Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration

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The study of long-distance migration provides insights into the habits and performance of organisms at the limit of their physical abilities. The Arctic tern *Sterna paradisaea* is the epitome of such behavior; despite its small size (<125 g), banding recoveries and at-sea surveys suggest that its annual migration from boreal and high Arctic breeding grounds to the Southern Ocean may be the longest seasonal movement of any animal. Our tracking of 11 Arctic terns fitted with miniature (1.4-g) geolocators revealed that these birds do indeed travel huge distances (more than 80,000 km annually for some individuals). As well as confirming the location of the main wintering region, we also identified a previously unknown oceanic stopover area in the North Atlantic used by birds from at least two breeding populations (from Greenland and Iceland). Although birds from the same colony took one of two alternative southbound migration routes following the African or South American coast, all returned on a broadly similar, sigmoidal trajectory, crossing from east to west in the Atlantic in the region of the equatorial Intertropical Convergence Zone. Arctic terns clearly target regions of high marine productivity both as stopover and wintering areas, and exploit prevailing global wind systems to reduce flight costs on long-distance commutes.

at-sea hotspot | global wind systems | geolocator | trans-equatorial migration

Developments in tracking technologies in the last three decades have revolutionized our understanding of movements of wide-ranging marine predators during both the breeding and nonbreeding periods (1–4). Until recently, minimum device sizes restricted deployments on seabirds to albatrosses, large petrels, and shearwaters (>400 g) (3–7), neglecting smaller species which, arguably, have even greater migratory capabilities and are potentially more sensitive indicators of the status of marine ecosystems (8, 9). These include a species long regarded as the classic exponent of long-distance migration in vertebrates, the Arctic tern (*Sterna paradisaea*).

The Arctic tern exhibits a circumpolar breeding distribution at high latitudes of the northern hemisphere and winters at high latitudes in the southern hemisphere (10, 11). The species nests on the ground, and is an opportunistic plunge-diving and surface-dipping feeder, with a diet comprising mainly small fish and large zooplankton (12, 13). There were several early attempts to infer its movements (14, 15), but the first comprehensive review (16) was presented by Salomonsen in 1967. He suggested that the main wintering areas were most likely to be off the southern tip of Africa and South America, and that Arctic terns might circumnavigate the Antarctic continent in early spring before initiating their northbound migration. This appeared to be supported by subsequent radar and visual observations of terns migrating from the Bellingshausen Sea to the Weddell Sea (17). It has been suggested that Arctic terns complete the southbound migration in a step-wise fashion, moving between rich feeding grounds, and may use high altitude migration flights to cross large expanses of land, such as the Greenland ice sheet (18, 19). Until now, there was little information on the northward return to the colony, but it was generally believed to start in March and occur more rapidly and over a wider front (20, 21). Several authors (10, 11) have attempted to estimate the total distance traveled during this impressive annual migration, typically quoting a figure of 40,000 km.

Although many (but not all) of these suppositions have subsequently proved correct, they were based on limited banding recoveries and at-sea observations, and hence inevitably reflected a range of potential biases (including, respectively, spatial and temporal variability in recovery effort, and lack of information on provenance, age, and status of individuals). Nor could they provide information on variation among individuals and populations in the phenology of migration, flight paths, or preferred wintering habitats. With the aim of providing much greater detail on individual movement patterns, we developed miniature (1.4-g) archival light loggers (geolocators) similar to those used in a recent study of passerines (22), for deployment on Arctic terns at two Arctic colonies.

Results and Discussion

With an accuracy of ~185 km in flying seabirds (23), the geolocators were used to document the migration routes, stopover sites, and wintering areas of Arctic terns from colonies in high-Arctic Greenland ($n = 10$) and Arctic Iceland ($n = 1$). At the end of the breeding season, tagged birds traveled southwest to a stopover region of deep water in the eastern portion of the Newfoundland Basin and the western slope of the mid-North Atlantic Ridge between 41–53° N and 27–41° W, in which they remained for an average ± SD of 24.6 ± 6 days (Fig. 1). This previously unknown oceanic hotspot for terns was located at the junction between cold, highly productive northern water and warmer, less-productive southern water, and was characterized by high *Chl. a* concentrations and high eddy variability (24, 25). Between 5 and 22 September 2007, all 11 birds continued their migration southeast toward the West African coast. South of the Cape Verde Islands (~10° N), however, migration routes diverged: seven birds continued to fly south parallel to the African coast, whereas four others crossed the Atlantic to follow the east coast of Brazil. Birds in both groups ceased their directed southbound transits at ~38–40° S, and shifted to a pattern of predominantly east–west movements. Three birds then traveled east into the Indian Ocean (one as far as 106° E). All birds subsequently moved south, spending the austral summer (December–March) south of 58° S and between 0 and 61° W in the Atlantic sector of the Southern Ocean. This region, which includes the Weddell Sea, is particularly productive, and supports higher densities of a key prey

