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Article

A red knot as a black swan: how a single bird shows navigational abilities during repeat crossings of the Greenland Icecap

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Despite the wealth of studies on seasonal movements of birds between southern non-breeding locations and High Arctic breeding locations, the key mechanisms of navigation during these migrations remain elusive. A flight along the shortest possible route between pairs of points on a sphere ('orthodrome') requires a bird to be able to assess its current location in relation to its migration goal and to make continuous adjustment of heading to reach that goal. Alternatively, birds may navigate along a vector with a fixed orientation ('loxodrome') based on magnetic and/or celestial compass mechanisms. Compass navigation is considered especially challenging for summer migrations in Polar regions, as continuous daylight and complexity in the geomagnetic field may complicate the use of both celestial and magnetic compasses here. We examine the possible use of orientation mechanisms during migratory flights across the Greenland Icecap. Using a novel 2 g solar-powered satellite transmitter, we documented the flight paths travelled by a female red knot *Calidris canutus islandica* during two northward and two southward migrations. The geometry of the paths suggests that red knots can migrate across the Greenland Icecap along the shortest-, orthodrome-like, path instead of the previously suggested loxodrome path. This particular bird's ability to return to locations visited in a previous year, together with its sudden course changes (which would be appropriate responses to ambient wind fields), suggest a map sense that enables red knots to determine location, so that they can tailor their route depending on local conditions.

Keywords: migration, orientation, navigation, tracking, orthodrome, loxodrome

Introduction

In response to predictable changing environmental conditions, many birds seasonally migrate between two places on Earth, e.g. commuting from high latitude breeding grounds to lower latitude non-breeding grounds (Alerstam 1990a, Berthold et al. 2003, Winkler et al. 2016). The intermediate geographic routes followed by individuals are



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now being revealed by means of ever-smaller tracking devices (Gill et al. 2009, Klaassen et al. 2011). The main mechanisms of orientation (i.e. directed movement, Able 2000) enabling birds to navigate (i.e. charting a course to a remote destination) along migratory routes have been suggested to include the (simultaneous) use of celestial- and magnetic compasses (Emlen 1975, Able 1995, 1999, Wiltschko and Wiltschko 1996, Gould and Grant Gould 2012, Hansson and Åkesson 2014) in combination with other sources of information including landmarks (Alerstam 1976, Wiltschko and Wiltschko 2015), infrasound (Hagstrum et al. 2000), smell (Papi et al. 1971, Wikelski et al. 2015), and information communicated by peers (Chernetsov et al. 2004, Loostra et al. 2019). The availability and function of most of these orientation mechanisms have been demonstrated in laboratory experiments (magnetic compass; Wiltschko and Wiltschko 1972, Sandberg et al. 1991, Sandberg 1992, celestial compass; Emlen 1975), and in experiments with free-flying birds with manipulated senses or endogenous clocks (Schmidt-Koenig 1960, Keeton 1971, Schmaljohann et al. 2013, Wikelski et al. 2015). How birds use, or combine, these orientation mechanisms during migratory navigation, remains largely unknown even today (Barrie 2019).

Travel along the shortest possible route between pairs of points on a sphere (the ‘orthodromic pathway’ or ‘great circle route’) requires continuous adjustment of the heading towards the goal (Imboden and Imboden 1972). For a moving individual, to be able to correct its course en route implies that the individual knows where it is relative to its goal (i.e. have a map sense, Gould and Grant Gould 2012). An alternative strategy to navigate towards a remote goal is by vector navigation. Vector navigation enables migrating birds to maintain a pre-determined orientation (Able 1995, Guilford et al. 2011, Gould and Grant Gould 2012, Hansson and Åkesson 2014, Åkesson and Bianco 2016) and orient along geographic-and/or magnetic loxodrome routes (also called ‘rhumbelines’). These routes, by definition, are longer than orthodromes, but may be easier to achieve because of the constant heading (Imboden and Imboden 1972, Gudmundsson and Alerstam 1998).

To investigate the orientation mechanisms in operation during natural migration, theoretical flight path geometries based on assumptions of alternative vector navigation strategies can be compared with observed individual migration routes (Alerstam 1996, Sandberg and Holmquist 1998, Alerstam and Gudmundsson 1999b, Muheim et al. 2003, 2018, Guilford et al. 2011, Åkesson and Bianco 2017, Sokolovskis et al. 2018). The most informative comparison would be for summer migrations along trajectories close to the geographic and the magnetic poles, where the challenging ‘cue environment’ would help disclose possible orientation mechanisms. Here, constant daylight conditions complicate the calibration of time-compensated sun compass mechanisms while the stars are invisible and thus useless for orientation. At the same time, irregular geomagnetic field lines may complicate the use of magnetic cues close to the magnetic North Pole (Kiepenheuer 1984, Alerstam 1990a, b,

Alerstam and Gudmundsson 1999b, Alerstam et al. 2001, Muheim et al. 2003, but see Sandberg et al. 1991, 1998, Åkesson et al. 2001).

