



FEATURE ARTICLE

Seasonally specific responses to wind patterns and ocean productivity facilitate the longest animal migration on Earth

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ABSTRACT: Migratory strategies of animals are broadly defined by species' eco-evolutionary dynamics, while behavioural plasticity according to the immediate environmental conditions en route is crucial for energy efficiency and survival. The Arctic tern *Sterna paradisaea* is known for its remarkable migration capacity, as it performs the longest migration known by any animal. Yet, little is known about the ecology of this record-breaking journey. Here, we tested how individual migration strategies of Arctic terns are adapted to wind conditions and fuelling opportunities along the way. To this end, we deployed geolocators on adult birds at their breeding sites in Svalbard, Norway. Our results confirm fundamental predictions of optimal migration theory: Arctic terns tailor their migration routes to profit from (1) tailwind support during the movement phase and (2) food-rich ocean areas during the stopover phase. We also found evidence for seasonally distinct migration strategies: terns prioritize fuelling in areas of high ocean productivity during the southbound autumn migration and rapid movement relying on strong tailwind support during the northbound spring migration. Travel speed in spring was 1.5 times higher compared to autumn, corresponding to an increase in experienced wind support. Furthermore, with their pole-to-pole migration, Arctic terns experience approximately 80% of all annual daylight on Earth (the most by any animal), easing their strictly diurnal foraging behaviour. However, our results indicate that during migration daylight duration is not a limiting factor. These findings provide strong evidence for the importance of interaction between migrants and the environment in facilitating the longest animal migration on Earth.



Geolocator tagged Arctic tern *Sterna paradisaea* at a breeding site in Svalbard, Norway.

Photo: Martins Briedis

KEY WORDS: Arctic tern · *Sterna paradisaea* · Daylength · Geolocator · Global wind systems · Long-distance migration · Migration phenology · Migration strategy · Ocean productivity

1. INTRODUCTION

Bird migration usually comprises an interchange of an active flying phase, when energy is consumed, and a stationary stopover phase, when fuel is restored by food intake (Alerstam & Lindström 1990, Hedenström & Alerstam 1998). This is especially true

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for flapping migrants (e.g. waders and songbirds) that fuel their flight by burning energy, as opposed to soaring migrants (e.g. raptors and albatrosses) that often take advantage of thermals or topography-induced air uplifts, to cover large distances with minimal energy expenditure. For flapping flyers, this means that, while on migration, extended time needs to be spent at stopover sites refuelling and storing energy reserves to power the upcoming flight bouts (Hedenström & Ålerstam 1997). Because the rate of energy expenditure during the flight phase is usually much higher than the rate of fuel deposition on stopovers, visiting high-quality stopover areas en route is of high importance for efficient and successful migration (Ålerstam 2011). One of the main ways to reduce the expenditure of stored energy during flapping flight is to exploit prevailing wind regimes and adjust migration routes to take a full advantage of wind assistance for covering large distances rapidly (Kranstauber et al. 2015). Thus, maximizing fuelling rates on stopovers and minimizing energy expenditure during the flight bouts are the 2 key aspects of migration energetics for species that use powered flight for their migration (Ålerstam 2003).

The overall migration duration of birds is largely dependent on fuelling rates (Lindström 2003), while tailwind support can significantly facilitate faster travelling during the movement phase (Green 2004). Daylength regime (day:night ratio) has also been suggested to have considerable effect on the total migration duration of diurnally foraging species because of limited daylight hours available for fuelling (Bauchinger & Klaassen 2005). As the season progresses and migrants move across latitudes, they experience changes in the daylength regime, which can slow down or speed up their migration depending on the time of the year, latitude and species' activity cycle (nocturnal vs. diurnal migrants and nocturnal vs. diurnal foragers). For most species, migration should be shorter (and faster) when daylength is longer and there is more time for fuelling (Kvist & Lindström 2000, Bauchinger & Klaassen 2005).

All these aspects should be especially important for trans-equatorial migrants that cover long distances between their breeding and non-breeding areas. On the extreme range of the migration distance spectrum is the Arctic tern *Sterna paradisaea* that annually migrates over 50 000 km between the breeding areas in the Arctic and the non-breeding areas in Antarctica (Storr 1958, Egevang et al. 2010). Despite a recent surge in tracking studies on Arctic terns (Egevang et al. 2010, Fijn et al. 2013, McKnight et al. 2013, Volkov et al. 2017, Ålerstam et al. 2019), significant gaps remain

in our understanding about the ecology of this record-breaking migration. To travel such vast distances across all climatic zones, exploitation of environmental settings for efficient travel may be crucial, as the seemingly favourable shortest route may not be optimal. By arching migration corridors according to the tailwind support and further fine-tuning the routes to pass through areas of high ocean productivity, migrants can sustain the energy-demanding flight phase by stopping over and refuelling at sites where food resources are abundant. Furthermore, while residing at the breeding and non-breeding sites, Arctic terns are exposed to 24 h daylight, enabling flexible interchange between foraging and resting time. In contrast, during migration terns are exposed to shifts between day and night as they pass through intermediate latitudes. Because Arctic terns are strictly diurnal foragers (McKnight et al. 2013), feeding and refuelling during migration are limited to the available daylight hours. This may force terns to feed during the day and travel at night if rapid and short-duration migration is advantageous.

In this study, we used geolocator tracking to, first, describe migration patterns and non-breeding areas of the Arctic terns breeding in the high Arctic (Svalbard, Norway) at the northern limits of the species' distribution range (BirdLife International 2018). Second, we tested how individual migration routes and stopover sites are adapted to take advantage of wind support and food availability en route. We hypothesized that the longest animal migration on Earth is facilitated by wind assistance during the flight phase and abundance of food resources during the refuelling stopover phase, which is further eased by extended daylength hours throughout the journey. Hence, we predicted that (1) the chosen migration routes of the tracked Arctic terns will be adapted so that the birds benefit from tailwind support during both southbound and northbound migrations; (2) the stopover sites of the terns will be located in areas of higher ocean productivity compared to passage areas (McKnight et al. 2013); (3) the terns will time their migration to cross the Equator near the equinoxes, enabling longer foraging hours in both hemispheres (Ålerstam 2003).

