Seasonal variation in migration strategies used to cross ecological barriers in a Nearctic migrant wintering in Africa

Don-Jean Léandri-Breton[1], Jean-François Lamarre[1,2] and Joël Bêty[1]

[1]Département de Biologie et Centre d'études nordiques, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, QC, G5L3A1, Canada

[2]Polar Knowledge Canada, 29C Mitik Street, Cambridge Bay, Nunavut, X0B0C0, Canada

Corresponding author: Don-Jean Léandri-Breton, Département de Biologie et Centre d'études nordiques, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, QC, G5L3A1, Canada. E-mail: don-jean.leandri-breton@uqar.ca

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Abstract

Ecological barriers such as oceans, mountain ranges or glaciers can have a substantial influence on the evolution of animal migration. Along the migration flyway connecting breeding sites in the North American Arctic and wintering grounds in Europe or Africa, Nearctic species are confronted with significant barriers such as the Atlantic Ocean and the Greenland icecap. Using geolocation devices, we identified wintering areas used by Ringed Plovers nesting in the Canadian High-Arctic and investigated migration strategies used by these Nearctic migrants along the transatlantic route. The main wintering area of the Ringed Plovers (n = 20) was located in Western Africa. We found contrasting seasonal migration patterns, with Ringed Plovers minimizing continuous flight distances over the ocean in spring by making a detour to stop in Iceland. In autumn, however, most individuals crossed the ocean in one direct flight from Southern Greenland to Western Europe, as far as Southern Spain. This likely resulted from prevailing anti-clockwise winds associated with the Icelandic low-pressure system. Moreover, the plovers we tracked largely circumvented the Greenland icecap in autumn, but in spring, some plovers apparently crossed the icecap above the 65°N. Our study highlighted the importance of Iceland as a stepping-stone during the spring migration and showed that small Nearctic migrants can perform non-stop transatlantic flights from Greenland to Southern Europe.

Keywords: Ecological barriers, Transatlantic migration, Migration detour, Geolocator, Shorebirds, Charadrius hiaticula

Introduction

Ecological barriers such as mountain ranges, oceans, desert or glaciers can have a substantial influence on the evolution of animal migration routes (Moreau 1972, Berthold 2001, Alerstam et al. 2003). Among birds, crossing large ecological barriers can involve highly demanding non-stop flights, as refuelling along the way is not possible (Alerstam 2001). Although long-distance migrants can display a high level of metabolic efficiency during continuous flights (Kvist et al. 2001), such flights can involve extreme physiological efforts (Piersma 2011) and increase mortality risk due to unpredictable weather encountered *en route* (Newton 2008). Moreover, migrants need additional energy to carry the extra fuel reserves required for long non-stop flights (Pennycuick 1975, Alerstam 2001). Migrants appear to minimize such costs by often making significant detours to reduce distances over ecological barriers (Alerstam 2001), unless wind patterns are favourable for a direct barrier crossing (Erni et al. 2005, Liechti 2006, Alerstam 2011). Such detours are often undertaken even though crossing the barriers is within the migrants' potential flight range capacities (Alerstam 2001).

Although the ability to cross or circumvent barriers requires complex adaptations (Henningsson and Alerstam 2005, Corman et al. 2014), some migration routes evolved despite the presence of major barriers along the way (e.g. Gill et al. 2009, Johnson et al. 2011, Klaassen et al. 2011, DeLuca et al. 2015). The migration flyway between breeding grounds in the North American Arctic and wintering quarters in Europe and Africa is indicative of the capacity of some species to cross extensive barriers during migration. Species using this flyway are typically confronted with the Greenland ice cap, which can be circumvented (Wilson 1981), and the North Atlantic Ocean, which cannot be avoided. Although this impressive transatlantic migration has been the subject of investigation for decades (e.g. Snow 1953, Salomonsen 1967, Alerstam 1996, Thorup et al. 2006), the migration strategies of most migrants using this route remain poorly known. At least nine nearctic species breeding in Eastern Canada and/or Western Greenland are known to use the transatlantic flyway, including two goose species (Brent Goose *Branta bernicla hrota* and Greater White-fronted Goose *Anser albifrons flavirostris;* Gudmundsson et al. 1995, Fox et al. 2013), one passerine (Northern Wheatear *Oenanthe oenanthe leucorhoa*, Bairlein et al. 2012), and six shorebird species (Cramp and Simmons 1983, Delany et al. 2009): Red Knot (*Calidris canutus islandica*), Sanderling (*Calidris alba*), Dunlin (*Calidris alpine arctica*), Purple Sandpiper (*Calidris maritima*), Ruddy Turnstone (*Arenaria interpres interpres*) and Ringed Plover (*Charadrius hiaticula psammodromus*).

