the Pacific Ocean, and the first migration routes of US birds breeding above the Arctic Circle. We report that the majority of Arctic terns tracked globally are using one of 3 southbound migration routes: (1) Atlantic West Africa route, (2) Atlantic Brazil route, and (3) Pacific coastal route, and are returning to the Northern Hemisphere using one of 2 northbound migration routes: (1) Mid-ocean Atlantic route or (2) Mid-ocean Pacific route.

### 4.1. Spatial commonalities of Arctic tern routes

We identified that Arctic terns from the same Canadian breeding colonies may use divergent coastal West African or East South American routes during southbound migration through the Atlantic (Fig. 1), a pattern also observed in Arctic terns from Green-

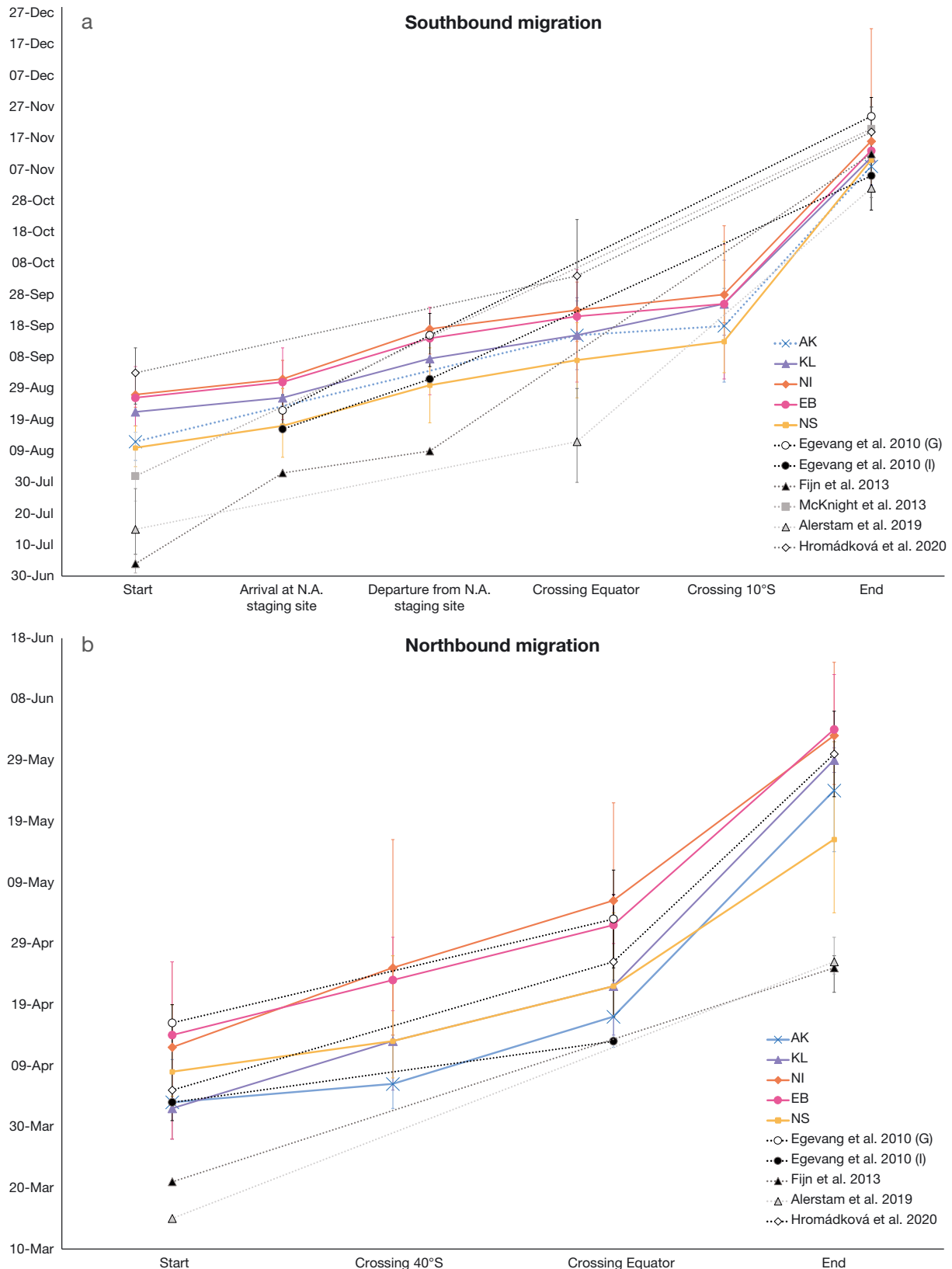


Fig. 5. Comparison of timing between the North American Arctic tern colonies in this study and other Arctic tern tracking studies (where timing information was available) during various stages of southbound and