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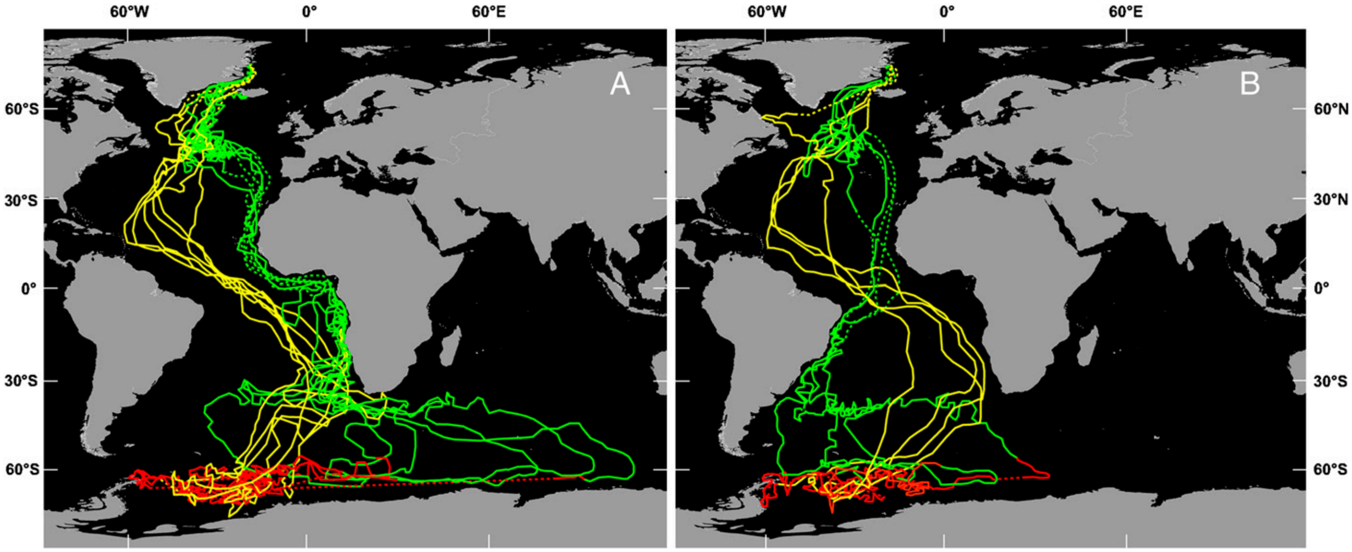

Fig. 1. Interpolated geolocation tracks of 11 Arctic terns tracked from breeding colonies in Greenland ($n = 10$ birds) and Iceland ($n = 1$ bird). Green = autumn (postbreeding) migration (August–November), red = winter range (December–March), and yellow = spring (return) migration (April–May). Two southbound migration routes were adopted in the South Atlantic, either (*A*) West African coast ($n = 7$ birds) or (*B*) Brazilian coast. *Dotted lines* link locations during the equinoxes.

for many seabirds, Antarctic krill (*Euphausia superba*), than elsewhere in the Southern Ocean (26).

All birds began the return migration to breeding colonies in early–mid April, always traveling over deep water at considerable distance from continental shelf margins, and taking a sigmoidal route, counterclockwise around the South Atlantic and clockwise around the North Atlantic gyres. Upon return in late May to the same general stopover region in the North Atlantic used during the southbound migration, two individuals transited rapidly west through the area, three remained there for 3–6 days before continuing to the north, and the remaining five birds appeared not to pause or deviate from their general course. Thus, there was little indication that the area was particularly important for northbound terns. Although the Arctic tern from Iceland began its outbound and return migration earlier than the Greenland-breeding birds (Table 1), there was no obvious difference in migration routes between this individual and some of the terns from Greenland. Thus, the emerging pattern for transequatorial migrants is of a high degree of mixing of birds from different breeding populations in wintering areas, as evident in this study and previous ones (5, 7, 27). This contrasts with the dominant strategies of southern hemisphere albatrosses, which, despite a similar capacity for long-distance migration and hence overlap, nevertheless tend to show a high degree of between-population segregation in nonbreeding distributions (28).