When confronted with major barriers where alternative routes over suitable habitats are not possible, migrants usually cross where the barrier extent is reduced, thus minimizing long-distance flights (Alerstam 2001). Along the Nearctic-European flyway, Iceland is known to be an important stepping-stone for migrants, significantly reducing the non-stop transatlantic flight (Wilson 1981, Alerstam 1996). In late spring, high numbers of migrants gather in Western Iceland (Wilson 1981, Gudmundsson and Gardarsson 1993), and large flocks have been reported to depart from the West coast towards the Greenland ice cap (Alerstam et al. 1990). Although it has been assumed that nearctic migrants can also stop in Iceland during the autumn migration (Wilson 1981, Dietz et al. 2010), a non-stop transatlantic flight could have evolved as an adaptation to prevailing winds over the North Atlantic Ocean (Salomonsen 1967, Alerstam 1996). South of Iceland, a low-pressure system is regularly moving eastwards, forming anticlockwise prevailing winds (Serreze et al. 1997, Summers et al. 2014). In autumn, migrants could thus be able to use favourable winds along the south flank of the depression to cross the ocean in one non-stop flight. For instance, all Nearctic Purple Sandpipers, followed during one year, skipped Iceland during their autumn migration and flew directly from Eastern Canada or Southern Greenland to their wintering grounds in Ireland or Scotland (Summers et al. 2014), a distance of over 2500 km. For nearctic species wintering further south (e.g. in Africa), stopping in Iceland would represent a much greater detour compared to a direct flight (Alerstam 1996). Aerodynamic models suggested that wind-assisted Nearctic Northern Wheatears would be able to cross the Atlantic Ocean in a direct flight from Southern Greenland or Eastern Canada to West Africa, which represents a 4200 km non-stop journey (Thorup et al. 2006, Delingat et al. 2008).

Along with the Wheatear, the Ringed Plover breeding in the Canadian Arctic migrates along the transatlantic route and thus represents a good model to examine migration strategies used to cross major ecological barriers. Nearctic Ringed Plover populations are suspected to migrate to the main wintering sites of the species along the eastern Atlantic coasts (i.e. Africa), but empirical evidence is lacking (Delany et al. 2009, Dunn et al. 2010). Using geolocation devices deployed over three years, we investigated the wintering areas and seasonal variation in migration strategies of Ringed Plovers nesting on Bylot Island in the Canadian High-Arctic. We identified stopover sites and migration routes used by Ringed Plovers to cross the Atlantic Ocean during both autumn and spring migrations. We expected plovers to take a northerly route in spring and use Iceland as a stepping-stone, therefore reducing continuous long-distance flights over the ocean before reaching their breeding grounds in the Canadian High-Arctic. However, because of prevailing anticlockwise winds associated with the Icelandic low-pressure system (Alerstam 1996, Summers et al. 2014), we expected that birds would take a more southerly route in autumn and perform direct transatlantic flights.

Material and methods

Our study site was located on Bylot Island (73°08'N, 80°00'W), Nunavut (Canada), near the northwest limit of the breeding distribution of the Ringed Plover (Cramp and Simmons 1983). Incubating birds were captured on their nest using bownet traps and were marked using unique colour-band combinations. From 2014 to 2016, 72 adult Ringed Plovers were fitted with geolocators (38 males and 34 females). We used Intigeo-W65A9 geolocators (MigrateTechnology, Ltd.) attached on a leg flag to track individuals. The geolocators with the flag weighted 0.93 ± 0.03 g, which represented on average 1.5 ± 0.1% of an individual's body mass (males = 63.5 ± 4.0 g, females = 62.4 ± 4.8 g).