2. MATERIALS AND METHODS

2.1. Field work

Our study site was located in Longyearbyen on the island of Spitsbergen, Svalbard archipelago (78° 14' N, 15° 39' E). We captured 30 breeding indi-

viduals during late stages of egg incubation between 8 and 14 July 2017, using tent spring traps placed on their nests. All captured birds were marked with unique colour ring combinations and equipped with multi-sensor archival data loggers (geolocators; model Intigeo-W65A9-SEA, Migrate Technology) that were fixed to the colour rings. Geolocators were set to sample ambient light intensity every minute and store maximal values at 5 min intervals. Temperature was sampled every 5 min, storing maximal and minimal values at 4 h intervals; immersion and conductivity measures were sampled every 30 s, storing the sum of samples scored as wet and maximal conductivity every 4 h.

The geolocators including colour rings weighed 1.06 ± 0.05 g (SD), which never exceeded 1.2 % of the body mass of the tagged birds (106.2 ± 7.6 g, $n = 30$). Sex of all tagged individuals was determined molecularly using a droplet of blood taken from the brachial vein (Griffiths et al. 1998, Fridolfsson & Ellegren 1999, Ležalová-Piálková 2011), as the accuracy of sexing Arctic terns in the field is typically lower than 74 % (Fletcher & Hamer 2003, Devlin et al. 2004).

In the following season between 27 June and 12 July 2018, we managed to recapture 16 birds with geolocators (53 %) at the same breeding colony. At least 7 more of the previously tagged birds were sighted in the breeding colony (total return rate = 77 %), but we failed to recapture them. This was mainly due to high predation rate of the nests in this season by Arctic fox *Vulpes lagopus* leading to frequent relocation or disappearance of the individuals whose nests were depredated.

Body mass of the tagged individuals was higher upon recapture and removal of the geolocators compared to the time of deployment a year earlier (2017: 104.6 ± 8 g [$n = 16$], mean capture date = 10 July; 2018: 110.9 ± 7.6 g, mean capture date = 4 July; paired t -test: $t_{14} = -2.691$, $p = 0.018$; data met the assumption of normality and homogeneity of variances based on a Shapiro-Wilk normality test and an F -test, respectively). Thus, geolocators apparently did not have a negative effect on the body condition of the tagged individuals (Brlík et al. 2020).

2.2. Data analyses

2.2.1. Geolocator tracking

All data analyses were done in R version 3.5.1 (R Core Team 2018). To calculate the geographic positions of the terns, we first log-transformed light inten-

sity recordings from the retrieved geolocators to derive sunrise and sunset times (twilight events) using the 'preprocessLight' function in the R-package 'TwGeos'. Further, we used the R-package 'FLightR' to estimate geographic locations of the tracked individuals (Rakhimberdiev et al. 2017). During both breeding and non-breeding periods, tracked Arctic terns were exposed to 24 h daylight, thus making it problematic to use these stationary periods for calibrating the light data. Sunsets and sunrises were recorded only during migration periods and during an approximately 2 mo long period before the spring migration when the birds were at an unknown location at the non-breeding sites. Within the latter period, we identified extended periods when birds were stationary before the spring migration by visually inspecting recorded sunrise and sunset times. We then used the 'find.stationary.location' function to estimate the geographic location of this unknown site and used it for calibration.

Further, we followed standard analysis procedures in 'FLightR' as outlined by Lisovski et al. (2020). 'FLightR' uses a template fit method to compute a spatial likelihood surface for each twilight event. A posterior distribution of the likeliest migration path and its credible intervals are then derived via particle filtering. Because the conductivity (salinity) recording on all of our geolocators indicated that whenever geolocators were immersed, birds were in saltwater, we set 0 probability for birds occurring in areas that were further than 50 km away from the shoreline. For 1 track (BH004, see Fig. S1e in the Supplement at www.int-res.com/articles/suppl/m638p001_supp.pdf), the imposed spatial mask led to a failure of the particle filter; therefore, the analyses for this geolocator were run without a spatial mask. Finally, we used the 'stationary.migration.summary' function to determine stationary periods that were longer than 6 twilight events (3 d) and arrival/departure dates from them. For this, we defined 20 % as the minimum probability of movement.

Using high-frequency data, McKnight et al. (2013) showed that Arctic terns typically do not rest on water, as only a small fraction of time (0.5 ± 0.22 h d⁻¹ at most in August) is spent floating. Thus, immersion recordings should approximately reflect the daily rate of feeding dives. Based on this, we used the cumulative daily count of the number of times the geolocator was immersed in water as a proxy for estimating the feeding rate across the annual cycle.

We used ANOVA to test if there were differences in migration parameters (migration timing, speed, distance, feeding rate, etc.) between males and females.

We used Bartlett's test of homogeneity of variances and a Shapiro-Wilk normality test to test homogeneity of variance and assumption of normality, respectively. In 3 migration parameters (onset of spring migration, migration distance in autumn and migration speed in autumn), homogeneity of variances and assumption of normality were not met, and in 1 migration parameter (total migration distance), only the assumption of normality was not met. Thus, we filtered outlying values from these 4 migration parameters. After excluding outlying values, total migration distance and migration speed in autumn met both assumptions. For onset of spring migration and migration distance in autumn, we used the nonparametric Wilcoxon rank sum test. Since no differences were found in any of the tested migration parameters, we pooled data of both sexes for all further analyses. Travel speed (km d^{-1}) is defined here as the total distance travelled divided by the total number of days spent on migration in each migration season.

