Variation in migration behaviours used by Arctic Terns (*Sterna paradisaea*) breeding across a wide latitudinal gradient

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Abstract

Arctic Terns (*Sterna paradisaea*) share a few routes to undertake the longest annual migrations of any organism. To understand how the wide spatial range of their breeding colonies may affect their migration strategies (e.g., departure date), we tracked 53 terns from five North American colonies distributed across 30° of latitude and 90° of longitude. While birds from all colonies arrived in Antarctic waters at a similar time, terns nesting in the Arctic colonies migrated back north more slowly and arrived to their breeding grounds later than those nesting in the colony farther south. Arrival dates in Antarctic waters coincided with the start of favourable foraging conditions (i.e., increased ocean productivity), and similarly arrival dates at breeding colonies coincided with the start of local favourable breeding conditions (i.e., disappearance of snow and ice). Larger birds followed a more direct southbound migration route than smaller birds. On both southbound and northbound migrations, daily distances travelled declined as time spent in contact with the ocean increased, suggesting a trade-off between resting/foraging and travelling. There was more unexplained variation in behaviour among individuals than among colonies, and one individual had a distinctive stop around Brazil. Terns nesting in the Arctic have a narrow time window for breeding that will likely increase with continuing declines in sea ice and snow. Departing Arctic Terns likely have few clues about the environmental conditions they will encounter on arrival, and their response to environmental changes at both poles may be assisted by large individual variation in migration strategy.

Key words: migration, Arctic Terns, individual variation, phenology, timing, latitudinal variation

Declarations

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Code availability: The analyses used R packages available on CRAN or Github.

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Introduction

Trans-equatorial migratory seabirds cover vast distances at sea, with the Arctic Tern (*Sterna paradisaea*) known for the longest migration of any organism (Egevang et al. 2010; Fijn et al. 2013; Wong et al. 2021). Using miniaturized light-level geolocators, researchers have shown that Arctic Terns display seasonally distinct migration strategies (McKnight et al. 2013; Hromádková et al. 2020) and that individuals from distant breeding colonies can share similar migration routes (Wong et al. 2021). However, these studies have primarily focused on inferring population-level movements of Arctic Terns and identifying key marine habitats used in migration (Egevang et al. 2010; Fijn et al. 2013; McKnight et al. 2013; U.S. Fish & Wildlife Service 2013; Alerstam et al. 2019; Hromádková et al. 2020; Redfern and Bevan 2020; Wong et al. 2021), with less attention paid to the potential effects of latitudinal differences in breeding sites and individuals' physical characteristics on migratory behaviour and phenology.

Arctic Terns display important seasonal differences in migration behaviour. Southbound migratory behaviour appears to be driven primarily by the phenology and distribution of food-rich marine stopover sites, with terns stopping frequently to refuel (McKnight et al. 2013). In contrast, during the northbound migration, terns use strong tailwinds to travel back to their breeding grounds quickly, a pattern presumably driven by a need to secure favourable nesting sites and initiate breeding as earlier as possible (Hromádková et al. 2020). Many other long-distance migratory birds have faster northbound than southbound migrations, and take migration routes that favour foraging or weather conditions (Nilsson et al. 2013; Hahn et al. 2014; Horton et al. 2016).

Arctic Terns from different colonies vary in when they cross important migratory landmarks (Wong et al. 2021), suggesting that breeding location may affect their migratory behaviour. The influence of breeding latitude on migratory patterns of birds varies considerably (Fifield et al. 2014; Ramos et al. 2015; Neufeld et al. 2021). Migration distance affects whether a species is likely to use a time- or energy-minimizing strategy (Anderson et al. 2019). Within species, the association between breeding site latitude and migration patterns is less clear. For example, while breeding latitude has no effect on the southbound departure dates of Herring Gulls (*Larus smithsoniansus*; Anderson et al. 2020), Bar-tailed Godwits (*Limosa lapponica baueri*) that nest farther north depart later (Conklin et al. 2010). Arctic Terns breed in the Northern hemisphere across a large latitudinal range (~40°, Hatch et al. 2020). We expect that this wide latitudinal range may explain some of the observed variation in migration timing (Wong et al. 2021), especially since breeding and foraging opportunities for birds nesting in the Arctic are more time-constrained than those of birds nesting in temperate zones due to factors such as later melt of snow and sea-ice farther north (e.g., Mallory and Forbes 2007).

Variation in migratory behaviour among individuals is known to have important relationships with the survival and reproduction of birds. For example, a bird’s arrival date to its nesting site can be linked to its probability of breeding (Bêty et al. 2004), and the previous or current year's breeding status of an individual can modulate its migration pattern (Catry et al. 2013; Bogdanova et al. 2017). Consequently, understanding individual variation in migratory behaviour can provide important insights into the potential for migration patterns to have carry-over effects into the breeding season, and the reproductive health of a population. Individual variation in migratory behaviour can be inferred from tracking devices through differences in movements (e.g., daily distance covered), behaviours (e.g., contact with water as indication of foraging/resting), and timing (e.g., start date, duration; Phillips et al. 2017).

To understand the factors that explain spatial and temporal variation in Arctic Tern migratory behaviour, we deployed geolocators and analyzed the movement tracks and activity patterns of 53 nesting individuals from five breeding colonies across Canada and Alaska, USA. For both southbound and northbound migrations, we determined the factors that best explained: 1) migration-level differences in departure dates, arrival dates, duration, total distance travelled, and time spent with their leg immersed in salt water; and 2) daily-level differences in distance travelled and time spent with their leg immersed in salt water. Our study provides a novel examination of how intraspecies differences in breeding site latitude affects migratory behaviour, as well as insights into individual migratory variation that is often overlooked by population-level descriptions of migration routes.