Geographic locations of marked birds were calculated using the threshold method (Hill and Braun 2001). Sunset and sunrise were determined with IntiProc software (Migrate Technology Ltd, v1.03) and then processed with R package GeoLight 2.0.0 (Lisovski et al. 2015). Prior to deployment, geolocators were calibrated on a rooftop in Mont-Joli (Québec, Canada), resulting in a sun elevation angle ranging from -6.7° to -7.4° (-7.0° ± 0.18, n = 18). Twilight events were identified using a threshold of 3 lux. Stationary periods were separated from movement periods using the ChangeLight function (probability of change = 0.9 quantile) with a minimum staging period set at 2 days (Lisovski and Hahn 2012). The Hill-Ekstrom calibration method was used to refine the location estimate by calculating the sun elevation angle for each stationary period (Hill and Braun 2001, Ekstrom 2004). Discrimination between stationary and movement locations was verified visually using maps and graphs of longitude and latitude against date to identify clear shifts indicating bird movements. Sunrise and sunset data were filtered using the LoessFilter function with two interquartile ranges as thresholds to remove extreme outliers. The precision of locations was calculated using calibration data only and resulted in a mean error of 163 ± 75 km (n = 20), which is comparable to other studies (see Lisovski et al. 2012 and references therein).

Around the equinoxes, day length is similar around the globe; therefore, the estimation of latitudes is inherently imprecise. However, longitudes can still be reliably known (Lisovski et al. 2012) and can be used to identify stopover sites during predominately east-west migration movements (Porter and Smith 2013).

Following visual inspection of data, asymmetric periods associated with the equinoxes (Ekstrom 2004) were defined as 5 days prior to the autumnal equinox to 20 days after, as well as 20 days prior to the vernal equinox to 5 days after. However, equinoxes had very little effects on the estimation of travel routes and only affected the last autumnal migration bouts of 7 individuals (out of 20). We used longitudes and geographic features (e.g. coastlines) to estimate timing of the last migration bouts. This was not possible for two individuals for which arrival date at the wintering site could not be estimated properly. One staging site was used only during the autumnal equinox, so we also used longitudes and geographic features to estimate the site location. For the northernmost part of the migration tracks, we repeated the analysis described above using a light threshold of 50 units to account for extensive daylight during polar summer (Porter and Smith 2013). This approach allowed us to detect additional staging sites or to better estimate the migration timeline in these northern regions. We ran a sensitivity analysis using higher light thresholds (up to 200 units), but no other staging sites were detected. We smoothed movement periods by calculating average position over a 3-position moving window. We use this 3-position average to get more realistic movement tracks (i.e. to include movements away from the shortest route) while excluding erroneous movements caused by noise in light data. Averaging over longer periods, however, can result in the exclusion of real detours taken by birds. For each stationary period, longitude and latitude estimates were averaged to illustrate the stopover site. During stationary periods with predominantly east-west coastlines, locations over open waters more than 150 km offshore were relocated on the coast using longitude only (Porter and Smith 2013). We considered that an individual had reached the wintering site when we could not detect clear shifts in locations for >60 days. Migration tracks were mapped on Azimuthal Orthographic Projection in QGIS 2.10.1.

Exact arrival and departure dates at the breeding site were unknown because of extensive daylight during Arctic summer. Hence, we calculated migration rates (km/day for the overall migration) using the first (in autumn) and last (in spring) date when a bird was located, which typically occurred in Greenland (< 1800 km away from the breeding site). Individuals that did not stop in Greenland during the spring migration (5 out of 17) were excluded from statistical comparison of their migration rates. Distances between two subsequent staging sites were calculated using orthodromic (great circle route) distances and the ellipsoid method ("distVicentyEllipsoid" in R package Geosphere 3.4.3). Reported values are therefore the minimum potential distances and detours travelled by individuals between two staging sites (i.e. excluding locations during movement periods). Because geolocation gives only two locations per day, we estimated flight duration using departure and arrival times determined as follows: the departure time was set at half of the time interval between the last stationary location and the first subsequent movement location, and the arrival time was set at half of the time interval between the last known movement location and the first subsequent stationary location. Means for all variables are reported along with their standard deviations.