We set out to investigate potential orientation mechanisms during the crossing of the Greenland Icecap by a red knot *Calidris canutus islandica*. Of the six described subspecies of red knot, the *islandica* subspecies spends most of the year in the large intertidal systems of northwest Europe. During northward migration most of the population visits known major stopover sites in western Iceland before they continue to migrate north to breed on the tundra in the Canadian High Arctic (Davidson and Wilson 1992, Piersma 2007, Buehler and Piersma 2008). *Islandica* knots have been suggested to cross the Greenland Icecap during both north- and southward migrations (Gibson 1922, Bent 1927, Morrison 1975, Dick et al. 1976). Observations of departing flocks in western Iceland were consistent with this suggestion (Alerstam et al. 1990, Gudmundsson 1993). Given that the destination area of this species is located in the challenging ‘cue environment’ close to the geographic- and the magnetic North Pole, no vector navigation strategy is known that would enable migrants to cross Greenland along a path with a constant geographic heading (Alerstam 1990b, Alerstam et al. 1990, Sandberg and Holmquist 1998). However, radar tracking on the coast of eastern Greenland suggested that red knots migrating between their spring staging area on Iceland and their breeding grounds on Ellesmere Island, Canada, travelled along a geographic loxodrome rather than the shorter orthodrome (Alerstam et al. 1986, 1990, Alerstam 1990b).

Acknowledging that unique and improbable observations can yield important insights in (ecological-) phenomena (the ‘black swan’ phenomenon, Taleb 2010), we present the details of four cross-Greenland flights by a single red knot to evaluate the possible orientation mechanisms used by this high latitudinal migrant. We compare the actual geometries of migratory tracks with the previously reported geographic loxodrome route (Alerstam et al. 1986), as well as the corresponding orthodromic routes. However, recognizing that the geometry of migratory tracks reflects the use of specific orientation mechanisms only in uniform worlds (Muheim et al. 2018), we also assess the influence of the moving medium, the winds, during the flights.

Material and methods

Paula, the focal bird

This red knot of the *islandica* subspecies was caught in mist nets at a high tide roost in the Dutch Wadden Sea (Richel, 53°17′31.67″N, 05°07′57.63″E) on 10 April 2016. The bird was an adult female, weighed 140 g, and showed moult of body feathers into the breeding plumage, indicating that she was physiologically preparing to breed. The bird, named ‘Paula’, received a metal ring (with inscription Z083055), a black flag and four colour rings (combination: N7PGRG, see Spaans et al. 2011).

Immediately after capture, Paula was moved to the Experimental Shorebird Facility of the NIOZ Royal Netherlands Institute for Sea Research on the island of Texel (53°00'N, 04°47'E), where she was housed with nine other red knots in an indoor aviary (4.5 m deep, 1.5 m wide and 2.3 m high). The aviary was equipped with rubber-coated concrete floors constantly irrigated with running seawater; it included a basin with sandy sediment from the Wadden Sea. The birds had free access to trout food pellets (Produits Trouw, Vervins, France) and natural prey (mud snails *Peringa ulvea*) as well as fresh water for drinking and bathing in a separate tray.

Paula was tagged with a pre-production prototype of a solar-powered rechargeable Argos 3 Platform Terminal Transmitter (PTT) weighing only 2.5 g (l×w×h=20×10×7 mm + 210 mm antenna), produced by Microwave Telemetry, Inc. When sufficiently charged, this PTT transmits signals to the Argos satellite system every 50 s, and when signals are received by a polar-orbiting satellite, the perceived Doppler shift in signal frequency of successive transmissions is used to estimate the position of the transmitter (CLS 2016).

To allow for an acclimatization period in a safe environment away from predators and with ample availability of food, four days prior to release the PTT was mounted on Paula using a backpack configuration (Chan et al. 2016). Within minutes of being equipped with the PTT, Paula resumed normal behaviour and within a day, the PTT was completely preened under the back feathers and invisible except for the antenna. Before release, a few back feathers were clipped to better expose the solar panel; note that these feathers would have regained their original length after moult in autumn 2016. In an outdoor aviary we verified that the transmitter was functioning correctly. On 22 April, after 12 days in captivity and with a body mass of 151 g, Paula was released at mid-day during low tide in the Mokbaai on Texel (53°00'20.74"N, 04°45'48.60"E), together with five other red knots.

Spatial analyses

Since we were especially interested in the trajectories of migratory flights, Argos data were filtered using a rate-based filter algorithm set for a high rate of speed (130 km h⁻¹) and a relaxed minimum redundant distance (10 km) suitable for summarizing long-distance flights (Douglas et al. 2012). During filtering all standard-quality locations (i.e. location classes 3, 2, 1; for details on Argos location classes see CLS 2016) were retained while low-quality locations (i.e. location classes 0, A, B and Z) were retained only if they passed filter thresholds. Ground speed was calculated between successive retained locations by means of the great circle distance (function *gdist()* from the *Imap* package (Wallace 2012) and the time (UTC) elapsed between two locations.

Departure and arrival times and the intervening flights were determined from the visual inspection of the tracks (Google Earth ©). Departure locations were defined as the last location on land with a ground speed < 20 km h⁻¹

(Chan et al. 2019) and arrival locations as the first location on land with ground speed < 20 km h⁻¹. Intermediate locations were defined as 'migratory flights' and were labeled as 'northward' or 'southward' migration together with a unique identifier for each migratory flight by year (number of migratory flights per year is 4 for 2016, and 5 for 2017, see Fig. 1 and Supplementary material Appendix 1 Table A1 for the migration scheme for both years).