2.2.2. Ocean productivity

We used ocean productivity data to compare if stopover sites of terns were located in areas with potentially higher food resource abundance as compared to passage areas (migration corridors). We defined polygons for stationary sites in a radius of 2° around the median location of the stationary sites earlier established by the 'stationary.migration.summary' function. Migration corridors were defined as lines connecting twice-daily positions within the migration periods with 1° wide buffer around them and excluding stationary sites.

We downloaded gridded (0.167° grid) weekly ocean productivity data from the Ocean Productivity website of the Oregon State University (www.science.oregonstate.edu/ocean.productivity/; Behrenfeld & Falkowski 1997) and extracted productivity values for all grid cells within the defined stationary areas and migration corridors corresponding to the specific weeks. Grid cells that did not contain productivity data were omitted from the analyses. Because ocean productivity data were positively skewed, we transformed the values using the natural logarithm.

2.2.3. Wind support

To evaluate the role of wind assistance in facilitating the migration, we obtained wind data from the

European Centre for Midrange Weather Forecast (ECMWF; <https://www.ecmwf.int/>). Wind data were averaged across the full migration period of the tracked terns (autumn 2017: 24 Aug–27 Nov, spring 2018: 31 Mar–6 Jun) for each $4 \times 4^\circ$ grid across the area between 85°N – 85°S and 80°W – 35°E . Because Arctic terns typically migrate at low altitudes near the water surface (Gudmundsson et al. 1992, Hedenström & Åkesson 2016) we used wind measurements at the surface level. We then used the 'NCEP.Air-speed' function from the R-package 'RNCEP' (Kemp et al. 2012) to calculate wind support for each movement segment (twice-daily positions and movement direction between them) along the migration routes of the tracked individuals.

2.2.4. Daylength

We used the light recording data from the geolocators to estimate the total amount of daylight hours experienced by individual terns throughout the annual cycle. Further, we calculated daylight duration at various latitudes across the year using the R-package 'suncalc' (Thieurmél & Elmarhraoui 2019). Daylight duration was calculated as the time between civil dawn and civil dusk when the geometric centre of the Sun is 6° below the horizon, which approximately matches light recording sensitivity of the geolocators' light sensor.

3. RESULTS

3.1. Migration and non-breeding areas

Terns departed their breeding site in Svalbard in late August–early September (Box 1) and migrated to a stopover area in the north Atlantic. Further, 9 individuals followed the west coast of Africa with later stopovers in the southeast Atlantic, while 7 individuals followed the east coast of South America with stopover sites in the southwest Atlantic (Fig. 1a). Interestingly, 2 individuals (BH011 and BH024, both females) made a loop at the beginning of the southbound migration and returned to Svalbard in early October before continuing their southward movement into tropical latitudes (Fig. S1i,p). Migration parameters are summarized in Box 1.

At the end of the southbound migration, all tracked individuals crossed the Antarctic Circle, entering the 24 h daylight zone; thus, location data from late November until early to mid-February are not avail-

Box 1. Summary data (mean and range) of key migration and non-breeding period parameters of 16 geolocator-tracked Arctic terns from a breeding colony in Longyearbyen, Svalbard

Autumn migration	
Start date	3 Sep (24 Aug–11 Sep)
Crossing Equator	4 Oct (23 Sep–22 Oct)
End date	19 Nov (5–27 Nov)
Total migration duration (d)	78 (68–93)
Migration distance (km)	22900 (19500–34800)
Travel speed (km d ⁻¹)	294 (258–420)
Non-breeding period	
Wintering latitude	South of 63° S
Wintering longitude	55° W–94° E
No. days at non-breeding site	137 (127–153)
Movement distance (km)	10812 (5279–19480)
Spring migration	
Start date	5 Apr (31 Mar–16 Apr)
Crossing Equator	26 Apr (17 Apr–11 May)
End date	30 May (23 May–6 Jun)
Total migration duration (d)	54 (39–64)
Migration distance (km)	24800 (19600–29700)
Travel speed (km d ⁻¹)	435 (334–518)
Total track length (km)	58500 (50200–78500)
Total daylight hours	6985 (6750–7232)

able. Between February and April, non-breeding sites of all but 1 bird were located in the Weddell Sea (Box 1, Fig. 2). The outlier individual travelled to the Indian Ocean, residing at ca. 100° E longitude.

Another individual crossed the Drake Passage between Antarctica and South America in late March, thus entering the Pacific Ocean before commencing the northbound migration. Overall, the terns were highly mobile during the non-breeding period covering several thousand km and residing at multiple sites during their 4–5 mo long non-breeding period in Antarctica (Box 1). Throughout the non-breeding period, all birds were exposed daily to sub-zero temperatures (Figs. S1 & S2).

Terns started the northbound migration in early April (Box 1), following an S-shaped migration pattern through the Atlantic (Fig. 1b). Longer stopover periods were scarce until the end of the migration period, when the birds arrived in the northern Atlantic residing at the same stopover region as at the beginning of the southbound migration. During this stopover period, the terns increased their feeding rate more than 2-fold (as implied by the number of times the birds were recorded being in water) as compared to the rest of the annual cycle (Fig. 3). Travel speed for all individuals was higher during the northbound migration compared to the southbound migration (paired t -test: $t_{15} = -9.56$, $p < 0.001$; Box 1), and birds arrived back at the breeding colony in late May–early June, having completed an average round trip migration distance of 58 500 km (range: 50 200–78 500 km; Box 1).