Results

From 2015 to 2017, we recaptured 29% of the individuals previously equipped with a geolocator on Bylot Island (n = 7 breeding individuals per year; total of 11 males and 10 females). Overall, we acquired 17 annual migration tracks (from 9 males and 8 females) and 3 incomplete tracks (full autumn migration and wintering grounds only, for 1 male and 2 females). We also obtained one additional incomplete annual track (full autumn migration) from a geolocator that recorded 1.5 years of migration data for one individual. We illustrated this additional migration path in our results (Figure 1) but did not use it in our statistical analyses to avoid pseudoreplication.

Ringed Plovers travelled a total round-trip migration distance of 17059 ± 1004 km (n = 17) between their breeding site in the Canadian Arctic and their wintering grounds in Africa (Figure 1). All but one individual spent the winter in Western Africa (southernmost Western Sahara, Mauritania, Senegal, Gambia and Guinea-Bissau) between 12°27’N and 22°39’N of latitude (mean latitude 16°23’ ± 2°36’ N in Southern Mauritania, n = 19). The remaining individual wintered in Northern Morocco (32°00’ N), with possible site itinerancy between Morocco and Southern Spain. After leaving the breeding site in autumn, individuals were detected for the first time on Baffin Island (Canada) or Greenland (<1500 km from the breeding site) between August 1 and August 11 (mean date: August 5, n=20). They reached their wintering sites between August 25 and October 28 (mean: September 11, n=18) and left their wintering sites between February 24 and May 8 (mean: April 15, n=17). For details on migration schedule of each individual, see supplementary material Appendix 1 Table A1.

Autumn migration strategies

All individuals stopped along the southwest coast of Greenland (Figure 1), which represented the first extended stopover detected during the autumn migration (stopover duration: 10.0 ± 4.5 days, range = 3.5-24.0

days, n = 20). All but one individual circumvented Greenland by the South and avoided the ice cap or crossed it near the southern tip, where its extent is substantially reduced. Among the 20 individuals, 7 individuals stopped for two days or more near the southernmost tip of Greenland, avoiding the ice cap entirely. Individuals used different strategies to cross the Atlantic Ocean, with 16 plovers (out of 20) skipping Iceland and migrating directly to Western Europe. Among them, 5 individuals flew directly from Southern Greenland to Spain, which represented a 3840 ± 363 km non-stop flight over water performed in 2.5 ± 0.5 days (range: 2.0 to 3.0 days). In contrast, 4 individuals used Iceland as a stepping-stone before reaching Western Europe and crossed the ocean in two shorter bouts of 1530 ± 267 km and 1798 ± 126 km over water. The detour by Iceland significantly increased the distance travelled between Greenland and Spain compared with individuals that skipped Iceland and flew directly to Spain (25.4 ± 13.1% longer; 4816 ± 503 km vs. 3840 ± 363 km; $t(5.3) = -3.3$, $p=0.02$).

Spring migration strategies

During the spring migration, all individuals (n = 17) followed the Atlantic coast of Western Europe and all but one stopped in the northern part of the British Isles (Figure 1; stopover duration: 11 ± 6.5 days, range = 4-29 days). A much higher proportion of individuals stopped in Iceland in spring than in autumn (15 out of 17 individuals spent ≥ 2 days in Iceland vs. 4 out of 20 individuals, respectively; Fisher's exact test, odds ratio=26.2, $p<0.0001$). One individual probably made a very short stopover in Iceland (<2 days), while the other likely skipped Iceland by following a more southerly route, far from the Icelandic coast, before reaching the southernmost tip of Greenland in 2.5 days (Figure 1, top-right panel, in grey). Plovers that stopped in Iceland (n = 15) departed from this stopover site between May 15 and June 3, and among them, 10 individuals made a stopover in Southern Greenland between May 17 and June 8. It was not possible to locate birds above 65° of latitude North because of the extensive daylight. As we were not able to get a single position for 5 individuals following their departure from Iceland, it suggests that they crossed the Greenland ice cap at relatively high latitudes (i.e. above 65°N). The 10 individuals that partly avoided the ice cap and made a stopover in Southern Greenland travelled a distance of at least 3033 ± 238 km between Iceland and their breeding site. This represented an average detour of 633 ± 238 km (20.4 ± 6.2% longer) compared with a direct flight of 2400 km across the Greenland ice cap from Iceland to the breeding site. For details about individual schedule of the transatlantic crossing, see supplementary material Appendix 1 Table A2.