Materials and methods

Data collection

We tagged 108 nesting Arctic Terns from five breeding colonies (four Arctic colonies and one temperate colony) in North America: Alpine, Alaska (70.35°N, 151.03°W, *n* = 23), Country Island, Nova Scotia (45.06°N, 61.32°W, *n* = 25), East Bay, Nunavut (64.01°N, 82.07°W, *n* = 20), Karrak Lake, Nunavut (67.25°N, 100.25°W, *n* = 10), and Nasaruvaalik Island, Nunavut (75.83°N, 96.30°W, *n* = 30, Fig. 1). In this paper, we refer to the four colonies studied in Alaska, USA and Nunavut, Canada as the "Arctic colonies". We used bownets and attempted to capture nesting terns during late incubation (June-July) to minimize the risk of nest abandonment. Birds were first captured in 2017 (see Wong et al. (2021) for details), and fitted with an Intigeo archival light-level geolocator (GLS; model W65 Migrate Technology Ltd., Cambridge, UK; 1 g total mass, < 2% of tern's body mass) attached to a Darvic color band on the tarsus. All birds also received a United States Geological Survey/Canadian Wildlife Service (USGS/CWS) metal leg band. The tags were attached with metal contact pins (used to record conductivity and to connect to a computer interface) facing up toward the bird's body to limit abrasion by contact with rocks. Intigeo tags recorded light intensities (lux) once every 5 min, as well as minimum and maximum temperatures (Celsius), number of salt water immersions (dry = 0, wet =1), and maximum conductivity levels every 4 h (range: 0 - 127). We recaptured tagged terns in 2018 and 2019 following their return to the breeding sites. We recorded multiple morphological measurements for most birds (see Wong et al. 2021) but selected total head length (cm) and body mass (g) as indices of body size. For Arctic Terns, head length differs between sex and has been used as a proxy of structural size, while mass has been used as a proxy of body condition (Devlin et al. 2004; Mallory et al. 2017; Baak et al. 2020), and although the values of these indices vary amongst individuals, they did not differ across colonies (Online Resource). While we did not systematically assess the nesting success of the terns we tagged, many of them were observed on their nests after tagging. Some field teams confirmed that none of the tagged birds abandoned their nest (e.g., Alaska), and similarly no abandonment after banding was observed in our previous work on Country and Nasaruvaalik Islands. All research was conducted under approved animal care protocols (Acadia University ACC 04-17; National Zoological Park ACUC Protocols 15-20, 18-06) and scientific permits (e.g., Environment and Climate Change Canada (ECCC) Banding: 10694, Government of Nunavut Wildlife License 2018-038; US Federal Bird Banding Permit: 09700, Alaska Scientific Permits: 17-162, 18-156).

Data processing

We recovered 58 of the 108 deployed GLS tags, but only 53 of these tags contained usable data: Alpine, AK (*n* = 8), Country Island, NS (*n* = 15), East Bay, NU (*n* = 7), Karrak Lake, NU (*n* = 4), and Nasaruvaalik Island, NU (*n* = 19). While 28 of the 53 tags were recovered in the second year (July 2019; Alpine, AK: *n* = 2; Country Island, NS: *n* = 2; East Bay, NU: *n* = 5; Nasaruvaalik Island, NU: *n* = 19), we only used the data from the first migration cycle for our analyses since the tags recovered in the second year stopped recoding data partway through the second migration cycle (October-November 2018). One individual from East Bay, NU and one from Country Island, NS were missing some of the physical measurements, and thus any statistical analysis requiring these covariates (see below) excluded these two individuals.

To investigate differences in behaviours along migratory routes, we analyzed the wet/dry readings recorded from leg-mounted tags. Intigeo tags recorded a ‘wet’ reading every 30 s and summed these readings across 4 h intervals (up to a maximum of 480 wet readings per 4 h). These wet readings only recorded immersion in salt water, as determined by conductivity levels > 63. Thus, we interpreted these wet readings as the animal landing on, or plunge diving in, the ocean, or any behaviour resulting in their leg being immersed in salt water. In our analyses, we summed wets readings over a period of 24 h, which we refer throughout as daily numbers of wets. This 24-h period is based on the pre-set times of the loggers rather than based on calendar days. For individuals with extended “dry periods” (i.e., more than one day with zero wet readings), we also explored the raw conductivity data to assess whether some of these dry periods were in fact spent in contact with fresh or brackish water (conductivity levels between 1 and 63).

We used the R packages *TwGeos* (Wotherspoon et al. 2016) and *SGAT* (Sumner et al. 2009; Lisovski and Hahn 2012; Lisovski et al. 2020) to estimate Arctic Tern locations from the raw light, immersion, and salt water temperature data collected by the tags; see Wong et al. (2021) for details. Briefly, *SGAT* uses a Bayesian framework to combine tag data with prior information on (i) the twilight error distribution, and (ii) the flight speed distribution, as well as (iii) a land and sea surface temperature (SST) mask based on satellite maps from NOAA (Reynolds et al. 2007), to sample the most likely locations of each individual. SST/land masks generally assigned very low probability to terrestrial locations. However, when an individual's tag did not record salt water readings for more than three days, higher probability was assigned to locations on land. In addition, for individuals assessed to be dry for multiple days, we fitted the model without the SST/land mask to visually assess the likelihood of terrestrial locations.

For all of our analyses, we defined southbound and northbound migrations as travel between the breeding colony in the northern hemisphere and the crossing of 54°S. To differentiate foraging trips while at colonies from the start of the southbound migration, we detected when individuals crossed a 300 km buffer around each colony for the last time. We chose a 300 km buffer as it is close to the median daily distance travelled by terns in this study during their southbound migration (293 km day^{-1}). We chose 54°S as it removed the wintering behaviour of all birds in our study (i.e., it removed multi-day clusters of locations in Antarctica). Thus, migration here excluded movement in the northern breeding grounds and in the Antarctic non-breeding grounds. Travel distances were calculated using the great elliptic distance between two consecutive positions, with the function ‘distVincentyEllipsoid’ in the R package *geosphere* (Hijmans et al. 2019). Since positions were predicted at the time of sunset and sunrise, the time of day associated with the locations differed each day. To have consistent measures of distance moved per day and to be able to link distance moved with behavioural measures, we interpolated the daily distance traveled to the pre-set times of the wet readings.

This study focuses on investigating factors that affect the total distance traveled and the duration of the migration. However, impediments to light-based geolocation during the polar summers (i.e., when there is less than two hours darkness) precluded having reliable locations at the start and end of the tracks for many individuals (Wong et al. 2021), resulting in truncated migrations. To correct for these data gaps and standardize the treatment of the data for all birds, we estimated the missing distance travelled as the straight-line distance between the last (for southbound, first for northbound) reliable migration location outside the 300 km buffer and the colony. Similarly, we estimated the missing distance travelled in the Southern hemisphere as the straight-line distance between the first (for southbound, last for northbound) location north of 54°S and the closest point on the 54th parallel. To correct and standardize dates of departure/arrival, and thus migration duration, we estimated how many days were required to travel that straight-line distance if they travelled 300 km day^{-1}. The 300 km speed value we selected could impact our estimated departure/arrival dates and duration of migration, and thus any further analyses. To assess the impact of this value on our results, we explored using unique speed values estimated for each individual (Online Resource).