In contrast to previous models of PTTs (Gill et al. 2009, Senner et al. 2015, Chan et al. 2016), the 2g PTT had no duty cycle, but rather transmitted whenever it was sufficiently charged. Under sunny conditions this provided numerous locations per day (average number of locations per day during migration 2016; n=14 and 2017; n=6). However, the transmitter was picked up more frequently at higher latitudes (since Argos satellites are polar-orbiting), and when Paula was in flight rather than on the ground. When the intermittent in-flight location data did not reveal appropriate departure or arrival times, we estimated those times by extrapolating the average speed (range 53–64 km h⁻¹) of each migratory flight from the last location in flight, or, for departure time, backward from the first location in flight. Throughout this manuscript we report measured distances based on filtered Argos location estimates. Since we did not continuously track the bird, local movements and slight deviations along flight paths may have been overlooked and thus overall distances moved may be underestimated. Hence, reported distances represent minimum distances traveled.

Orthodrome or loxodrome routes?

Geographic orthodrome and loxodrome paths between Iceland and Ellesmere Island were simulated by means of the functions *gcIntermediate()* and *destPointRhumb()* of the *geosphere* package (Hijmans 2019), with a resolution of 1 point per kilometer between previously assigned departure and arrival locations. Since Paula's tracks crossed Iceland without stops during both southward migrations (a pattern predicted by Dietz et al. 2010), we assigned 'pseudo-'arrival locations and arrival times by means of the locations where she first crossed the Icelandic coastline and the average groundspeeds of the respective migratory flights.

We calculated the mean distance and standard deviation of each transmitter location to their nearest locations on the simulated orthodrome and geographic loxodrome paths with the function *dist2Line()* of the *geosphere* package (Hijmans 2019). For each crossing of the Greenland Icecap, these deviations from the orthodrome and geographic loxodrome were compared by means of a two sided t test using the function *t.test()* of the *stats* package. All analyses were done in the R environment (v 3.6.3; <www.r-project.org>).

Wind effects

To explore the effect of winds on migration path, we used NCEP Reanalysis data from <<http://www.esrl.noaa.gov/psd/>> provided by the NOAA/OAR/ESRL PSD, Boulder,

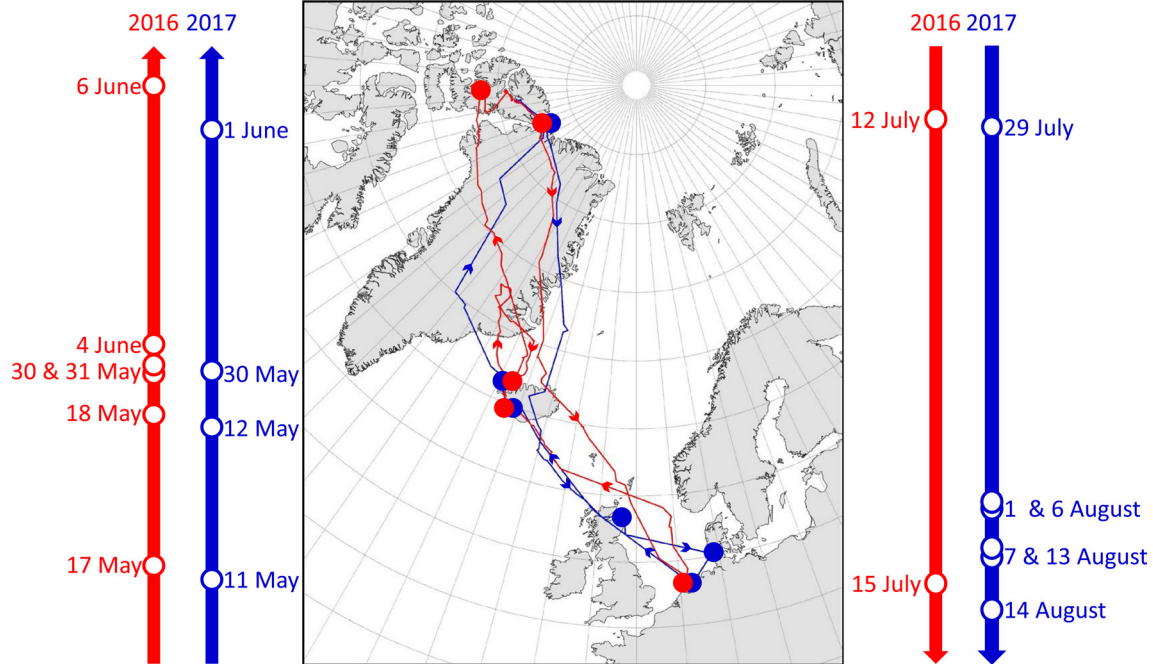


Figure 1. Flight paths of a single satellite-tracked red knot during 2 years. Northward and southward migrations in 2016 (red) and 2017 (blue) are shown on an Azimuthal Equidistant map projection. Open circles in the timelines (left = northward migration, right = southward migration) correspond to solid circles in the map and represent stopovers in 2016 (red) and 2017 (blue). Arrowheads indicate the flight direction.