northbound migration. Each symbol represents the mean colony date at the specified migration event computed from the total number of individuals in that colony (detailed summary in Tables S2 & S3), and the bars indicate the range of dates observed for each colony (where available). Solid lines represent colonies in which the time of crossing at each migration event was available, while dashed lines represent colonies in which the timing of only some migration events were available. Note Egevang et al. (2010) tracked terns from Greenland (G) and Iceland (I), and McKnight et al. (2013) did not record a northbound migration

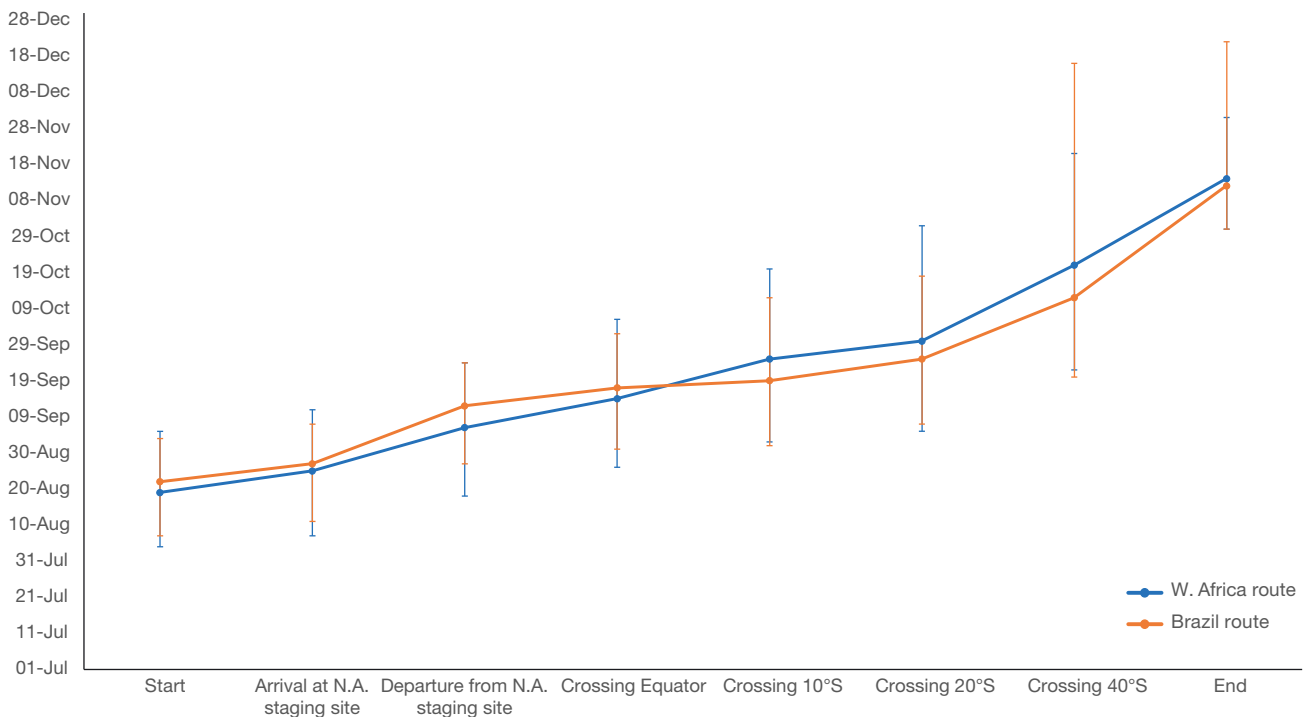


Fig. 6. Comparison of migration timing between Arctic terns using the West Africa route ( $n = 22$ ) or the Brazil route ( $n = 23$ ) during southbound migration through the Atlantic Ocean. The point denoted at each migration event represents the mean date of crossing, and the bars represent the range of dates for individuals using that route