The Greenlandic birds exhibited clear synchrony in timing of migration, all reaching the North Atlantic stopover site, departing the wintering area and crossing the Equator within a few days of each other (Table 1), but there was no indication that they traveled together in the same flocks. Similarly, at-sea observations suggest that flock sizes of migrating terns are typically very small (<15 birds) (17), and recent results (7) from studies of other migrant seabirds also indicate high levels of synchrony in timing of passage through restricted flyways and no evidence of persistent associations between individuals (including members of a pair).

The routes used for both the southbound and northbound migrations showed a high level of congruence with parts of those taken by Manx shearwater (*Puffinus puffinus*) and Cory's shearwater (*Calonectris diomedea*), which also winter in the South Atlantic, albeit considerably farther north than Arctic terns (5, 6). It would appear, therefore, that the terns' small size is no handicap to exploiting the prevailing global wind systems (clockwise in the North, and counter clockwise in the South Atlantic), in a similar way to that of shearwaters (27), and confirms similar suggestions made several decades ago for terns (29). The efficiency of tern flight paths is illustrated by the return

Table 1. Phenology of migration stages of Arctic terns from colonies in Greenland ($n = 10$) and Iceland ($n = 1$)

	Greenland birds ($n = 10$)	Iceland bird ($n = 1$)
Arrival at North Atlantic stopover site	22 Aug (16–27 Aug)	16 Aug
Time spent at North Atlantic stopover site	24.6 Days (10–30 days)	16 days
Departure from North Atlantic stopover site	15 Sep (5–22 Sep)	1 Sep
Arrival in wintering region	24 Nov (25 Oct–30 Nov)	5 Nov
Time spent in wintering region	149 Days (139–173 days)	151 days
Departure from wintering region	16 Apr (12–19 Apr)	3 Apr
Date passing Equator on northbound migration	3 May (25 Apr–7 May)	13 Apr
Duration of northbound migration	40 Days (36–46 days)	41 days
Duration of southbound migration	93 Days (69–103 days)	80 days

Arrival and departure dates and durations are given as mean with range in parentheses.

Table 2. Summary of distances traveled during migration stages of Arctic terns (Greenland and Iceland birds combined, $n = 11$)

Migration segment	Distance traveled
Total distance traveled on migration	70,900 km (59,500–81,600 km)
Distance traveled on southbound migration	34,600 km (28,800–38,500 km)
Distance traveled per day on southbound migration	330 $\text{km}\cdot\text{day}^{-1}$ (280–390 $\text{km}\cdot\text{day}^{-1}$)
Distance traveled on northbound migration	25,700 km (21,400–34,900 km)
Distance traveled per day on northbound migration	520 $\text{km}\cdot\text{day}^{-1}$ (390–670 $\text{km}\cdot\text{day}^{-1}$)
Distance traveled within winter site	10,900 km (2,700–21,600 km)

migration from Antarctica to south Greenland (c. 60° N), an average distance of 24,270 km (range 20,070–27,790 km) covered in only 40 days (range 36–46 days), with average travel distances of 520 $\text{km}\cdot\text{day}^{-1}$ (range 390–670 $\text{km}\cdot\text{day}^{-1}$). As birds seem to have been exploiting favorable winds, travel (ground) speed will be higher than air speed. Nevertheless these flight speeds are of the same order as the maximum range speed (9.7 ms^{-1}) calculated from aerodynamics theory, and mean groundspeeds observed using radar (11.3 ms^{-1}) (17), which would correspond to 838 and 976 $\text{km}\cdot\text{day}^{-1}$, respectively, if birds were to fly nonstop (which is, of course, unlikely). Overall, the northbound migration took less than half the time (40 vs. 93 days), despite being three quarters the length (25,700 vs. 34,600 km) of the southbound journey. Indeed, the average annual distance traveled, from departing the breeding site in August to return in late May/early June (i.e., excluding movements within the breeding season) was 70,900 km (range 59,500–81,600 km). This is the longest round-trip animal migration ever recorded electronically (3, 5, 7). As our estimates of travel distance, and hence speed, were affected by the fractal dimension of the flight path (i.e., the step length for the distance measurements) (30), and by the considerable errors inherent in geolocation (23), they are not directly comparable with previous studies. Nevertheless, the tracked birds were considered to travel nearly twice the total distance generally cited for the annual Arctic tern migration. As Arctic terns can live for more than 30 years (31), the total distance traveled in a lifetime may exceed 2.4 million km, equivalent to approximately three return journeys to the Moon.