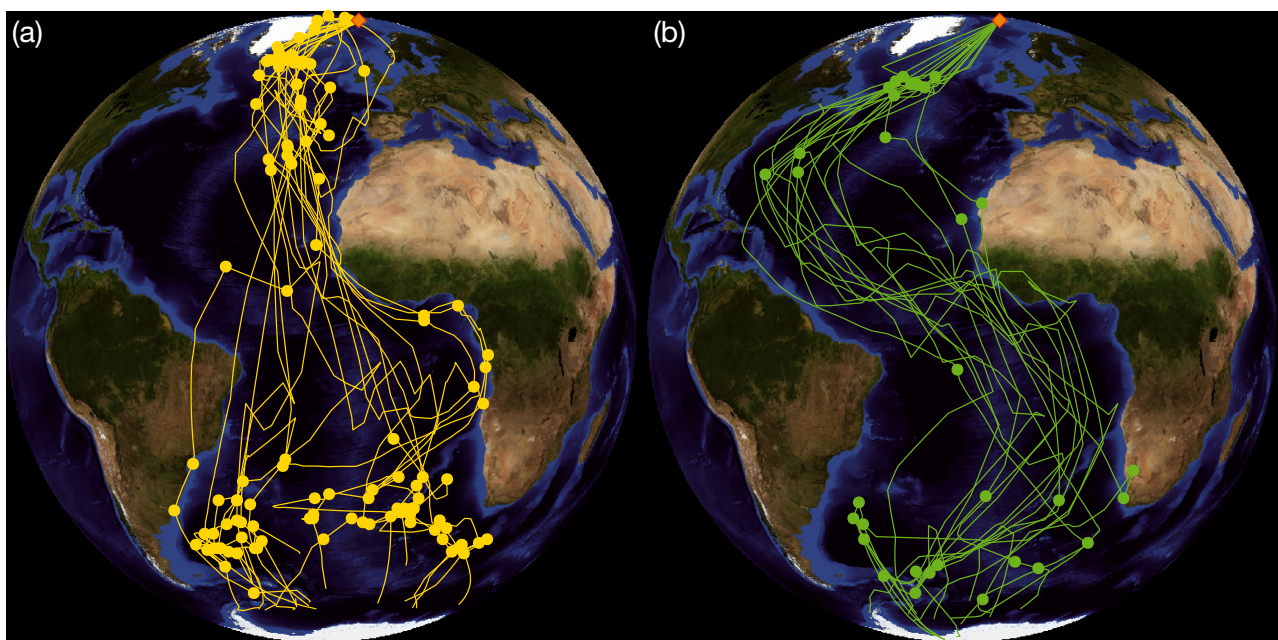


Fig. 1. Migration routes and stopover areas of 16 geolocator-tracked Arctic terns during (a) southbound and (b) northbound migration. Breeding site in Longyearbyen, Svalbard, is marked with an orange diamond, stopover sites longer than 3 d are marked with dots. Background map source: Blue Marble Next Generation, <https://visibleearth.nasa.gov/collection/1484/blue-marble>

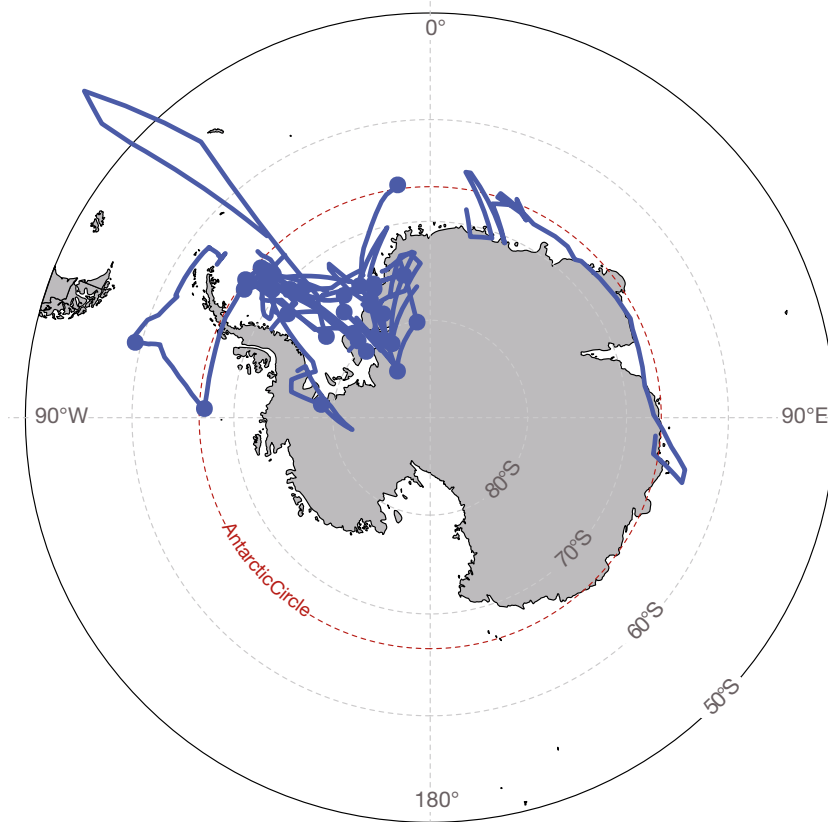


Fig. 2. Non-breeding areas (February–April) of 16 geolocator-tracked Arctic terns. Stationary sites where birds remained for at least 7 d are marked with dots; lines show movements within the non-breeding areas. Location data from late November (after the southbound migration) until early-mid February are not available due to 24 h daylight as all birds resided south of the Antarctic Circle

3.2. Migration routes and wind support

In both seasons, terns on average benefited from tailwind support along their chosen migration routes (Figs 4 & 5). During the southbound migration, terns on average experienced $0.4 \pm 0.6 \text{ m s}^{-1}$ (SD) tailwind support, while during the northbound migration the experienced tailwind support was substantially stronger, averaging $2.2 \pm 1.2 \text{ m s}^{-1}$ (paired t -test: $t_{15} = -5.34$, $p < 0.001$; Fig. 5). Testing for the wind support on reversed migration routes (travelling along the spring routes in autumn and autumn routes in spring) revealed that terns would experience significantly more headwinds in both migration seasons (southbound migration: $-2.1 \pm 0.8 \text{ m s}^{-1}$, paired t -test: $t_{15} = 8.36$, $p < 0.001$; northbound migration: $-0.2 \pm 0.7 \text{ m s}^{-1}$, paired t -test: $t_{15} = 6.81$, $p < 0.001$; Fig. 5).