land, Iceland, Maine (USA), and Svalbard (Norway) (Fig. 4; Egevang et al. 2010, US Fish & Wildlife Service 2013, Hromádková et al. 2020). Arctic terns in the Pacific Ocean shared similar coastal routes for a major portion of their southbound migration (Fig. 1; McKnight et al. 2013). During the return northbound migration, our findings indicated that Atlantic and Pacific Arctic tern colonies exhibit latitudinally similar east–west directional movements, and each group takes one main offshore route to their breeding grounds (Fig. 3). This pattern supports other Atlantic Arctic tern studies (Egevang et al. 2010, US Fish & Wildlife Service 2013, Hromádková et al. 2020), but our study is the first to report a northbound migration route for Pacific-breeding Arctic terns. We also provide evidence that Arctic terns use the same southbound migration routes across years (Figs. 1, S1 & S2). This similarity in routes between years and shared migration patterns with other Arctic tern colonies strongly suggests that the migration routes used by Arctic terns in our study are likely the main migration routes used by this species.

Arctic tern migration routes are also used by other trans-equatorial seabird species. Sabine's gulls *Xema sabini* used similar southbound coastal routes along the east Pacific Ocean (Davis et al. 2016), while sooty shearwaters *Ardenna grisea* and south polar skuas

*Stercorarius maccormicki* followed similar northbound Pacific routes (Shaffer et al. 2006, Kopp et al. 2011). Use of 2 divergent routes during southbound migration over the Atlantic Ocean, towards West Africa and eastern South America, has been observed in long-tailed skuas *S. longicauda* (Gilg et al. 2013) and Cory's shearwaters *Calonectris borealis* (Dias et al. 2011). Meanwhile, Sabine's gulls (Stenhouse et al. 2012, Davis et al. 2016), Manx shearwaters *Puffinus puffinus* (Guilford et al. 2009), and Leach's storm petrels *Oceanodroma leucorhoa* (Pollet et al. 2019) followed one of the 2 coastal Atlantic southbound routes. During northbound migration, Cory's shearwaters (González-Solís et al. 2007, Dias et al. 2012), sooty shearwaters (Hedd et al. 2012), and south polar skuas (Kopp et al. 2011) share the same movement trajectories and temporal patterns as northbound Arctic tern routes. These similarities suggest that the Pacific and Atlantic routes used by Arctic terns are not species-specific, but are also important for many other trans-equatorial migratory seabirds.

Wind and food availability may both play a role in driving these shared migration patterns. Favourable tailwinds have been used by long-distance migrants to reduce energetic costs by up to 30% (Liechti & Bruderer 1998, Shaffer et al. 2006, González-Solís et al. 2007, 2009, Felicísimo et al. 2008, Egevang et al.

2010, Kopp et al. 2011). Winds blowing clockwise in the North Atlantic and counter-clockwise in the South Atlantic likely influence Arctic tern movement towards coastal waters, to avoid oncoming headwinds south of the Equator during southbound migration (Fig. 1; Liechti 2006). During northbound migration, the continual movement of all tracks east before heading westward at 40° S (Fig. 3) is likely also a result of global wind patterns. Strong westerly winds, known as the Roaring Forties at 40° S, and even stronger westerly gale-force winds at 50° S and 60° S (the Furious Fifties and Screaming Sixties, respectively) likely push terns east until winds ease past 40° S (NOAA 2021). These wind patterns could also explain why terns take coastal southbound routes, as the land can help break the effect of these winds at southern latitudes (NOAA 2021). In contrast, during northbound migration, the fastest possible route (e.g. utilizing offshore prevailing winds) may be prioritized by terns to reach their breeding grounds in the least amount of time. For Cory's shearwaters, low-cost 'wind highways' were preferentially used over the shortest great circle migratory routes (Felicísimo et al. 2008), and low food availability around the Equator (associated with the warm oligotrophic waters) also altered flight paths (Dias et al. 2012). In Baltic and South Alaskan-breeding Arctic terns, migratory movements coincided with the seasonal shift of oceanic productive zones (McKnight et al. 2013, Alerstam et al. 2019). Recently, Hromádková et al. (2020) suggested the influence of wind or food on route choice is seasonally dependent. During southbound migration, Norwegian-breeding Arctic terns in the Atlantic were guided by productive stopover sites, and opted for these sites even with oncoming headwinds (Hromádková et al. 2020). Meanwhile, during northbound migration, Arctic terns took advantage of prevailing wind patterns and had fewer stopovers due to greater energy reserves from the non-breeding season, resulting in a faster migration rate than the southbound migration (Hromádková et al. 2020). Indeed, all Canadian-breeding Arctic terns stopped at the highly productive North Atlantic staging site (Grand Banks hotspot) used by many other migrating seabird species, including Arctic terns of Greenland, Iceland, and the Netherlands (Egevang et al. 2010, Boertmann 2011, Fijn et al. 2013, Gilg et al. 2013, van Bemmelen et al. 2017). In the Southern Hemisphere, the junction of warm and cold water and high eddy variability creates an area of high primary productivity off the Namibian and Brazilian coast, known as the Benguela current and Brazil current, respectively (Hutchings et al. 2009, Katsura-