Potential drivers of migration-level behavioural differences

To investigate differences in migration behaviours for both the southbound and northbound migrations, we examined factors associated with five migration metrics: start date, end date, duration, distance travelled, and mean number of wet readings per day (higher values can be interpreted as an animal spending more time in behaviours that result in its leg-mounted tag being immersed in salt water). We first assessed whether migration metrics differed across colonies using ANOVAs.

To understand the potential drivers of colony and individual differences, we also assessed whether these five migration metrics were related to the latitude of the breeding colony, the total head length (a proxy of structural size), and body mass (a proxy of body condition). Because only a small portion of individuals was genetically sexed, we could not explore sexual differences directly. We hypothesized that individuals spending more time landing, plunge diving, or more generally with their leg immersed in the ocean, would take longer to complete their migration. Thus, we additionally assessed whether start date, end date, duration, and distance travelled were associated with the mean number of wet readings per day.

For the independent analysis of each migration metric, we use the R packages *nlme* (Pinheiro et al. 2019) and *MuMIn* (Bartoń 2020) to fit the full range of linear mixed-effect models and to model-average parameter estimates. We checked for correlation between covariates, which were all lower than 0.7, and thus deemed to be independent predictor variables (Dormann et al. 2013). To facilitate comparison of the effects of covariates, we centered and scaled all covariates. To ensure that the effect of colony latitude was not confounded by other potential colony differences (e.g., local habitat conditions) or the ocean taken to complete migration (see Wong et al. 2021), we added ocean/colony as nested random effects.

Potential drivers for daily-level movement and behavioural differences

To understand differences in daily migratory behaviour, we explored the potential factors associated with the daily distance travelled and daily number of wet readings. We investigated the potential associations of these two metrics with the latitude of the individual’s colony, its head length, and its body mass. For daily distance, we were also interested in knowing whether it was associated with the amount of time spent with their legs immersed in salt water. For both southbound and northbound migrations, we used linear mixed-effects models. Since each individual is likely to have similar behaviours on consecutive days, we expected (and observed) autocorrelation in the time series of daily values of distance moved and number of wet readings for each individual. To account for this temporal autocorrelation, we added a correlation structure (using ‘corAR1’ argument in the *lme* function of the *nlme* R package) to the mixed-effects models (Pinheiro et al. 2019). To account for individual and colony variability in daily movement not explained by our covariates, we used an individual random effect nested within a colony random effect (i.e., colony/individual). Our original full linear mixed-effects models showed clear trends in the residuals that suggested changes in the variance (e.g. heteroscedasticity; Schielzeth et al. 2020). To account for this violation of model assumptions, we added a power variance structure to the model (using function ‘varPower’ in the *nlme* R package; Pinheiro et al. 2019). As for the migration-level analyses, we used the R packages *nlme* and *MuMIn* to fit the full range of daily-level linear mixed-effect models and to model-average parameter estimates. Given that daily numbers of wets were count data, we reproduced these analyses using a variety of generalized linear mixed-effect models (for details, see Online Resource). We again checked for correlation between covariates, and centered and scaled all covariates.

All means are presented ± standard deviation.

Results

Difference in duration between southbound and northbound migrations

For all colonies, Arctic Terns spent more days migrating south than north (Fig. 2A) and, similarly, total distance traveled was longer during the southbound than northbound migration (Fig. 2B). On average, Arctic Terns spent 90 ± 9 d and travelled 33,806 ± 2,839 km on their southbound migration, while they spent 48 ± 12 d and travelled 22,906 ± 3,473 km on their northbound migration. The total number of wet readings per individual was higher during the southbound migration compared to northbound migration (southbound: mean = 30,185 ± 12,944 wets; northbound: 23,368 ± 9,554 wets). However, the individual variation was large and 21 individuals (40%) had a higher total number of wet readings during their northbound migration. In addition, terns had higher mean number of wet readings per day during their northbound migration compared to their southbound migration (Fig. 2C).

Potential drivers of migration-level behavioural differences

For the southbound migration, colonies significantly differed in terms of start date, duration, and average wet readings per day (Table 1, Fig. 3 B, F, J), but not in terms of end date and total distance travelled (Table 1, Fig. 3 D, H). For the northbound migration, colonies significantly differed in terms of start date, end date, duration, and total distance travelled (Table 1, Fig. 4 B, D, F, H), but not in terms of average wets per day (Table 1, Fig. 4 J). We found only two significant relationships explaining the variation in migration-level behavioural metrics. The first was a negative relationship between head length and total distance travelled during the southbound migration (Fig. 3 G), indicating that larger terns covered less distance in their migration to Antarctica. The second was a positive relationship between colony latitude and the end date of the northbound migration (Fig. 4 C), indicating that terns breeding at higher latitudes arrived later at their breeding grounds. While not statistically significant, we found similar positive relationships between colony latitude and both duration and distance travelled during the northbound migration (Fig. 4 E, G).

Potential drivers for daily-level movement and behavioural differences

At the daily-level, we found three significant relationships explaining variation in daily distance travelled. The first two were negative relationships between numbers of daily wets and daily distance travelled for both the southbound and northbound migration (Fig. 5 A, C), indicating that on days where terns spent more time with their legs immersed in salt water, they traveled less distance. The third was a negative relationship between colony latitude and daily distance on the northbound migration (Fig. 5 C), indicating that terns breeding farther north covered less distance daily. There were no significant relationships explaining variation in the daily number of wets (Fig. 5 B, D, Online Resource).

Individual variation

While we did not find any significant relationships between individual physical characteristics (head length or mass) and daily migratory behaviour (Fig. 5), the standard deviations of the individual random effects suggested substantial individual variation (Table 2). The standard deviations of the individual random effects for the two full models of daily number of wets were larger than the standard deviations of the colony random effects and the standard deviation associated with the residuals (Table 2). These results indicate that there was more unexplained variation among individuals than among colonies and that the variation between individuals accounted for a large part of the overall daily variation in daily wets. Such individual variation can be visualized through differences in movement and patterns in the wet readings (Fig. 6).