Overall, Ringed Plovers travelled a total distance of 8508 ± 530 km in autumn (n=20) and of 8645 ± 529 km in spring (n=17). When compared to a hypothetical direct flight of 6890 ± 428 km between the breeding and wintering sites of individuals (n = 17), it represented a total detour of 1088 ± 316 (range 582 to 1641; 12.9 ± 3.4% longer) in autumn and 1320 ± 302 km (range 779 to 1778 km; 15.2 ± 3.0% longer) in spring. The total detour flown by individuals in spring was longer than the one flown during the autumn migration (paired t-test, $t(16)=-3.2$, $p=0.003$, mean difference = 232 km). Migration rates between the Greenland stopover and the wintering site averaged 226 ± 67 km per day during fall migration (range 61-339 km/day, n = 18), which was faster than the spring migration for the same part of the migration route (169 ± 40 km per day, range 60-214 km/day, n=12; LMER, $p<0.001$, estimate=48.1, SE=14.3 with "individual" as random effect). This pattern was similar in all years ($\chi^2(1) = 2.8$, $p = 0.01$) and for both sexes ($\chi^2(1) = 0.5$, $p = 0.5$). Spring migration rate for the 5 individuals not detected in Greenland in spring (and therefore excluded for the seasonal comparison) averaged 167 ± 69 km per day (range 107-271 km/day) between the winter site and the last stopover detected (i.e. Iceland).

Discussion

Our study revealed that Ringed Plovers nesting in the Canadian High-Arctic overwinter mainly in Western Africa and use contrasting seasonal migration strategies along the Nearctic-European Flyway. As expected, individuals followed a more northerly route in spring, largely using the British Isles and Iceland as stepping-stones and minimizing long-distance flights over the ocean. In autumn, however, we found higher intra-population variability in migration routes, with most individuals skipping Iceland. Our results showed that nearctic migrants can perform a direct transatlantic flight from Greenland to Southwestern Europe and confirmed that the Ringed Plover is one of the Nearctic species with the longest migration along the transatlantic route. Nearctic birds likely use wind assistance for their transatlantic flights (Summers et al. 2014) and we suggest that seasonal variation in migration strategies observed in Ringed Plovers partly result from prevailing anticlockwise winds associated with the Icelandic low-pressure system (see below).

Wintering areas of Ringed Plovers

Our data indicate that the main wintering area use by Ringed Plovers nesting on Bylot Island is located south of the wintering grounds used by the southern breeding populations, including the British Isles, the coastal Baltic Sea, North Sea and Southern Scandinavia and the Icelandic breeding populations (Taylor 1980, Wernham 2002, Delany et al. 2009, Thorisson et al. 2012). The Ringed Plover is a well-known example of species migrating according to a "leap-frog pattern" where populations breeding in the North typically migrate to wintering grounds located further south compared to the southern breeding populations (Salomonsen 1955). Our results are consistent with this general pattern and indicate that Canadian Ringed Plovers spend the winter at similar latitudes to the few Northern Scandinavian breeding plovers tracked so far (see Lislevand et al. 2016). Interestingly, individuals from the easternmost breeding population (Chukotka, Russia) and tracked with geolocators spent winter in the Arabian Peninsula and Northeast Africa (Tomkovich et al. 2017). This suggests an east-west divide in the species wintering distribution with western breeding birds wintering in West Africa and Europe and eastern breeding birds wintering in East Africa and Middle East. Integrating migration data of several Ringed Plover populations, including those breeding at the northern limit of the species distribution, would likely give new insights into the evolutionary processes behind the leap-frog migration pattern.