Our study demonstrated heterogeneity in migration routes within a population, yet clear migratory connectivity between populations. We confirmed that the main wintering region was the marginal ice zone around Antarctica, which agrees with at-sea observations (ref. 18 and references therein). Given that the highest densities of Arctic terns in the Southern Ocean have been observed in the Weddell Sea (17), and that a very high (likely >50%) proportion of the worlds Arctic terns breed in Greenland and Iceland (13), the wintering areas used by our tracked birds may well be typical of the majority of the North Atlantic population. Thus, the long-term changes in duration and extent of winter sea ice, and declines in abundance of Antarctic krill in this region (26, 32) should be viewed with considerable concern.

Material and Methods

We fitted miniature archival light loggers (Mk14 geolocators, mass 1.4 g; British Antarctic Survey), attached to plastic leg rings (mass of logger, ring, tape, and cable tie: 2.0 g, ~1.9% of adult body mass), to 50 breeding Arctic terns in July 2007 at Sand Island (74° 43′ N, 20° 27′ W), Young Sound, Northeast Greenland. An additional 20 geolocators were deployed on Arctic terns at Flatey Island (65° 22′N; 22° 55′W), Breiðafjörður, Iceland, in June 2007. The following season, a minimum of 21 birds equipped with loggers (>42%) were observed at Sand Island, but only 10 loggers (20%) were retrieved. At Flatey Island, four birds were resighted (20%), and one (5%) logger was retrieved. All recaptured birds were in good physical condition and no significant difference ($t = -1.57$, $P = 0.133$, df = 18, $n = 10$) could be detected in their body mass between the 2 years (mean ± SD in 2007 and 2008: 106.0 g ± 6.3 and 110.3 ± 6.0, respectively). The average clutch size of breeding pairs in 2008 at Sand Island equipped with loggers was 1.3 (± 0.43, $n = 8$), whereas clutch size in control birds the same year was 1.7 (±0.48, $n = 60$). Although poor in power of analysis because of low sample size in the logger group, a one-sided Fisher's exact test indicated no statistical difference ($P = 0.038$) between the two groups. Not all birds observed at colonies in 2008 could be recaptured; some birds were clearly breeding, but the nest could not be located or the targeted bird would not enter the trap; others were likely to be nonbreeders or failed breeders, which are very difficult to capture. In one case (Iceland), the nest of an equipped bird was abandoned after being trampled by domestic sheep before the bird could be trapped.

Although fidelity at the regional level is high in nesting Arctic terns (33), dispersal to neighboring breeding colonies occurs frequently (33–36) and is likely driven by food availability, presence of predators, disturbance, or changing climatic conditions. The only study to apply modern capture–mark–recapture techniques to adult Arctic terns showed a low reencounter probability, ranging from 0.12 to 0.74, depending on colony and year (33).

Ten of the 11 loggers retrieved were downloaded successfully, providing a full year of migration data (July 2007 to July 2008). Six months of migration data were extracted from the remaining logger. Light data were processed following the approach of Phillips et al. (23). Times of sunrise and sunset were calculated from light records and converted to location estimates using TransEdit and BirdTracker (British Antarctic Survey) using thresholds of 10, an angle of elevation of −4.7°, and applying the compensation for movement. Locations were unavailable at periods of the year when birds were at very high latitudes and experiencing 24 h daylight. In addition, only longitudes were available around equinoxes, when day length is similar throughout the world. Overall, after omitting periods with light level interference and periods around equinoxes, the filtered data sets contained between 166 and 242 days of locations for each individual (mean = 207.2 days, SD = 20.58, $n = 10$). The data set contained two daily positions, after fitting points to a smooth line, travel distances were calculated in ArcMap (ESRI) using great circle distances (Table 2). A straight-line path was assumed between the preceding and succeeding valid fix around periods when locations were unavailable (discussed above). The only exceptions were during the autumn migration around the west African coast, where it was assumed that birds did not cross land and the projected route was altered to follow the coast, and for movement north and south to the breeding colonies in Greenland and Iceland from 60° N. As positions obtained from geolocators exhibit a relatively low accuracy, we used a conservative approach when calculating distances and speed, and hence values presented here should be regarded as minimum estimates. Great-circle distances were calculated using the mean of the two daily positions, interpolating between adjacent valid locations across periods when data were unavailable because of proximity to the equinox or light level interference. Stopover sites were identified following the approach of Guilford et al. (6); where latitudinal movements were <0.8° over a 0.5-day period, they smoothed over 3 days.

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