Such individual variation was exemplified by one individual (BF423 from Nasaruvaalik Island, NU) that exhibited a long period of “dry” travel (i.e., without immersing their leg in salt water) and had movement patterns that suggested it likely spent part of this time in eastern Brazil during its southbound migration (Fig. 7). This presumed period of time on, or near, land was supported by an absence of wet recordings across an 8-d span. When using the SST/land mask to estimate the locations, only two daily locations fell on land (Fig. 7 A, B). However, this SST/land mask assigns low probability to land locations and cannot account for higher water temperatures present in shallow and protected waters. When estimating the locations without using the SST/land mask, all eight daily locations associated with zero daily wet readings, and an additional 27 locations, fell on land (Fig. 7 C, D). The tag recorded wet readings only when it was immersed in salt water. However, the maximum conductivity data showed that 22 out of 43 readings during this eight-day period were completely dry. The remaining 21 readings were associated with fresh or brackish water suggesting that the tag may have been immersed in water from an estuary, lake, or river, or was in contact with rain. While this eight-day period comprised only 7% of all days with conductivity data (8 out 116 days), it contained 55% of all conductivity readings exactly equal to zero (i.e., completely dry). The southbound migration of this individual was estimated to be 120 days, the longest estimated southbound migration duration of all birds in our study (mean for all colonies: 86 ± 10 d; mean for Nasaruvaalik Island colony: 83 ± 11 d). Despite departing from the breeding colony at a similar date (August 24) as other Nasaruvaalik Island individuals (mean: August 22 ± 4 d), BF423 was the last individual to arrive at the non-breeding grounds by over one month (estimated arrival date of December 23 compared to mean of November 14 ± 13 d for Nasaruvaalik Island colony and November 10 ± 10 d for all colonies). With the exception of one additional individual (BF334), for which the raw conductivity data suggested that water may have infiltrated the tag, all the other individuals immersed their leg in salt water at least a few times each day.

Discussion

Collectively, our tracking of Arctic Terns from five colonies across North America confirms that terns generally take a relatively shorter, quicker northbound migration to arrive at colonies at different times, compared to a longer, slower, southbound migration which allows birds from most colonies to arrive in the Antarctic at approximately the same time. However, despite the thousands of kilometers and the tens of degrees of latitude separating colonies, southbound migration behaviour was generally similar across colonies, and northbound behaviour differed principally for the southernmost colony, while birds from the Arctic colonies exhibited similar migration metrics. In contrast, our results suggest a high level of individual variability in migratory behaviour, and that larger birds may use more direct southbound routes. Our study is the first to provide evidence suggesting that an individual Arctic Tern can spend an extended period around Brazil, with periods on land and in contact with fresh or brackish water, during migration.

Many bird species, including Arctic Terns, exhibit a slower southbound migration and a faster northbound migration (Egevang et al. 2010; Fijn et al. 2013; Nilsson et al. 2013; Schmaljohann 2018; Alerstam et al. 2019; Hromádková et al. 2020). Rapid northbound migrations and early arrival at breeding sites are generally attributed to competition for, and early selection of, nest sites at the beginning of the breeding season (Bêty et al. 2004; Smith and Moore 2005), and are linked to increased reproduction and chick survival (Smith and Moore 2005), which in turn has important carry-over fitness consequences for birds (Catry et al. 2013; Bogdanova et al. 2017). Arctic Terns prioritize favourable tailwind support over food availability during the northbound migration (Hromádková et al. 2020), suggesting benefits to early arrival at breeding sites. In contrast, slower southbound migration has been attributed to longer time spent at stopover sites, where they rest and refuel (Schmaljohann 2018). For Arctic Terns breeding in Svalbard, Norway, or Alaska, USA, food-rich stopover sites were also the primary driver of their routes during southbound migration (McKnight et al. 2013; Hromádková et al. 2020). Thus, the phenological differences in migration timing observed in this study further support that migration strategies for many birds are seasonally-specific and likely driven by spatiotemporal patterns in ocean productivity during their southbound journey, and a need to arrive quickly at their breeding grounds during their northbound journey.

While the movement patterns we observed indicate that terns may be foraging and resting more during the southbound migration compared to northbound migration, terns appeared to spend less of their day landing on the ocean or plunge diving during the southbound migration. One interpretation of these results could be that terns undertook a more indirect southbound route, including spending time at important foraging sites (Davies et al. 2021; Wong et al. 2021), but that they spent more time flying in search of food and/or foraging in flight (e.g., via contact dipping, Holbech et al. 2018), thus foraging without immersing their legs in the ocean. Using such foraging behaviours would cause wet readings to underestimate the time birds spend foraging (McKnight et al. 2013). Further exploring terns' foraging behaviour during migration, including the importance of contact dipping, would require either direct visual observations, or higher quality and resolution movement data such as those collected by GPS and multi-sensor tags (e.g., Liechti et al. 2018; Corbeau et al. 2020).

While the estimated start date of the southbound and northbound migrations differed significantly between colonies, surprisingly there were no significant relationships between the estimated start date and colony latitude, suggesting that other factors may have been more important in driving the start of migration. For southbound migration, the timing of departure from colonies may be more flexible than the timing of arrival at key feeding (refueling) areas to match peak food availability (Egevang et al. 2010; Davies et al. 2021). The estimated end date of the southbound migration did not differ among colonies, suggesting that all birds may be targeting arrival in Antarctica around November, just when the austral summer and broad scale increases in marine productivity begin (Smith Jr et al. 2000; Ducklow et al. 2001; Park et al. 2017). Due to the limitations of light-based geolocation during polar summers, the start of the southbound migration and the end of the northbound migration were truncated for many individuals, and our correction provided coarse estimates of these dates (Online Resource). As such, further studies may be required to disentangle finer patterns in migration phenology. Such studies would be facilitated by the use of more accurate positioning technologies, including the use of newly-developed small and long-lasting GPS units (see Seward et al. 2021 and Morten et al. 2022 for GPS data recorded from Arctic Terns during the breeding period).

The duration, distance travelled, and end date of the northbound migration differed significantly among colonies. These three metrics were all positively related to colony latitude, although only the relationship with end date was significant. In addition, at the daily-level, colony latitude had a negative effect on daily distances covered during the northbound migration, suggesting that arrival at breeding colonies may be driven by local conditions, rather than by the distance to colonies. Overall, birds breeding in Country Island, NS, travelled farther each day and arrived at their colony at least two weeks earlier than all of the Arctic colonies. We expected these later arrival dates at Arctic colonies, given that snow melts at nesting sites, and sea-ice breakups in adjacent foraging areas, occurs in early to mid June (e.g., Levermann and Tøttrup

2007; Smith et al. 2010; Egevang and Frederiksen 2011; Mallory et al. 2017). Arctic-breeding birds have a small window of time in which to breed (e.g., Mallory and Forbes 2007; Moe et al. 2009; Sauve et al. 2019). In years when melt is very late, thereby leaving nesting areas snow-covered, foraging areas ice-covered, and nesting islands accessible to land predators by ice, terns often skip breeding (Levermann and Tøttrup 2007; Egevang and Frederiksen 2011; Mallory, unpubl. data). Despite these challenges, terns likely nest at high latitudes due to benefits such as fewer competitors for nest sites and food supplies, reduced predation pressure (McKinnon et al. 2010; Hatch et al. 2020), and predictable, abundant food resources near many of the nesting colonies (e.g., polynyas; Maftei et al. 2015; Pratte et al. 2017; Baak et al. 2020).