After excluding the 2 outlying individuals that made a loop at the beginning of the autumn migration and had exceptionally high travel speeds, there was no relationship between wind support and individual southbound travel speed ($\beta = -0.72 \pm 7.38$, $F_{1,12} < 0.01$, $r^2 = 0.01$, $p = 0.924$), while there was a positive relationship between the experi-

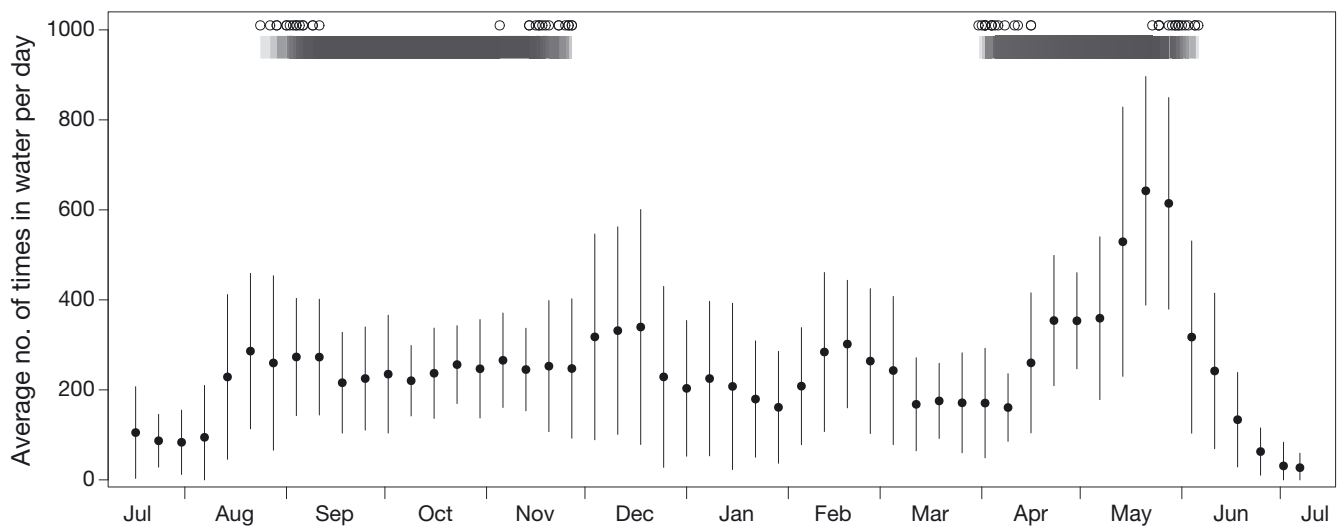


Fig. 3. Weekly average ($\pm$ SD) number of times per day when geolocators were submerged in water during the annual cycle. Migration periods are marked with grey bars on top (higher colour intensity corresponds to overlapping migration periods of more individuals) and individual timings of start and end of migration are indicated by open circles

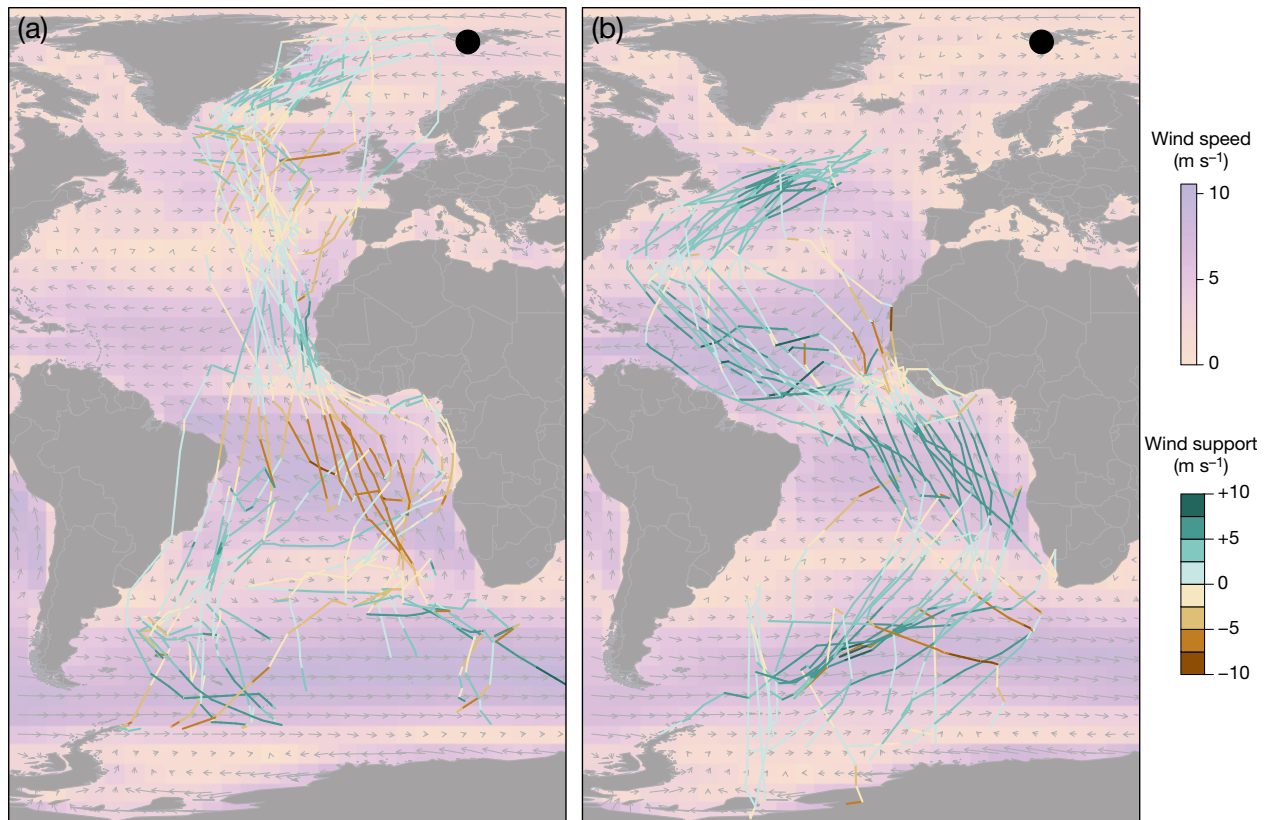
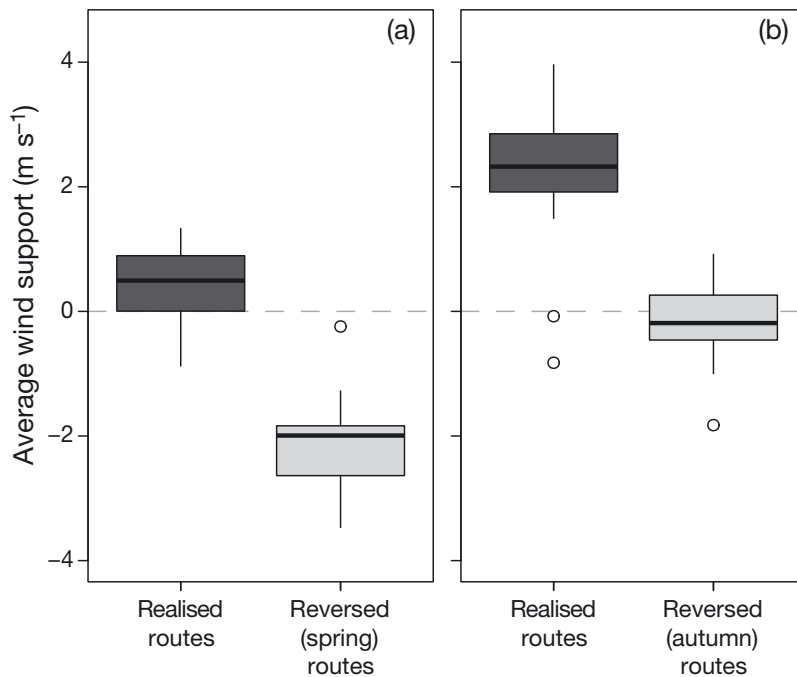