Barriers, wind and migration strategies of Nearctic birds

Most Ringed Plovers we tracked made a stopover in South Greenland, thereby largely avoiding the ice cap in autumn. In spring, however, one third of the individuals that stopped in Iceland could not be located after their departure, suggesting that they crossed the ice cap above 65°N, where extensive daylight did not allow us to obtain a position using geolocators. Direct crossing in spring has previously been supported by visual observations of knots, turnstones and Brent Geese departing from Iceland and heading towards the Greenland ice cap (Alerstam et al. 1990) and confirmed by radar and visual observations of migrants over the ice cap (Alerstam et al. 1986). Moreover, Salomonsen (1950) reported that Ringed Plovers, turnstones and knots, although common passing migrants in West Greenland, were absent in Southwest Greenland in spring, suggesting they cross the ice cap further north. Satellite telemetry also confirmed that White-fronted Geese (Fox et al. 2003) and Brent Geese (Gudmundsson et al. 1995) departing from Iceland cross the Greenland ice cap near or above 65°N during spring migration, where the ice cap rises >2500m in height.

The seasonal variation in ocean crossing strategies observed in Ringed Plovers may be common in other transatlantic birds. Nearctic Purple Sandpipers wintering in the British Isles make a detour in spring, with a majority of tracked individuals stopping in Iceland before reaching Greenland or Canada (Summers et al. 2014). Moreover, passages of nearctic shorebirds in Iceland are typically marked by high peaks in abundance of Red Knots, Ruddy Turnstones and Sanderlings in spring that are much less pronounced in autumn (Wilson 1981), suggesting that some birds use a more northerly route in spring. Based on visual observations (Snow 1953, Williamson 1958), leg-ring recoveries (Alerstam 1996) or departure fuel load at stopover sites (Dierschke et al. 2005), Nearctic Wheatears also appear to take a more northerly route in spring and a more direct transatlantic flight to Western Europe in the autumn. Whimbrels (*Numenius phaeopus*) breeding in Iceland undertake a fast and direct transoceanic flight in autumn to reach their wintering site in West Africa, while most individuals make a stopover in Europe during spring migration (Carneiro et al. 2019). Such transatlantic flight could be facilitated by better wind condition with individuals experiencing more wind support in autumn than in spring (Alves et al. 2016, Carneiro et al. 2019).Contrasting seasonal migration strategies, with migrants largely avoiding the ocean in spring but making long transoceanic flights in autumn, have been associated with favourable wind patterns in other migration flyways. For instance, selection of favourable winds can greatly facilitate the migration of Bar-tailed Godwits (*Limosa lapponica baueri*), which use distinct seasonal routes with an impressive transoceanic flight in autumn between Alaska and New Zealand, but largely limit their crossing of the Pacific Ocean in spring with a detour in East Asia (Gill et al. 2009, 2014). Similarly, many passerine and shorebird species breeding in eastern North America follow the landmass in spring but undertake a transoceanic flight over the Western Atlantic in autumn to reach the Caribbean or South America (Williams et al. 1977, Richardson 1979, Alerstam 1993). Such a transoceanic flight is also partly attributed to favourable wind patterns in autumn, with migrants taking advantage of northwest winds following strong cold fronts (Richardson 1979).

Seasonal and geographic consistency in prevailing wind patterns can create optimal flyways along which migrants can benefit from wind assistance (Kemp et al. 2010, Kranstauber et al. 2015), acting as a selective factor in the evolution of migration routes (Alerstam 1979, Gauthreaux et al. 2005). Some migratory flyways coincide with general airflows, which appear particularly important in the evolution of migration routes across extensive barriers such as the Sahara (Erni et al. 2005, Schmaljohann et al. 2009), the Western Atlantic Ocean (Richardson 1979) and the Pacific Ocean (Gill et al. 2009, 2014). Unless birds can benefit from wind assistance, migration routes that minimize continuous flight distances over ecological barriers should be favoured by natural selection (Alerstam 2001, Henningsson and Alerstam 2005).