Colorado, USA (Kalnay et al. 1996). We used the package *RNCEP* (Kemp et al. 2012a) to assess the wind data. The function `RNCEP.interp()` was used to obtain and interpolate *u*- and *v*-wind information in space and time for each received location (in degrees from north and in m s^{-1} ; Kemp et al. 2012a). We did not measure flight altitude, but after inspection of the elevation profile of the Greenland Icecap (with main levels of altitude between 2000 and 2500 m with the highest peak at 3300 m above sea level (a.s.l.); Alerstam et al. 1986), we obtained *u*- and *v*-wind components from the 700 mb atmospheric pressure level which corresponds to an altitude of roughly 3000 m a.s.l. (Alerstam et al. 1986). Flow assistance was then calculated for each location using the function `NCEP.Tailwind()`, assuming a fixed airspeed of 16 m s^{-1} (Shamoun-Baranes et al. 2010) and full compensation for wind drift (Chapman et al. 2011, Kemp et al. 2012b).

To assess possible effects of winds on the geometry of the migratory paths during the flights over Greenland, we used the function `NCEP.gather()` (Kemp et al. 2012a) to obtain the prevailing wind speed and direction at the time of crossing. Given the temporal resolution (every 6 h) and the spatial resolution (a 2.5° latitude \times 2.5° longitude) of the available wind data (Reanalysis 2 dataset, Kanamitsu et al. 2002), we queried the *u*- and *v*-wind components at 700 mb pressure level between $40^\circ 0' 0''\text{N}$, $90^\circ 0' 0''\text{W}$ and $90^\circ 0' 0''\text{N}$, $30^\circ 0' 0''\text{E}$ for the available time closest to the midpoint in time for each migratory flight (Fig. 2).

To visualize general wind conditions and flow assistance in one map, and in the absence of information of the bird's

flight altitudes, we used the 700 mb pressure level for wind calculations along the whole track. Following Alerstam et al. (1986) and Shamoun-Baranes et al. (2010), we repeated our analyses for the 500 and 925 mb pressure levels (5500 m and 766 m a.s.l.). As we found that differences in flow assistance at different pressure levels were trivial, these results are not presented.

Results

In 2016 and 2017, the 2 g solar PTT on Paula successfully transmitted data during two northward (mid-May to early June) and two southward migratory journeys (mid-July to mid-August; Fig. 1, Supplementary material Appendix 1 Table A1 for more details). In 2016 Paula departed from the Wadden Sea on 17 May, i.e. 25 days after release, and flew nonstop to western Iceland, where she moved among multiple nearby staging sites, all known for red knots (Wilson 1981, Gudmundsson and Gardarsson 1992, Morrison and Wilson 1992, Wilson and Morrison 1992).

On 30 May 2016, Paula left Iceland for what turned out to be a round trip back to Iceland. She first flew northwest across the Denmark Strait ($67^\circ 0' 0''\text{N}$, $24^\circ 0' 0''\text{W}$), then made a circuitous flight over part of the mid-eastern portion of the Greenland Icecap, before turning back to Iceland. This trip totalled 39 h and 1859 km (Fig. 1, Supplementary material Appendix 1–2 Table A1, Fig. A1). Paula departed Iceland again four days later on 4 June 2016 and made a nonstop,