We found that larger birds travelled less total distance during southbound migration than smaller birds. However, there was no such relationship between body size and daily distance travelled. These results, as well as the (non-significant) negative relationship between head size and migration duration, suggest that larger terns used more direct southbound migration routes than smaller ones. Because male Arctic Terns tend to be larger than females, and head size can be used to differentiate between sexes (Devlin et al. 2004; Baak et al. 2020), this relationship may indicate sex differences in migration strategy during the southbound migration. Many seabird species demonstrate sex differences in foraging and migration behaviours (Phillips et al. 2017). Various factors could result in sexual differences in the southbound migration behaviour of Arctic Terns, one of which could be associated to the known sexual difference in energy stores during the breeding season (Baak et al. 2020).

Individual variation in migration can be observed through differences in movements, space use, and feeding behaviour of many seabird species (Phillips et al. 2017). However, evidence for this has not been well-documented in Arctic Terns, in part because overall migration routes are similar for individuals from the same colony (Phillips et al. 2017; Wong et al. 2021), and until recently, tags that could capture these fine-scale behavioural differences were too large to be carried by Arctic Terns over long time periods. Nonetheless, for southbound and northbound migrations, our analyses suggest substantial individual variation in migration behaviour. The strong fitness benefits that may be conferred through different migration strategies (Bêty et al. 2004; Smith and Moore 2005), and the vast ocean areas spanned by these pelagic seabirds provide high potential for individual variation in migratory behaviour. Further understanding this variation will provide us important insights into the spatiotemporal plasticity of Arctic Tern migration patterns, which can in turn help us better predict the resilience of Arctic Terns to environmental changes such as ocean warming and reduced sea-ice cover (Comiso et al. 2008; Saba et al. 2015).

Our study suggest that an individual Arctic Tern could have spent an extended period on land during its migration (Fig. 7). Previous studies have shown that Arctic Terns make short overland flights during their migration (Duffy et al. 2013; Redfern and Bevan 2020). Redfern and Bevan (2020) showed that the majority of the tagged Arctic Terns breeding on the North Sea coast of the United Kingdom arrived and left their colony using an overland passage rather than through coastal routes, and reported associated inland sightings of Arctic Terns. Duffy et al. (2013) showed that five Arctic Terns migrating from Alaska likely crossed the Andes to reach the Atlantic Ocean off the coast of Argentina. These overland passages over the Andes lasted only 14.3-35.5h. In contrast, individual BF423 in this paper appears to have spent eight days on land, with potential trips to fresh/brackish water. In addition, this individual appears to have spent two months using the waters around Brazil. While their occurrence is rare, Arctic Terns have been sighted in Brazil across most months of the year and a broad latitudinal range, and include sightings far inland and on beaches (Olmos 2002; Dias et al. 2012). The prolonged stopover the individual in this paper made around Brazil appears to have delayed its arrival in Antarctica by over a month.

Overall, migration appears to be driven mainly by the goal of arriving when the conditions are favourable at both poles, the timing of which will continue to be influenced by climate change. Despite sharing this common goal, our analyses suggest individuals and colonies exhibit considerable variation in migratory behaviour. This large variation suggests that there is phenotypic plasticity in migratory behaviour of the world’s longest migrating organism. The question that now arises is whether this plasticity provides the resilience needed for Arctic Terns to adapt to environmental changes brought on by a warming climate.

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Table 1 ANOVA results for the assessment of whether the five colonies of Arctic Terns (*Sterna paradisaea*) significantly differed in the five migration-level behavioural metrics. See Table A2 for the equivalent results using the Kruskal-Wallis test.

Behavioural metric	*Southbound*		*Northbound*	
	F	*p*	*F*	*p*
Start date	27.24	< 0.0001	12.82	< 0.0001
End date	0.97*	0.4335	69.41	< 0.0001
Duration	2.94*	0.0298	19.54*	< 0.0001
Total distance	2.04	0.1042	13.96	< 0.0001
Average wets per day	4.43**	0.0040	1.40	0.2498

* Patterns in the residuals indicate slight deviation from Normality.

** Levene's test indicates that there may be heteroscedasticity.

Table 2 The standard deviations of the random effects and error of the full models for daily movement and behavioural metrics of Arctic Terns (*Sterna paradisaea*). The random effects for all models were defined as an individual random effect nested with a colony random effect.

Response	Covariates	*Southbound*			*Northbound*		
		Colony	ID	Residual	Colony	ID	Residual
Daily distance	Colony latitude, Daily wets, Head length, Mass	< 0.01	< 0.01	0.56	< 0.01	< 0.01	0.63
Daily wets	Colony latitude, Head length, Mass	1.17	123.26	13.83	0.13	151.59	26.82