Fig. 4. Wind support along the migration routes of 16 geolocator-tracked Arctic terns during (a) southbound and (b) northbound migration. Lines show the most likely migration paths coloured according to the wind support in each segment (brown: headwind, turquoise: tailwind). Directions of arrows indicate gridded wind directions and background heatmap shows wind speed; both are averaged across the migration period of the tracked Arctic terns. Breeding site in Longyearbyen, Svalbard, is marked with a black dot



enced wind support and individual northbound travel speeds ($\beta = 28.89 \pm 9.33$, $F_{1,14} = 9.6$, $r^2 = 0.41$, $p = 0.008$).

3.3. Stopover areas and ocean productivity

While on migration, terns spent on average 32 ± 7.9 d (SD) on stopover sites during the southbound migration and 10 ± 7 d

Fig. 5. Average wind support across the entire migration route for 16 geolocator-tracked Arctic terns during (a) southbound and (b) northbound migration. Wind support along the realised migration routes is shown in dark grey and reversed routes (spring routes in autumn and vice versa) are shown in light grey. Box plots show median values with interquartile ranges (IQR; boxes), whiskers extend to 1.5× the IQR, outliers are given as open circles

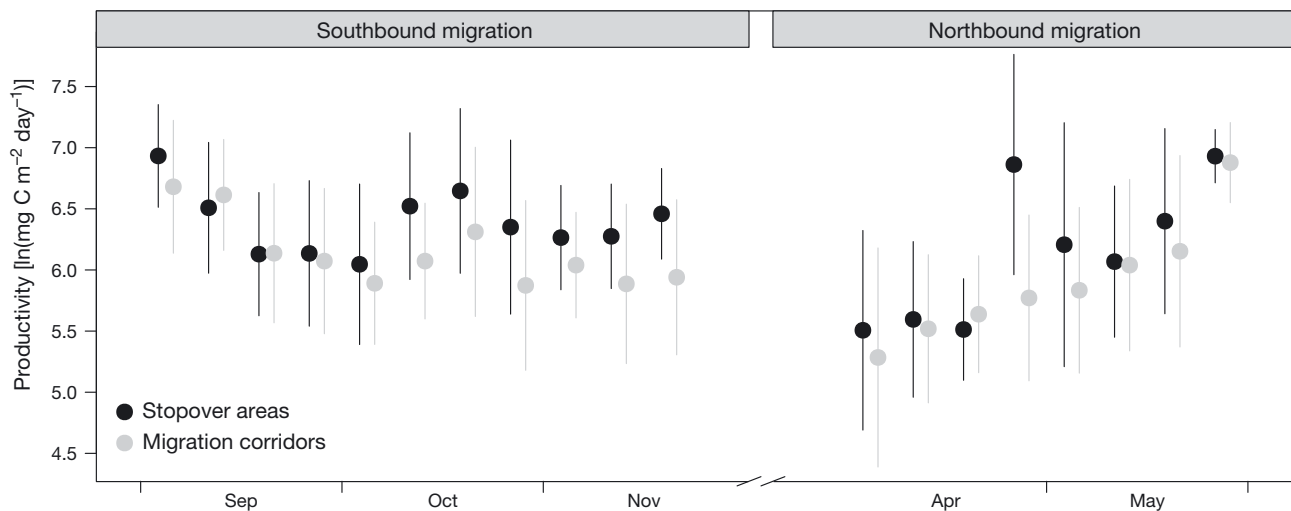


Fig. 6. Weekly ocean productivity at stopover areas (black circles) and migration corridors (grey circles) of Arctic terns during the southbound and northbound migration. Data are mean $\pm$ SD

during the northbound migration. Stopover sites of the tracked terns were located in areas where ocean productivity was higher (mean $\pm$ SD; $6.28 \pm 0.43 \ln[\text{mg C m}^{-2} \text{ d}^{-1}]$) as compared to migration corridors ($6.03 \pm 0.39 \ln[\text{mg C m}^{-2} \text{ d}^{-1}]$; paired t -test: $t_{18} = 3.87$, $p = 0.001$; Fig. 6). Weekly locations of stopover areas and migration corridors with the underlying ocean productivity maps can be found in Fig. S3.