gawa et al. 2014). Arctic terns using the coastal southbound West African and Brazilian routes likely exploit these currents and depend on the high food availability of these regions to complete their southbound migration.

Although there appears to be broad route homogeneity among most Arctic terns (even from widely separated breeding colonies), there are a few notable differences. In this study, Arctic terns tagged at a North Alaskan Arctic colony ( $n = 8$ ) used completely oceanic routes to reach their wintering grounds, in contrast to the overland migration at 40° S used by Arctic terns tagged at a South Alaskan sub-Arctic colony ( $n = 6$ ) (McKnight et al. 2013, Duffy et al. 2014). As a result, all Alaskan terns in the current study appeared to remain between 60° and 160° W, comparatively west of the Weddell Sea region used by previously tracked terns (McKnight et al. 2013, Duffy et al. 2014). Although the lack of Antarctic position data due to 24 h summer daylight makes validation of this assumption difficult, this suggests that North Alaskan terns in this study used a broader portion of the Antarctic ice shelf than South Alaskan terns. Another notable difference emerged in routes used by Canadian Arctic terns and those used by Arctic terns from the Baltic Sea and the Netherlands (Fijn et al. 2013, Alerstam et al. 2019). Although movements from 2 individuals (originating from Nova Scotia and Karrak Lake) showed more eastern movement into the Indian Ocean up until the Amery Ice Shelf, the majority of Canadian Arctic terns appear to overwinter in the Antarctic region between the Amery Ice Shelf and the Antarctic Peninsula (Fig. 1). The Amery Ice Shelf was also the easternmost extent of Antarctica used by Arctic terns from Maine, USA (US Fish & Wildlife Service 2013), and Arctic terns from Greenland, Iceland, Svalbard, and southern Alaska also overwintered in the Weddell Sea region of Western Antarctica (Egevang et al. 2010, McKnight et al. 2013, Hromádková et al. 2020). Thus, it appears that Arctic terns from Canada, Maine (USA), Greenland, Iceland, Svalbard, and southern Alaska (USA) may use a common Antarctic nonbreeding range, different from the more eastern Antarctic extent used by Arctic terns from the Baltic Sea and the Netherlands (Fijn et al. 2013, Alerstam et al. 2019).

#### 4.2. Timing of Arctic tern migration

Our results indicated that timing of migration was generally different across North American breeding colonies, although differences in crossing dates at

each latitude point typically fell within a 2 wk range (Fig. 5, Table S2). This suggests that North American Arctic terns used similar migratory routes, but at slightly staggered times from August to November (southbound migration) and April to June (northbound migration). These variations are likely related to differences in timing of breeding. For example, during northbound migration, Arctic terns from Nova Scotia reached their original breeding colony significantly earlier than other colonies in North America (Table S1, Fig. S3). This earlier arrival corresponds with the early breeding period of Nova Scotian birds. Nova Scotian Arctic terns complete breeding and dispersed from their colonies by mid-July (Loring et al. 2017). In contrast, Arctic terns from the Canadian High Arctic initiate nests in the first week of July (Mallory et al. 2017).