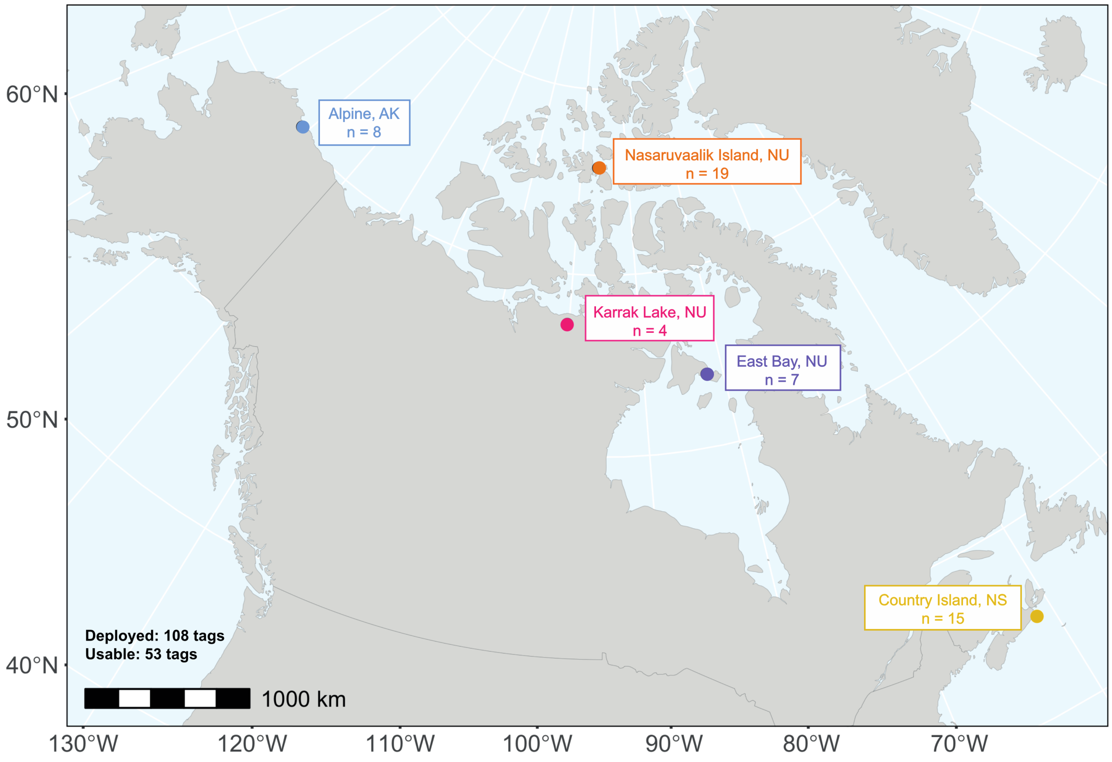

Fig. 1 Locations of the five Arctic Tern (*Sterna paradisaea*) breeding colonies where usable tags were deployed and retrieved, showing the number of tags with usable light data at each colony. Colony coordinates: Alpine, Alaska, USA (70.35°N, 151.03°W), Country Island, Nova Scotia, Canada (45.06°N, 61.32°W), East Bay, Nunavut, Canada (64.01°N, 82.07°W), Karrak Lake, Nunavut, Canada (67.25°N, 100.25°W), and Nasaruvaalik Island, Nunavut, Canada (75.83°N, 96.30°W).

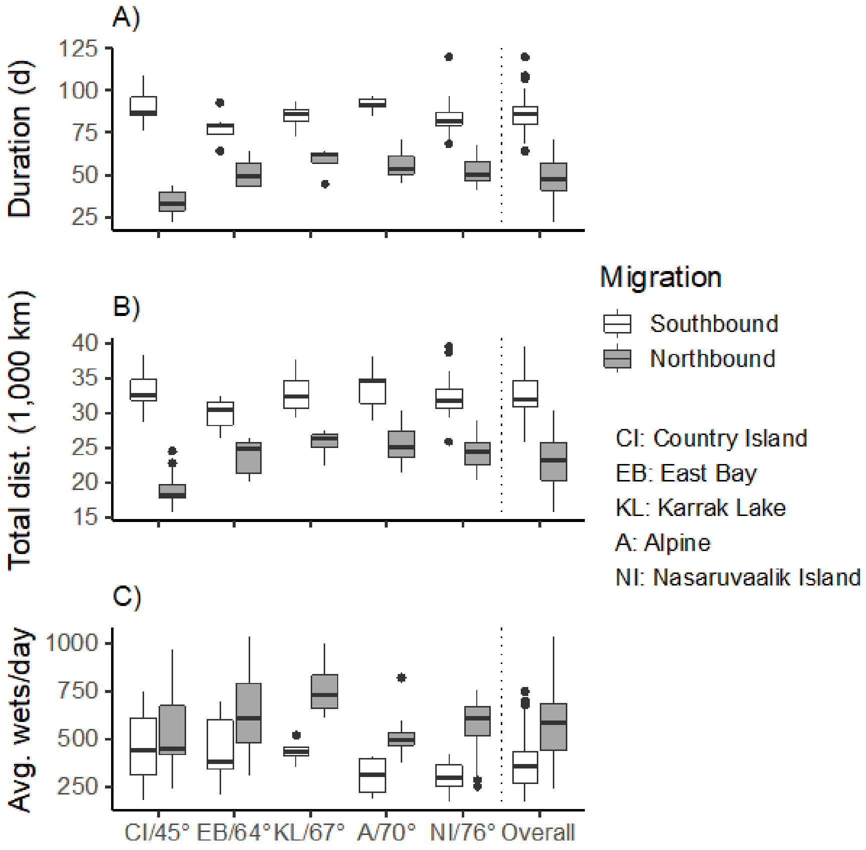

Fig. 2 Differences between the southbound and northbound migrations in terms of duration, total distance travelled (sum of path segments), and average number of times the tag recorded contact with salt water per day. The boxplots display the results from 53 individual Arctic Terns (*Sterna paradisaea*) tracked from five North American breeding colonies (CI = Country Island, NS, 45°N, *n* = 15; EB = East Bay, NU, 64°N, *n* = 7; KL = Karrak Lake, NU 67°N, *n* = 4; A = Alpine, AK, 70°N, *n* = 8; NI = Nasaruvaalik Island, NU, 76°N, *n* = 19), as well as the overall results for all colonies. Center lines of the boxplots represent the median, and the boxes themselves represent the interquartile range (IQR). Whiskers extend to 1.5 times the IQR, and the black points beyond these whiskers are the outliers.