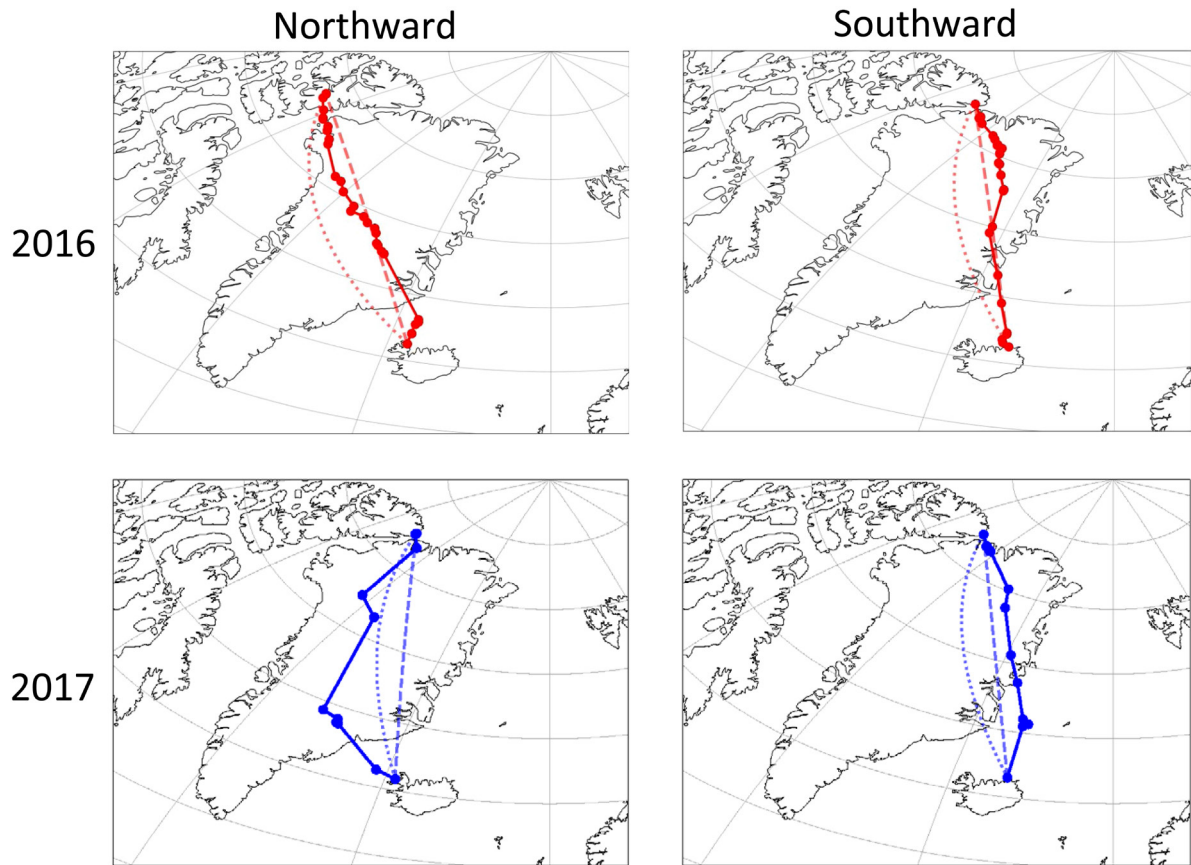


Figure 2. Orthodrome and geographic loxodrome paths. Maps show the northward (left) and southward (right) crossing of the Greenland Icecap in 2016 (red) and 2017 (blue) in relation to the orthodrome (dashed lines) and loxodrome (dotted lines) paths between Iceland and Ellesmere Island on an Azimuthal Equidistant projection. Red and blue circles show in-flight tracking locations.

37-h, 2404-km flight to Ellesmere Island, a known breeding area for *islandica* knots (Nettleship 1974, Whitfield et al. 1996, Fig. 1, Supplementary material Appendix 1 Table A1). After some initial small-scale directional movements on Ellesmere Island between 8 and 26 June 2016, we began receiving highly clustered locations indicative of a bird tending a nest (95% of the locations were within 7.5 km of the period's average, consistent with Argos location errors expected to remain after filtering the raw data with a 10 km redundancy threshold). After 18 days, Paula resumed small scale directional movements towards the settlement of Alert (82°30'6"N 62°20'53"W), before departing on southward migration on 12 July in what was a single nonstop flight of 60 h, covering 4091 km, to the Dutch Wadden Sea (Fig. 1, Supplementary material Appendix 1 Table A1).

In 2017 Paula flew from the Wadden Sea to Iceland on 11 May, 6 days earlier than in the previous year, and staged for 17 days mostly at the same staging sites she visited in 2016. Still six days ahead of the 2016 northward flight schedule, she flew 41 h over 2469 km to Ellesmere Island, this time arriving close to her departure location of the previous year, near Alert (Fig. 1, Supplementary material Appendix 1 Table A1). Within three days, she moved approximately 250 km inland to a site that she also visited briefly after nesting in

the previous year, and stayed at that locale for 26 days (95% of the locations were within 15.3 km of the period's average), indicating a breeding attempt. After subsequent small-scale movements, again in the direction of Alert, Paula flew back to Europe on 29 July, more than 2 weeks later than in 2016. In a nonstop flight of 68 h she covered 3333 km to northern Scotland. After a stop of five days, she crossed the North Sea to the Wadden Sea near Sylt, Germany. Staying there for three more days, she finally arrived in the Dutch Wadden Sea on 14 August, one month later than in 2016. She thereby completed southward migration passage in 136 flight hours and covered 4422 km (Fig. 1, Supplementary material Appendix 1 Table A1).

In 2016, Paula flew closer to the orthodrome than to the loxodrome path during both the northward (mean \pm SD, orthodrome: 50 \pm 36 km, loxodrome: 143 \pm 101 km; $t = -4.81$, $df = 37$, $p < 0.0001$) and the southward crossings of Greenland (orthodrome: 57 \pm 44 km, loxodrome: 171 \pm 108 km; $t = -5.07$, $df = 35$, $p < 0.0001$; Fig. 2a–b, Supplementary material Appendix 1 Table A1). In 2017, during northward migration the locations deviated considerably from the two possible geometric paths (mean \pm SD, orthodrome: 212 \pm 192 km, loxodrome: 142 \pm 136 km; $t = 0.99$, $df = 18$, $p = 0.33$ see Fig. 2c, Supplementary material Appendix

1 Table A1). During southward migration Paula flew closer to the orthodrome than the loxodrome (orthodrome: 66 ± 61 km, loxodrome: 115 ± 118 ; $t = -2.59$, $df = 21$, $p = 0.02$; see Fig. 2d, Supplementary material Appendix 1 Table A1).