In both southbound and northbound migrations, Arctic terns from the Netherlands and the Baltic Sea started migration 1–2 mo ahead of all other tern colonies (Fig. 6) as a result of an earlier breeding season (May–July; Fijn et al. 2013, Alerstam et al. 2019). Terns from the Baltic Sea and the Netherlands are also the only tracked Arctic terns to use the Indian Ocean/Tasman Sea at the end of their southbound migration (Fig. 5). Thus, these Western European terns may utilize the productive Indian Ocean/Tasman Sea belt for up to 2 mo to avoid competition with later-breeding Arctic terns in the Atlantic Ocean, despite the increased energy costs of a longer-distance migration (Alerstam et al. 2019). These differences suggest that although Arctic terns may share common migration route patterns, the timing of migration may differ as a result of asymmetric breeding periods and migration strategies. Nevertheless, the 1–2 mo period in which all tracked Arctic tern colonies of the world start (southbound: early July to early September; northbound: early March to mid-April) and end migration (southbound: mid-October to late December; northbound: early April to early June) on both their southbound and northbound journeys suggests that there is a ‘moving window’ of time where Arctic terns are present at each latitudinal crossing. The difference in the years that Arctic terns were tracked between studies also indicates that this timing, although staggered, is still relatively consistent within a 1–2 mo window throughout the year.

This same 1–2 mo window of southbound and northbound migrations is observed in other species of trans-equatorial seabirds that use the same general migration route patterns as Arctic terns. For example, long-tailed skuas start southbound migra-

tion in mid-August and arrive at their non-breeding grounds off southwestern Africa by late October (Gilg et al. 2013). Pacific and Atlantic migrating Sabine’s gulls started migrating in mid-late August and arrived at their nonbreeding grounds of coastal Peru and southwestern Africa by mid-November (Davis et al. 2016). Sooty shearwaters started their northbound migration from the Falkland Islands to the North Atlantic in late March and arrived in mid-April (Hedd et al. 2012). These similarities suggest that Arctic tern routes are not only shared with other migrating seabirds in space, but the general time in which seabirds are present in each of these areas of the ocean falls within a 1–2 mo window.

### 4.3. Conservation implications

The broad geographic range of Arctic terns requires a common framework to facilitate international cooperation and ensure that conservation action is also wide-ranging. Recently, the use of dynamic management tools, such as mobile marine protected areas (mMPAs) which shift across space and time, has been proposed under the 1982 United Nations Convention on the Law of the Sea (UNCLOS) (Maxwell et al. 2020). Dynamic management could offer protection for migratory seabirds that spans entire oceans, in which protection over such a large range would otherwise be unfeasible with traditional MPAs. For example, a more feasible dynamic mMPA for pelagic migrating seabirds may be one where management measures are only necessary during the most important times of the year where and when seabird migration is concentrated. Incorporating the temporal scale of seabird movement in marine spatial planning could also ensure that plans can accommodate variations in seabird life histories, such as from climate change or changes in human activity (Lennox et al. 2019). Our study provides information about the times of the year when Arctic terns and some other pelagic migrants may utilize the northern and southern portions of the Pacific and Atlantic Oceans during the start and end of southbound and northbound migrations, which can be used to inform future time-dependent conservation. While it is difficult to gather accurate position estimates during the Antarctic non-breeding period using light-level geolocators due to 24 h daylight during polar summer, the duration of time Arctic terns spend in their wintering ground is similar to the duration of migration. Further studies should identify whether Arctic terns use similar Antarctic wintering grounds and

whether mMPA or more traditional approaches should be used to protect these areas.

BirdLife International has called for migratory seabird protection under international agreements, such as the recent High Seas Treaty, to protect marine life in areas beyond national jurisdiction (United Nations General Assembly 2017). For migratory birds, identifying common multi-species flyways, such as the Waterbird Flyways for waterfowl and shorebirds (e.g. common terns *Sterna hirundo*), has been useful to facilitate political cooperation and cross-country management of their populations (UNEP/CMS Secretariat 2012). Identifying flyways, and thereby who is responsible for managing threats to birds, is particularly important for the conservation of pelagic seabirds such as Arctic terns because their use of the High Seas presents additional political challenges and necessitates cross-country negotiations (Harrison et al. 2018). Such multi-stakeholder cooperation has been successful in managing oceanic areas. Recently, the Oslo and Paris Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) Commission proposed a new MPA ('The North Atlantic Current and Evlanov Seamount MPA') for seabirds crossing the Atlantic on the High Seas (Ospar Commission 2018). International negotiations between 24 member states also recently designated the world's largest MPA in the Ross Sea, Antarctica, which includes a 'no take' zone prohibiting all fishing activities (Brooks et al. 2019). While our study shows that the migratory route patterns used by most studies of Arctic terns are generally similar in space and across years and that these migration routes may also be used by some other trans-equatorial seabird species, no official seabird flyways exists, and the observed routes of North American Arctic terns overlap little with the Waterbird Flyways (Fig. S4; Table S4). BirdLife International has assimilated the space use of many migratory seabirds globally through their Seabird Tracking Database (BirdLife International 2020a). Thus, the next step would be to perform a meta-analysis comparing the migration of a broad range of seabird species to identify the main multi-species 'seabird flyways'.