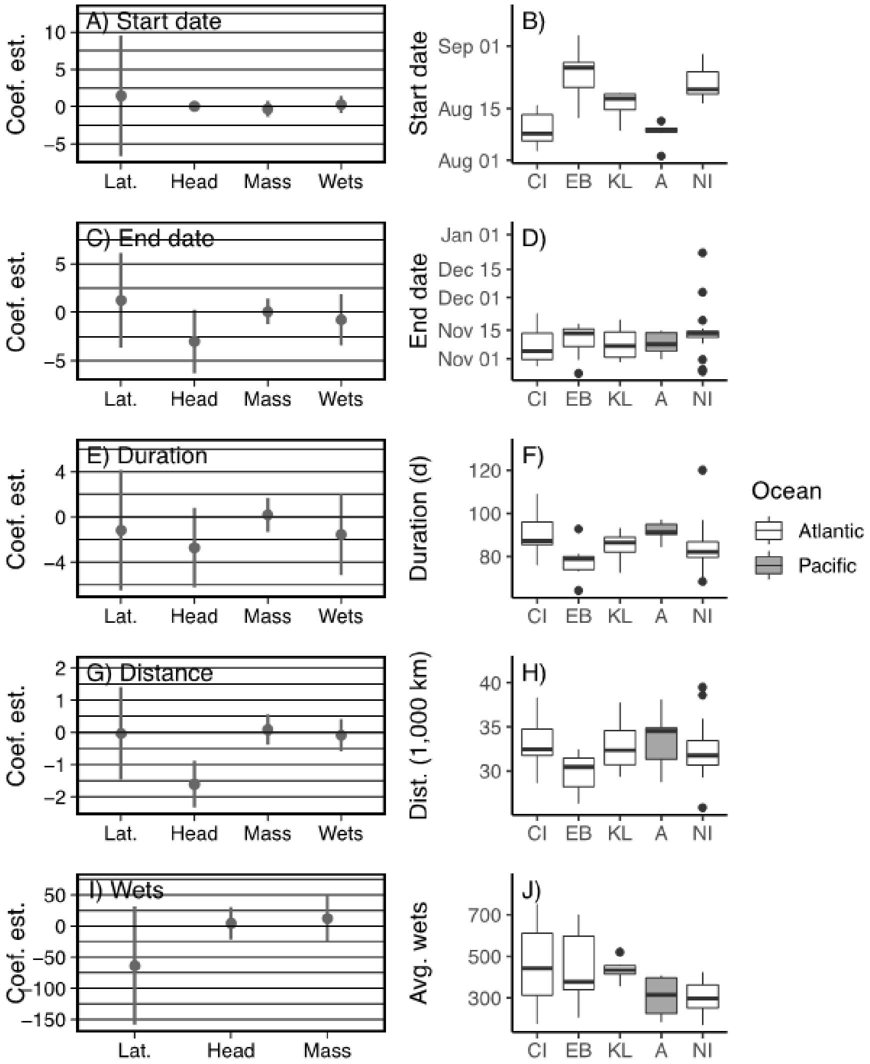

Fig. 3 Variation in the southbound migration-level behavioural metrics (A-B start date, C-D end date, E-F duration, G-H total distance travelled (sum of path segments), and I-J average number of wet readings per day) and relationship with the factors that may affect them (Lat. = colony latitude, Head = head length, Mass, and Wets = average number of wet readings per day). Panels A, C, E, G, and I, represent the model-averaged coefficient estimates and their confidence intervals. Panels B, D, F, H, and J represent the variation in the behavioural metrics for tracked Arctic Terns (*Sterna paradisaea*) across their different breeding colonies, ordered by colony latitude (CI = Country Island, NS, 45°N; EB = East Bay, NU, 64°N; KL = Karrak Lake, NU, 67°N; A = Alpine, AK, 70°N; NI = Nasaruvaalik Island, NU, 76°N).

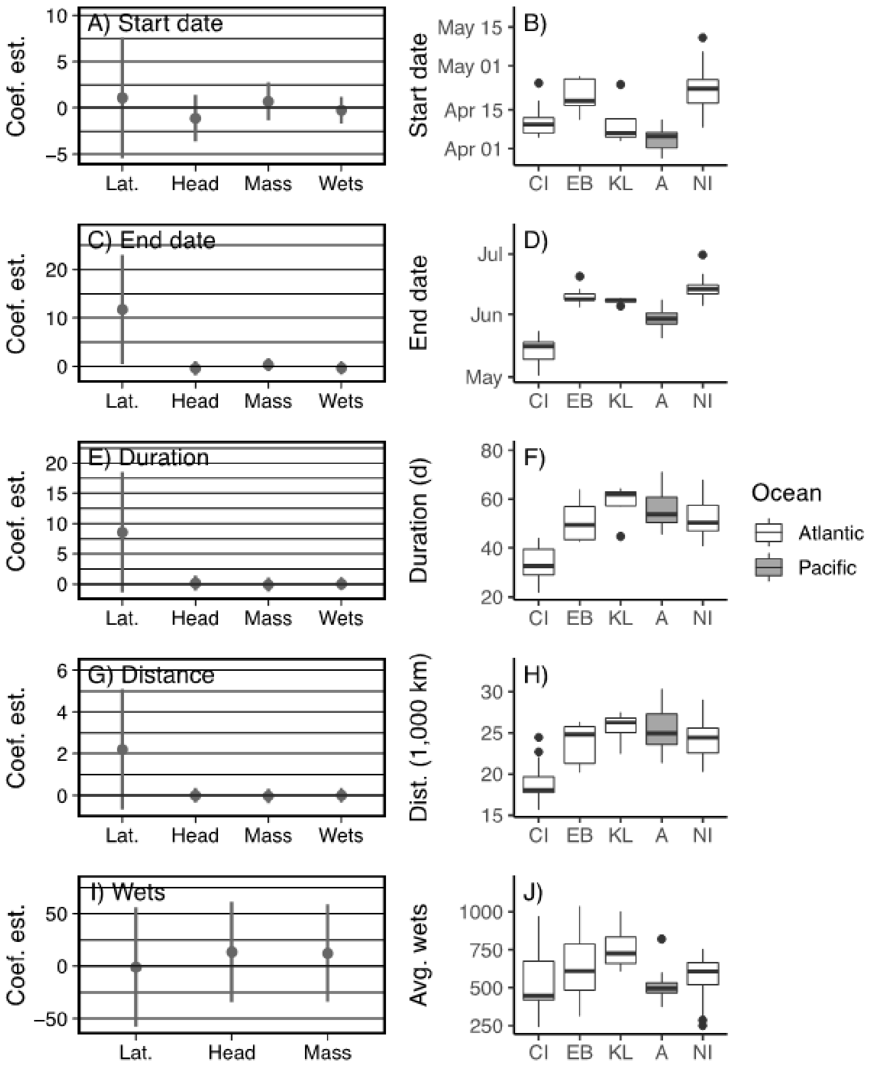

Fig. 4 Variation in the northbound migration-level behavioural metrics (A-B start date, C-D end date, E-F duration, G-H distance, and I-J average number of wet readings per day) and relationship with the factors that may affect them (Lat. = colony latitude, Head = head length Mass, and Wets = average number of wet readings per day). Panels A, C, E, G, and I, represent the model-averaged coefficient estimates and their 95% confidence intervals. Panels B, D, F, H, and J represent the variation in the behavioural metrics for tracked Arctic Terns (*Sterna paradisaea*) across their different breeding colonies, ordered by colony latitude (CI = Country Island, NS, 45°N; EB = East Bay, NU, 64°N; KL = Karrak Lake, NU, 67°N; A = Alpine, AK, 70°N; NI = Nasaruvaalik Island, NU, 76°N).