3.4. Migration timing and daylight hours

In both seasons and particularly in spring, terns on average crossed the Equator significantly later than the equinoxes (autumn average: $+12 \pm 8$ d (SD), t -test: $t_{15} = 6.402$, $p < 0.001$, spring average: $+38 \pm 6$ d; t -test: $t_{15} = 23.334$, $p < 0.001$; Fig. 7). Despite the low synchronisation between crossing the Equator and equinoxes, birds still on average experienced 6985 ± 123 h (SD) of daylight during the annual cycle, which corresponds to 79.7% of all available daylight on Earth per year ($365 \text{ days} \times 24 \text{ h} = 8760 \text{ h}$).

4. DISCUSSION

In this study, we show that Arctic terns breeding at 78°N in Svalbard migrate to non-breeding sites south

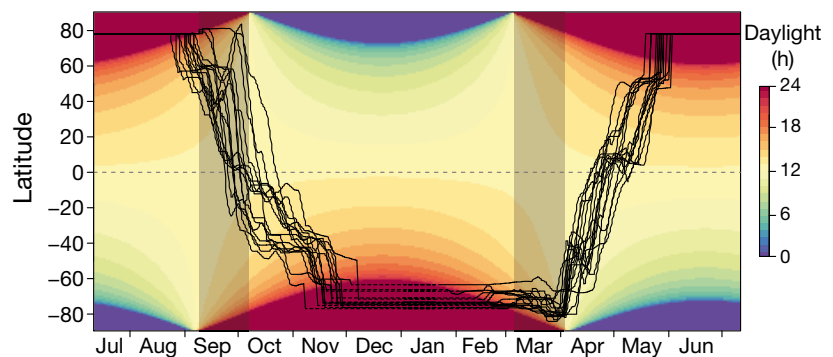


Fig. 7. Latitude and experienced daylight duration as a function of time across the annual cycle indicating the underlying phenological patterns of 16 individually tracked Arctic terns. The dashed parts of the black lines indicate the non-breeding period when birds were exposed to 24 h polar day making latitude estimates impracticable. Grey dashed line marks the Equator and shaded areas indicate periods 2 wk on either side of the equinoxes. Daylight duration was calculated as the time between civil dawn and civil dusk when the geometric centre of the sun is 6° below the horizon

of 63°S in the Weddell Sea covering up to 80 000 km on their round-trip journeys. This impressive migration is facilitated by tailwind support along the chosen migration routes in spring, and food-rich stopover areas for refuelling. Despite the low synchronisation between Equator crossing and equinoxes, which would allow for maximizing the experienced daylight (and thus, the amount of time when birds can forage), the tracked terns still experienced ca. 80% of all available daylight hours on the Earth per year, which is the most by any animal in the world. These findings suggest that the amount of time when the birds can feed is not the limiting factor during migration, but terns rather shift between seasonally specific

exploitation of tailwind support (in spring) and ocean areas of high food abundance (particularly in autumn) to facilitate their remarkable migration.

4.1. Migration, non-breeding areas and population comparison

In our study, we did not find differences in migration patterns between males and females, corresponding to earlier studies on trans-Equatorial migratory seabirds (Shaffer et al. 2006, Guilford et al. 2009, Magnúsdóttir et al. 2012, Mosbech et al. 2012). Arctic terns from Svalbard migrated to their non-breeding areas in Antarctica via 2 distinct routes following either the west coast of Africa or the east coast of South America; both of these routes are known from earlier studies (González-Solís et al. 2007, Guilford et al. 2009, Egevang et al. 2010, Fijn et al. 2013, Volkov et al. 2017, Alerstam et al. 2019). Similarly, the Weddell Sea, where most of our tracked terns over-wintered, has previously been established as a prime non-breeding area for Arctic terns breeding across various longitudes in the northern hemisphere (Egevang et al. 2010, Fijn et al. 2013, McKnight et al. 2013, Volkov et al. 2017).

Terns from our study site on average departed from Svalbard on 3 September, which is from 1 to 2 mo later than previously shown in studies from more southerly breeding areas (Table S1; Egevang et al. 2010, Fijn et al. 2013, Loring et al. 2017, Volkov et al. 2017, Alerstam et al. 2019, Redfern & Bevan 2020a). The late departure date of our tracked individuals corresponds with later departure of other species from northern latitudes (Butler et al. 1998, Gilg et al. 2013, Davis et al. 2016). As a general pattern, migratory birds breeding at higher latitudes depart from their breeding areas later than their southern conspecifics, owing to the later onset of the breeding season at high latitudes (Conklin et al. 2010, Briedis et al. 2016). Similarly, our tracked terns arrived at the breeding sites later than their conspecifics breeding at more southern latitudes (Egevang et al. 2010, Fijn et al. 2013, Loring et al. 2017, Volkov et al. 2017, Alerstam et al. 2019, Redfern & Bevan 2020a). Such population-level differences in migration timing can lead to significant variation in migration strategies, as different populations face different environmental conditions en route (González-Solís et al. 2009, Sittler et al. 2011, Hanssen et al. 2016). In the case of Arctic terns, Alerstam et al. (2019) suggested that population-specific migration strate-

gies are driven by intraspecific competition and different costs of migration. Subsequently, between-population differences in migration timing lead to population-specific wintering sites. Comparative assessment across populations corresponds with this hypothesis, as terns from Svalbard arrive in Antarctica relatively late compared to other populations and over-winter almost exclusively in the Weddell Sea. Breeding populations from lower latitudes arrive in Antarctica relatively earlier and often over-winter further east in the Indian Ocean (e.g. Alerstam et al. 2019, Redfern & Bevan 2020b).