In 2016, during the circuitous flight over the mid-eastern portion of the Greenland Icecap, Paula initially experienced positive flow assistance when she left Iceland. However, while she continued to fly north, she entered a narrow zone of headwinds (average flow assistance for this northbound flight = 0 m s^{-1} ; Fig. 3, panel 1a, Supplementary material Appendix 2 Fig. A1). During the southbound return flight to Iceland, she also experienced headwinds (average flow assistance -5 m s^{-1} ; Fig. 3, panel 1b).

During the subsequent complete northward crossing of the Icecap, Paula generally experienced low levels of flow assistance (average flow assistance = 1 m s^{-1}), with most wind support during the intermediate section. Before her arrival on Ellesmere Island she experienced weak headwinds (Fig. 3c). At departure on southward migration Paula experienced slight headwinds, however, favourable wind conditions and strong flow assistance prevailed during most of her crossing of the Greenland Icecap (average flow assistance = 3 m s^{-1} ; Fig. 3d). In 2017, Paula experienced weak to negative flow assistance during the northward flight over Denmark Strait and strong flow assistance during the second half of the flight across the Greenland Icecap (overall average flow assistance = 6 m s^{-1} ;

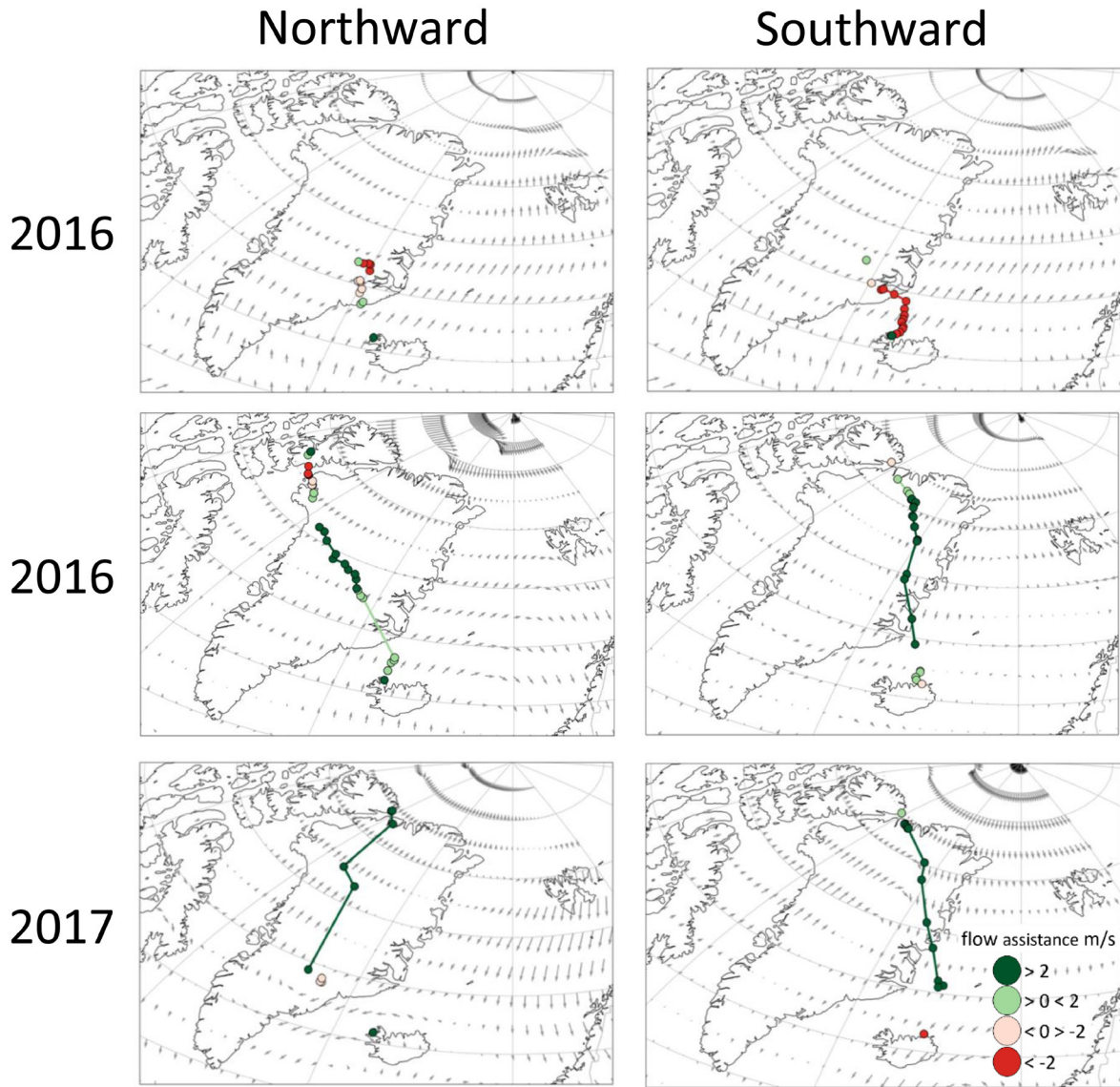


Figure 3. Flow assistance (m s^{-1}). Maps of calculated flow assistance at each tracking location during northward (left column) and southward (right column) migration, with positive flow assistance colored green (light green $< 2 \text{ m s}^{-1}$, dark green $> 2 \text{ m s}^{-1}$) and negative flow assistance (i.e. headwinds) colored red (light red $> -2 \text{ m s}^{-1}$, dark red $< -2 \text{ m s}^{-1}$). The spring 2016 circular flight (top row) that reached mid-eastern Greenland (a) before turning back to Iceland (b), and completed migrations in 2016 (middle) and 2017 (bottom row) on an Azimuthal Equidistant projection. Gray arrows show wind speed and direction midway during the respective migration.