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#### LITERATURE CITED

- ✦ Alerstam T (1991) Bird flight and optimal migration. *Trends Ecol Evol* 6:210–215
- ✦ Alerstam T, Bäckman J, Grönroos J, Olofsson P, Strandberg R (2019) Hypotheses and tracking results about the longest migration: the case of the Arctic tern. *Ecol Evol* 9: 9511–9531
- ✦ BirdLife International (2020a) Seabird tracking database. <http://www.seabirdtracking.org/> (accessed 12 December 2020)
- ✦ BirdLife International (2020b) Species factsheet: *Sterna paradisaea*. <http://datazone.birdlife.org/species/factsheet/arctic-tern-sterna-paradisaea> (accessed 18 November 2019)
- Boertmann D (2011) Seabirds in the central North Atlantic, September 2006: further evidence for an oceanic seabird aggregation area. *Mar Ornithol* 39:183–188
- ✦ Bracey A, Lisovski S, Moore D, McKellar A and others (2018) Migratory routes and wintering locations of declining inland North American common terns. *Auk* 135:385–399
- ✦ Brooks CM, Crowder LB, Österblom H, Strong AL (2019) Reaching consensus for conserving the global commons: the case of the Ross Sea, Antarctica. *Conserv Lett* 13: e12676
- Burnham KK, Burnham JL, Konkel BW, Johnson JA (2017) Significant decline observed in Arctic tern *Sterna paradisaea* population in northwest Greenland. *Seabird* 30: 39–50
- ✦ Croxall JP, Butchart SHM, Lascelles BG, Stattersfield AJ, Sullivan BJ, Symes A, Taylor P (2012) Seabird conservation status and threats: a global assessment of priorities. *Bird Conserv Int* 22:1–34
- ✦ Davis SE, Maftei M, Mallory ML (2016) Migratory connectivity at high latitudes: Sabine's gulls (*Xema sabini*) from a colony in the Canadian High Arctic migrate to different oceans. *PLOS ONE* 11:e0166043
- ✦ Dias MP, Granadeiro JP, Phillips RA, Alonso H, Catry P (2011) Breaking the routine: individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proc R Soc B* 278:1786–1793
- ✦ Dias MP, Granadeiro JP, Catry P (2012) Do seabirds differ from other migrants in their travel arrangements? On route strategies of Cory's shearwater during Its trans-equatorial journey. *PLOS ONE* 7:e49376
- Duffy DC, McKnight A, Irons DB (2014) Trans-Andean passage of migrating Arctic terns over Patagonia. *Mar Ornithol* 41:155–159
- ✦ Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc Natl Acad Sci USA* 107:2078–2081
- ✦ Felicísimo AM, Muñoz J, González-Solís J (2008) Ocean sur-