We found that terns increased their feeding rate before arrival at the breeding site in spring (Fig. 3). At least 2 potential explanations for this may be brought forward: (1) behavioural changes regarding increased floating on water. However, using high-frequency data, McKnight et al. (2013) showed that Arctic terns spend only a small fraction of time floating on water, deeming this an unlikely explanation. (2) Birds increased their feeding frequency before arrival at the breeding site. Earlier studies confirmed Arctic terns as income breeders (species that primarily use local resources for egg production; Drent & Daan 1980, Hobson et al. 2000, Mallory et al. 2017); thus, this increase in feeding rate should not be attributed to resource deposition for future egg production. Moreover, we found that both sexes increased their feeding rate, further ruling out this behaviour as part of the capital breeding strategy. Another explanation for the observed changes in feeding rate may be attributed to changing conditions in food availability. When food is abundant, birds may require less time for feeding (e.g. at the breeding sites), while when food is scarce it may require more effort and time to feed. However, ocean productivity data indicate high food availability at the place and time when the birds showed increased feeding rate, implying that food availability may not be the main driver behind the observed pattern. A more likely explanation may be preparation against the forthcoming reduction in feeding time due to courtship behaviour and incubation. This explanation is also supported by the reduced number of times when the birds were in water after their arrival at the breeding sites, suggesting that birds could at least partially be using previously stored reserves for body maintenance during egg incubation. Moreover, body mass of the tagged individuals captured during incubation showed a decline of 0.75 g d^{-1} over the capturing period, further supporting this premise.

4.2. Migration patterns and the environment

Our findings suggest that the terns benefit from using a looped migration strategy where southbound and northbound migration routes do not overlap. By adapting the migration routes to the prevailing wind patterns across the Atlantic Ocean, Arctic terns take advantage of tailwind support en route. During the autumn migration, wind support along the 2 main autumn migration flyways — southeastern and southwestern Atlantic — is essentially different. The overall net wind support during the autumn migration was negligible, and individuals migrating through the southeastern Atlantic generally experienced more headwinds. Following this flyway may have a trade-off between relying on wind support and fuelling at food-rich stopovers, as ocean productivity in the southeastern Atlantic during this time of year is higher compared to the southwestern Atlantic (i.e. the coasts of Brazil; Fig. S3a–k).

Wind support was particularly pronounced during the northbound migration when strong tailwinds likely contributed to the exceptionally fast travel speed of terns: a 1.5-fold increase compared to travel speed during the southbound migration (Fig. 4, Box 1; sensu Kemp et al. 2010). Similar increases in seasonal travel speed have also been found in other seabirds (Felicísimo et al. 2008, González-Solís et al. 2009). In contrast, Hensz (2015) did not find wind to be a significant predictor for travel speed during either southbound or northbound migration of Arctic terns. Wind exploitation might also be used in combination with a fly-and-forage strategy (Strandberg & Alerstam 2007) to further increase travel speed. A fly-and-forage migration strategy is advantageous when an individual carries enough energy reserves from the non-breeding grounds and does not need to frequently refuel at stopovers (Strandberg & Alerstam 2007).

Stopover use, however, seems to play a more important role in route choice during the southbound migration. Tracked birds navigated between stopover sites of high ocean productivity with migration corridors passing over areas of lower productivity (Fig. 6 & Fig. S3). Such patterns in Arctic terns were first documented by McKnight et al. (2013) as birds from Alaska migrated along the west coast of the Americas. Similar patterns were described in a study where terns were tracked from Greenland and Iceland (Hensz 2015). During both migration periods, one of the main stopover areas of our tracked birds corresponded with the well-known refuelling area for migrating seabirds in the North Atlantic (Cattray et al. 2011, Sittler et al. 2011, Gilg et al. 2013), also

known as the North Atlantic drift province (Longhurst 2010). According to Bourne & Casement (1996), Arctic terns are present in the area from late April until late October, with a distinct peak in August. This time window corresponds with breeding site departure dates of terns from lower (Egevang et al. 2010, Fijn et al. 2013, Loring et al. 2017, Volkov et al. 2017) and higher latitudes (our study; Box 1).

Because terns are exclusively diurnal foragers (McKnight et al. 2013), we predicted that they will time their migration to cross the Equator close to the autumnal and vernal equinoxes, thus experiencing the longest foraging hours (Alerstam 2003). However, during both migration seasons, terns crossed the Equator significantly later than the equinoxes, suggesting that available daylength is not a limiting factor during migration. The large variation we observed in Equator crossing dates of the tracked terns suggests that crossing time is rather flexible. Furthermore, on southbound migration, Arctic terns from a breeding site in Sweden crossed the Equator almost 2 mo earlier than terns in our study (Alerstam et al. 2019; Table S1). Such population differences indicate that the timing of crossing the Equator on a population level is mainly influenced by the timing of departure from breeding sites rather than by environmental conditions.

Collectively, our findings suggest that the slower southbound migration is primarily guided by commuting between food-rich stopovers, whereas the faster spring migration is adapted to take advantage of the prevailing wind patterns to facilitate a shorter migration duration. Disentangling the influence of environmental drivers behind seasonal migration strategies of Arctic terns brings us a step closer to understanding the ecology of the world's longest animal migration. Our results provide a means to better understand the delicate relationship between seasonal migration strategies of birds and variation in environmental conditions, which may be disrupted by the ongoing global climate change.

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