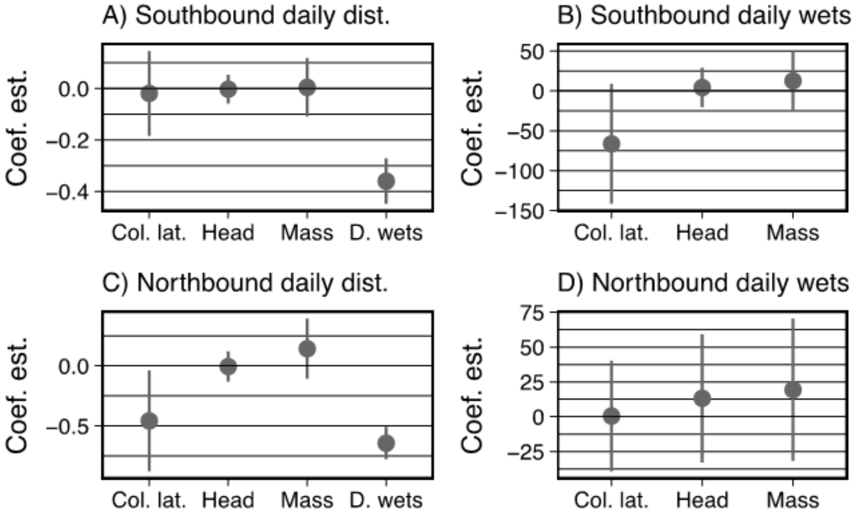

Fig. 5 Relationships (coefficients and 95% confidence intervals) between daily-level behavioural metrics measured for Arctic Terns (*Sterna paradisaea*) and the factors that may affect them (Col. lat. = colony latitude, D. wets = daily wets, Head = head size, Mass).

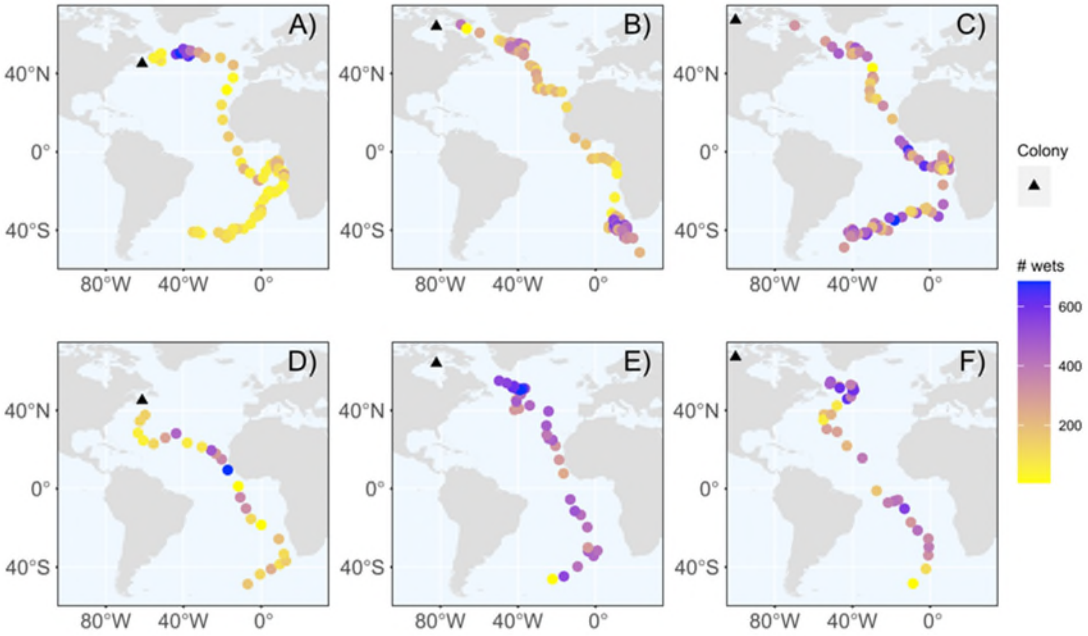

Fig. 6 Southbound (A-C) and northbound (D-F) migration of three Arctic Terns (*Sterna paradisaea*) demonstrating individual differences in migration behaviour. BF426 from Country Island, NS (A, D), BF369 from East Bay, NU (B, E), and BF432 from Karrak Lake, NU (C, F). The colour scale represents the number of wet readings per day. Each triangle represents the breeding colony of the individual.

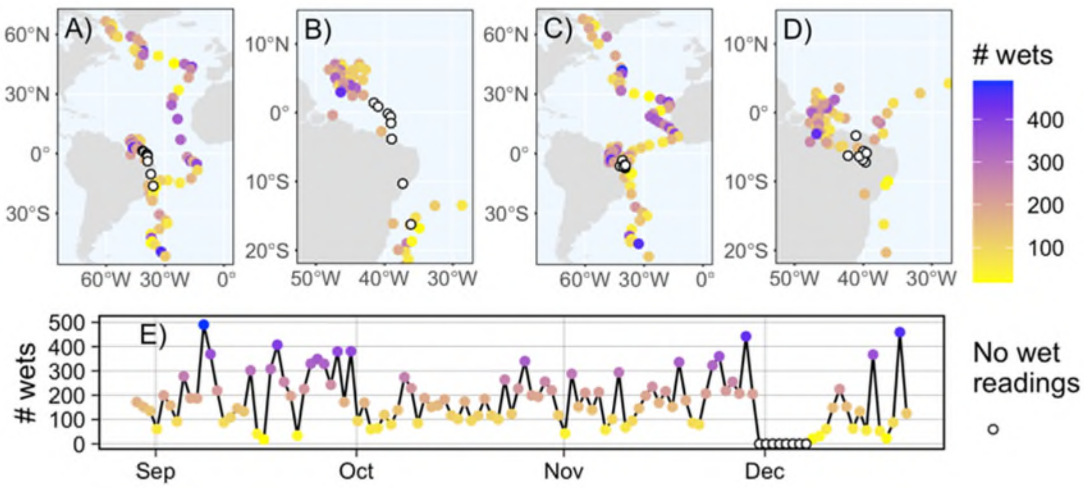

Fig. 7 Southbound migration of BF423, an individual Arctic Tern (*Sterna paradisaea*) that spent extended time around Brazil. Panels A-B represent the movement track estimated using the SST/land mask, while panels C-D represent the movement track estimated without the SST/land mask. Panels A and C show the complete track, while panels B and D focus on the area around Brazil where there were multiple days without immersions in salt water. Panel E shows the time series of wet readings of this individual. The colour scale represents the number of wet readings per day, specifically the number of wet readings in salt water. The black and white points highlight the days without any readings in salt water.