- face winds drive dynamics of transoceanic aerial movements. *PLOS ONE* 3:e2928
- ✦ Fijn RC, Hiemstra D, Phillips RA, van der Winden J (2013) Arctic terns *Sterna paradisaea* from the Netherlands migrate record distances across three oceans to Wilkes Land, East Antarctica. *Ardea* 101:3–12
- ✦ Gaston AJ, Mallory ML, Gilchrist HG (2012) Populations and trends of Canadian Arctic seabirds. *Polar Biol* 35: 1221–1232
- ✦ Gilchrist HG, Robertson GJ (1999) Population trends of gulls and Arctic terns nesting in the Belcher Islands, Nunavut. *Arctic* 52:325–331
- ✦ Gilg O, Moe B, Hanssen SA, Schmidt NM and others (2013) Trans-equatorial migration routes, staging sites and wintering areas of a high-Arctic avian predator: the long-tailed skua (*Stercorarius longicaudus*). *PLOS ONE* 8:e64614
- ✦ Gilroy JJ, Gill JA, Butchart SHM, Jones VR, Franco AMA (2016) Migratory diversity predicts population declines in birds. *Ecol Lett* 19:308–317
- ✦ González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Front Ecol Environ* 5:297–301
- ✦ González-Solís J, Felicísimo ÁM, Fox JW, Afanasyev V, Kolbeinsson Y, Muñoz J (2009) Influence of sea surface winds on shearwater migration detours. *Mar Ecol Prog Ser* 391:221–230
- ✦ Gudmundsson GA, Larsson B, Alerstam T (1992) Radar observations of northbound migration of the Arctic tern, *Sterna paradisaea*, at the Antarctic Peninsula. *Antarct Sci* 4:163–170
- ✦ Guilford T, Meade J, Willis J, Phillips RA and others (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proc R Soc B* 276:1215–1223
- ✦ Harrison AL, Costa DP, Winship AJ, Benson SR and others (2018) The political biogeography of migratory marine predators. *Nat Ecol Evol* 2:1571–1578
- Hatch JJ, Gochfeld M, Burger J, Garcia EFJ (2020) Arctic tern (*Sterna paradisaea*). In: Billerman SM (ed) *Birds of the world*. Cornell Lab of Ornithology, Ithaca, NY
- ✦ Hedd A, Montevecchi WA, Otley H, Phillips RA, Fifield DA (2012) Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. *Mar Ecol Prog Ser* 449:277–290
- ✦ Henri DA, Martinez-Levasseur LM, Weetaltuk S, Mallory ML, Gilchrist HG, Jean-Gagnon F (2020) Inuit knowledge of Arctic terns (*Sterna paradisaea*) and perspectives on declining abundance in southeastern Hudson Bay, Canada. *PLOS ONE* 15:e0242193
- ✦ Hromádková T, Pavel V, Flousek J, Briedis M (2020) Seasonally specific responses to wind patterns and ocean productivity facilitate the longest animal migration on Earth. *Mar Ecol Prog Ser* 638:1–12
- ✦ Hutchings L, van der Linden CD, Shannon LJ, Crawford RJM and others (2009) The Benguela Current: an ecosystem of four components. *Prog Oceanogr* 83:15–32
- Jodice PGR, Suryan RM (2010) The transboundary nature of seabird ecology. In: Trombulak SC, Baldwin RF (eds) *Landscape-scale conservation planning*. Springer Science, Berlin, p 139–165
- ✦ Kassambara A (2020) rstatix: pipe-friendly framework for basic statistical tests. R package version 0.5.0. <https://CRAN.R-project.org/package=rstatix>
- ✦ Katsuragawa M, Dias JF, Harari J, Namiki C, Zani-Teixeira ML (2014) Patterns in larval fish assemblages under the influence of the Brazil current. *Cont Shelf Res* 89:103–117
- ✦ Kopp M, Peter HU, Mustafa O, Lisovski S, Ritz MS, Phillips RA, Hahn S (2011) South polar skuas from a single breeding population overwinter in different oceans though show similar migration patterns. *Mar Ecol Prog Ser* 435:263–267
- ✦ Lennox RJ, Engler-Palma C, Kowarski K, Filous A, Whitlock R, Cooke SJ, Auger-Méthé M (2019) Optimizing marine spatial plans with animal tracking data. *Can J Fish Aquat Sci* 76:497–509
- ✦ Liechti F (2006) Birds: Blowin' by the wind? *J Ornithol* 147: 202–211
- ✦ Liechti F, Bruderer B (1998) The relevance of wind for optimal migration theory. *J Avian Biol* 29:561–568
- ✦ Lisovski S, Wotherspoon S, Sumner M (2016) TwGeos: Basic data processing for light-level geolocation archival tags. R package version 0.1.2. <https://github.com/slisovski/TwGeos/>
- ✦ Lisovski S, Bauer S, Briedis M, Davidson SC and others (2020) Light-level geolocator analyses: a user's guide. *J Anim Ecol* 89:221–236
- ✦ Loring PH, Ronconi RA, Welch LJ, Taylor PD, Mallory ML (2017) Postbreeding dispersal and staging of common and Arctic terns throughout the western North Atlantic. *Avian Conserv Ecol* 12:20
- ✦ Maftei M, Davis SE, Mallory ML (2015) Assessing regional populations of ground-nesting marine birds in the Canadian High Arctic. *Polar Res* 34:25055
- ✦ Mallory ML, Akearok J (2010) NWMB interim report: local knowledge and surveys on declines of Arctic terns near Rankin Inlet and Whale Cove. Nunavut Wildlife Management Board (NWMB), Iqaluit
- ✦ Mallory ML, Boadway KA, Davis SE, Maftei M, Diamond AW (2017) Breeding biology of Arctic terns (*Sterna paradisaea*) in the Canadian High Arctic. *Polar Biol* 40: 1515–1525
- ✦ Mallory ML, Davis SE, Maftei M, Fife DT, Robertson GJ (2018) Adult survival of Arctic terns in the Canadian High Arctic. *Polar Res* 37:1537710
- ✦ Maxwell SM, Gjerde KM, Connors MG, Crowder LB (2020) Mobile protected areas for biodiversity on the high seas. *Science* 367:252–254
- ✦ McKnight A, Allyn AJ, Duffy DC, Irons DB (2013) 'Stepping stone' pattern in Pacific Arctic tern migration reveals the importance of upwelling areas. *Mar Ecol Prog Ser* 491: 253–264
- ✦ NOAA (2021) What are the roaring forties? <https://oceanservice.noaa.gov/facts/roaring-forties.html> (accessed 23 May 2021)
- ✦ Oskar Commission (2018) Views sought on new marine protected area for seabirds. Oskar News. <https://www.ospar.org/news/views-sought-on-new-marine-protected-area-for-seabirds>
- ✦ Petersen A, Robertson GJ, Thorstensen S, Mallory ML (2020) Annual survival of Arctic terns in western Iceland. *Polar Biol* 43:1843–1849
- Pollet IL, Ronconi RA, Leonard ML, Shutler D (2019) Migration routes and stopover areas of Leach's storm petrels *Oceanodroma leucorhoa*. *Mar Ornithol* 47:55–65
- ✦ Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. [www.R-project.org/](http://www.R-project.org/)
- ✦ Redfern CPF, Bevan RM (2020) Overland movement and migration phenology in relation to breeding of Arctic