Fig. 3e). Just as in 2016, in 2017 Paula experienced relatively strong flow assistance during southward migration when flying over the Greenland Icecap (average flow assistance = 4 m s^{-1} ; Fig. 3f).

Discussion

Paula's flights confirm earlier predictions that red knots are able to traverse the Greenland Icecap during both north- and southward migration (Gibson 1922, Bent 1927, Morrison 1975, Dick et al. 1976, Gudmundsson 1993). However, contradicting earlier suggestions (Alerstam 1990b, Alerstam et al. 1990), she did not follow a geographic loxodrome when crossing the Greenland Icecap. In fact, in three out of the four crossings, the geometric shape of the track more closely resembled the shorter orthodrome route (Fig. 2).

At high latitudes the use of a magnetic compass and a time-compensated sun compass could lead migrants along geographic paths that closely resemble orthodromes (Alerstam 1990b, Alerstam et al. 1990). The magnetic compass mechanism is based on the axial alignment of the geomagnetic field in relation to gravity (i.e. the geographic field) (Wiltshko and Wiltshko 1972, Kiepenheuer 1984). Since the magnetic- and the geographic poles do not coincide, birds orienting along a constant magnetic course (i.e. magnetic loxodrome) are led along a changing geographic course (which also varies in space and time due to the movement of magnetic north; Alerstam and Gudmundsson 1999b, Muheim et al. 2003, 2018). Flying along a constant magnetic course requires frequent recalibrations of the magnetic compass direction depending on the local magnetic declination (Alerstam and Gudmundsson 1999b, Muheim et al. 2003, Supplementary material Appendix 3). Migrants departing from Iceland could navigate along orthodrome like routes towards Ellesmere Island by means of orientation along a constant magnetic course towards the magnetic North Pole, which is currently situated close to Ellesmere Island (Alerstam et al. 1990, Supplementary material Appendix 3 Fig. A2, A3). Orientation experiments at high latitudes suggest that songbirds are able to orient by means of geomagnetic cues even in close proximity to the magnetic North Pole (Sandberg et al. 1998, Åkesson et al. 2001).

In shorebird migrants with an endogenously controlled time keeping mechanism (Karagicheva et al. 2016), a time-compensated sun compass would enable the use of the predictable daily movement of the sun to navigate along a geographic loxodrome (Muheim et al. 2018). However, during long distance migration across longitudes, maintaining a constant heading requires the recalibration of the internal circadian time-keeping mechanism (Schmidt-Koenig 1990). If recalibration is absent, at high latitudes each degree of longitude transected by a migrating bird will lead to a course shift of 1° in latitude (Alerstam et al. 1990, Alerstam and Pettersson 1991). Therefore, the use of a time-compensated sun compass without adjustment for longitudinal time shifts

has been proposed to enable birds to fly along orthodrome-like routes (Alerstam et al. 1990, Alerstam and Gudmundsson 1999b, Muheim et al. 2018). The use of a sun compass calibrated in Iceland was previously suggested to enable orientation along an orthodrome route over the Greenland Icecap (Alerstam and Pettersson 1991, Alerstam et al. 2001, Gudmundsson et al. 2002), but empirical evidence is lacking. In both years Paula staged for two weeks on Iceland before crossing the Greenland Icecap. Her time spent at this stop-over offered the opportunity to recalibrate her internal clock to match the local time on Iceland. This would have allowed her to orient along an orthodrome route over the Icecap by means of a sun compass.

Inconsistent with Paula's non-stop flights over Greenland are the many ring recoveries of knots along the west and east coast of Greenland that indicate that at least some individuals make intermediate stops (Alerstam et al. 1986; <<https://wadertales.wordpress.com/2019/08/15/sixty-years-of-wash-waders/>>). Stops along the Greenland coast were also observed in satellite-tracked brent geese *Branta bernicla brota* and white-fronted geese *Anser albifrons flavirostris*, waterbirds that migrate from east to west across much narrower parts of the Icecap in southern Greenland and thus avoid the highest mountain peaks (Gudmundsson et al. 1995, Fox et al. 2003). Gudmundsson et al. (1995) suggest that the brent geese in their study followed a geographic loxodrome when crossing the Greenland Icecap by using topographical features in combination with a sun compass, under the assumption that the geese reset their endogenous clock from local Iceland time to Greenland time during a stop on the east coast of Greenland. Recent movement studies on smaller migrants carrying lightweight geolocators (i.e. northern wheatear *Oenanthe oenanthe leucorhoa*, Bairlein et al. 2012; purple sandpiper *Calidris maritima*, Summers et al. 2014; and ringed plover *Charadrius hiaticula psammodromus*, Léandri-Breton et al. 2019) suggest that most of these birds follow geographic loxodromes like the geese. However, some of the observed northward tracks suggest that individuals cross the Greenland Icecap above 65°N latitude, along routes that may approach orthodromes (Summers et al. 2014, Léandri-Breton et al. 2019). Unfortunately, the tracks end prematurely because the light-based geolocators used in these studies did not allow for estimation of locations under the constant daylight conditions present above the Arctic Circle during northern summer.