- terns *Sterna paradisaea*. *Ibis* 162:373–380
- ✦ Reynolds RW, Smith TM, Liu C, Chelton DB, Casey KS, Schlax MG (2007) Daily high-resolution-blended analyses for sea surface temperature. *J Clim* 20:5473–5496
- ✦ Shaffer SA, Tremblay Y, Weimerskirch H, Scott D and others (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc Natl Acad Sci USA* 103:12799–12802
- ✦ Stenhouse IJ, Egevang C, Phillips RA (2012) Trans-equatorial migration, staging sites and wintering area of Sabine's gulls *Larus sabini* in the Atlantic Ocean. *Ibis* 154:42–51
- ✦ Sutherland WJ (1998) Evidence for flexibility and constraint in migration systems. *J Avian Biol* 29:441–446
- UNEP/CMS Secretariat (2012) A bird's eye view on flyways: a brief tour by the Convention on the Conservation of Migratory Species of Wild Animals. UNEP/CMS Secretariat, Bonn
- ✦ United Nations General Assembly (2017) Resolution 72/249: International legally binding instrument under the United Nations Convention on the Law of the Sea on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction. <https://undocs.org/en/a/res/72/249>
- US Fish & Wildlife Service (2006) Alaska seabird information series: Arctic tern (*Sterna paradisaea*). US Fish & Wildlife Service, Anchorage, AK
- ✦ US Fish & Wildlife Service (2013) Field notes entry: geolocators reveal migratory pathway of Arctic terns. [www.fws.gov/FieldNotes/regmap.cfm?arskey=32639](http://www.fws.gov/FieldNotes/regmap.cfm?arskey=32639) (accessed 12 November 2019)
- ✦ van Bemmelen R, Moe B, Hanssen SA, Schmidt NM and others (2017) Flexibility in otherwise consistent non-breeding movements of a long-distance migratory seabird, the long-tailed skua. *Mar Ecol Prog Ser* 578:197–211
- ✦ Wotherspoon SJ, Sumner MD, Lisovski S (2013) R package SGAT: solar/satellite geolocation for animal tracking

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