Winds across the Greenland Icecap are usually determined by a high-pressure system northeast of Greenland and a low-pressure system to its south (Alerstam et al. 1986, Liechti 2006). As a result, the prevailing winds across the Icecap come from the northwest, resulting in generally unfavourable winds during northward migration, but mostly favourable winds during southward migration (Alerstam et al. 1986). Confirming previous findings for shorebirds (Gudmundsson 1993, 1994, Alerstam and Gudmundsson 1999a, Green et al. 2004), Paula departed under (light) tail wind conditions from Iceland as well as from Ellesmere Island (Fig. 3). She followed the orthodrome route most strictly immediately after

departures and just before arrivals, drifting away from the shortest path at intermediate sections of her flights (Fig. 2).

We considered the possibility that Paula's circuitous flight across part of Greenland in 2016 was an attempt to cross the Icecap, an attempt that was aborted because of deteriorating wind conditions during the traverse (Fig. 3a–b, Supplementary material Appendix 2 Fig. A1). A similar circuitous journey was actually observed in a satellite-tagged white-fronted goose by Fox et al. (2003). Although the goose departed from Iceland with following winds, it aborted the crossing of the Greenland Icecap and returned to the east coast of Greenland where it remained for the rest of the summer. In pectoral sandpipers *Calidris melanotos*, circuitous flights initiated with following winds have been suggested to be the outcome of group behaviour when multiple individuals with different directional preferences act to lead the group along a compromised course until they split up (Krietsch et al. 2020).

In all four crossings of the Greenland Icecap Paula experienced strong wind assistance at sections where she could afford to drift (i.e. at locations far from the goal locations). This was most pronounced during northward migration in 2017 when winds were considerably stronger than in 2016 (Fig. 3e). While Paula departed from Iceland in 2017 in a westerly direction (rather than in a northwesterly direction to the breeding grounds), she turned almost 90 degrees north at a point where strong southerly winds supported her all the way to the breeding grounds (Fig. 3e). Such distinct course changes have previously been explained by encounters with geographic features such as coasts, mountain ridges, rivers and anthropogenic structures (Ottooson et al. 1990, Kuyt 1992, Gudmundsson 1993, Gudmundsson et al. 1995, Alerstam 1996, Alerstam and Gudmundsson 1999a, Åkesson 2007). Empirical studies show that, at least in homing pigeons *Columba livia*, visual guideposts are important when birds are close to their destination (Wilkie et al. 1989, Lechelt and Spetch 1997, Biro et al. 2007). The observation that Paula arrived on Ellesmere Island in 2017 at the location from where she departed from the breeding grounds in 2016, suggests that she targeted specific memorized locations (Kok et al. 2020a). Orientation by means of visual landmarks during the crossing of the Greenland Icecap may be difficult if the landscape is homogenous. However, a broad overview of the landscape from the high altitude at which Paula may have been flying (Senner et al. 2018), together with the variable topography of the Icecap (reaching levels up to 3300 m a.s.l.; Alerstam et al. 1986), may contribute distinct visual cues to aid orientation.

As flying takes place in a medium that is moving itself at comparable speeds to the birds (Liechti 2006), migratory routes will only resemble the theoretically predicted geometric paths in a wind-still world, or when a bird completely compensates for wind drift (Alerstam 1979, Åkesson and Bianco 2016). Empirical evidence for the use of specific orientation mechanisms during natural migrations is therefore rather more challenging than what has been suggested (Gudmundsson and

Alerstam 1998, Sandberg and Holmquist 1998, Åkesson and Bianco 2017, Muheim et al. 2018, Sokolovskis et al. 2018, but see Guilford et al. 2011); it requires careful strategic elimination of senses that rule out the use of 'all but one' orientation mechanism. Indeed, 'tracks only tell us where a bird was at a given time, but they do not tell us why and by what means it was navigating' (Wiltshcko and Wiltshcko 2015). Nevertheless, the detailed observations of a single tracked individual (our 'black swan') crossing the Greenland Icecap on four occasions show us that red knots are in fact able to do just that. They may fly along the shortest, orthodrome-like path instead of the longer, previously suggested geographic loxodrome paths. Paula's ability to return to previously visited locations and fly primarily with following winds, together with the sudden, and fully appropriate course changes observed, suggest the use of a map sense that enables red knots to determine their location in relation to their goal and tailor their migratory route depending on previous experience and ambient wind fields.

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Data accessibility

The data and reproducible code is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.b8gth795> (Kok et al. 2020b). The tracking data used in this study are also accessible on Movebank (movebank.org, study name "Red Knot Piersma Paula Greenland").

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Supplementary material (available online as Appendix jav-02464 at <www.avianbiology.org/appendix/jav-02464>). Appendix 1.