Seasonal variation in migration routes and the use of stopover sites along the transatlantic migration could also be influenced by the final destination (breeding location), food availability and predation risk (Bauer et al. 2010). Higher food intake rates at stopover sites located closer to the breeding grounds could be an important factor shaping spring migration routes in shorebirds (Piersma et al. 2005), notably by providing favourable pre-breeding foraging conditions required to nest in the Arctic (Henningsson and Alerstam 2005). The use of a more northerly route in spring could allow transatlantic migrants to appraise conditions on the breeding areas (Carneiro et al. 2019) and to access good stopover sites allowing them to bring extra body reserves needed upon arrival on the breeding sites (Morrison et al. 2005, Gill et al. 2009). Transoceanic flights could be selected because open oceans provide routes with reduced risk of predation, particularly in autumn when adult avian raptors are joined by juveniles, increasing predator density (Lank et al. 2003)

Overall, it is likely that prevailing wind patterns over the North Atlantic Ocean partly explain the seasonal variation in migration strategies used by nearctic birds (Salomonsen 1967, Alerstam 1996). The Iceland stopover may be of a greater importance in spring by reducing continuous flight distance over the ocean when migrants would face unfavourable winds altering their ability to make a direct ocean crossing. In autumn, however, nearctic birds may benefit from the atmospheric pressure system over the North Atlantic Ocean (Serreze et al. 1997, Summers et al. 2014). Therefore, the Atlantic Ocean may act as a major barrier for nearctic migrants in spring because of headwinds, but not necessarily in autumn if they can use wind assistance. To our knowledge, no studies have yet fully described the consistency of favourable wind patterns over the North Atlantic Ocean and related these patterns to multi-year transatlantic migration datasets. This would be needed to rigorously investigate the effect of wind assistance on migration strategies of nearctic species.

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References

Alerstam, T. 1979. Wind as selective agent in bird migration. - Ornis Scand. 10: 76–93.

Alerstam, T. 1993. Bird Migration. - Cambridge University Press.

Alerstam, T. 1996. The geographical scale factor in orientation of migrating birds. - J. Exp. Biol. 199: 9–19.

Alerstam, T. 2001. Detours in bird migration. - J. Theor. Biol. 209: 319–331.

Alerstam, T. 2011. Optimal bird migration revisited. - J. Ornithol. 152: 5–23.

Alerstam, T., Hjort, C., Högstedt, G., Jönsson, P. E., Karlsson, J. and Larsson, B. 1986. Spring migration of birds across the Greenland Inlandice. - Meddelelser om Grønland Bioscience 21: 1–38.

Alerstam, T., Gudmundsson, G. A., Jönsson, P. E., Karlsson, J. and Lindström, Å. 1990. Orientation, migration routes and flight behaviour of Knots, Turnstones and Brant Geese departing from Iceland in spring. - Arctic 43: 201–214.

Alerstam, T., Hedenström, A. and Akesson, S. 2003. Long-distance migration: evolution and determinants. - Oikos 103: 247–260.

Alves, J. A., Dias, M. P., Mendez, V., Katrínardóttir, B. and Gunnarsson, T. G. 2016. Very rapid long-distance sea crossing by a migratory bird. - Sci. Rep.: 1–6.

Bairlein, F., Norris, D. R., Nagel, R., Bulte, M., Voigt, C. C., Fox, J. W., Hussell, D. J. T. and Schmaljohann, H. 2012. Cross-hemisphere migration of a 25 g songbird. - Biol. Lett. 8: 505–7.

Bauer, S., Ens, B. J. and Klaassen, M. 2010. Many routes lead to Rome : potential causes for the multi-route migration system of Red Knots, *Calidris canutus islandica*. - Ecology 91: 1822–1831.

Berthold, P. 2001. Bird migration: a general survey. - Oxford University Press.

Carneiro, C., Gunnarsson, T. G. and Alves, J. A. 2019. Faster migration in autumn than in spring: seasonal migration patterns and non-breeding distribution of Icelandic whimbrels *Numenius phaeopus islandicus*. - J. Avian Biol. 50: 1–8.

Corman, A. M., Bairlein, F. and Schmaljohann, H. 2014. The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird. - Behav. Ecol. Sociobiol. 68: 391–402.

Cramp, S. and Simmons, K. E. L. 1983. Handbook of the birds of Europe, the Middle East, and North Africa: The birds of the Western Palearctic Volume III: Waders to gulls. - Oxford University Press.

Delany, S., Scott, D., Dodman, T. and Stroud, D. 2009. The Wader Atlas: an atlas of wader populations in Africa and Western Eurasia. - Wetlands International and International Wader Study Group, Wageningen, NL.

Delingat, J., Bairlein, F. and Hedenström, A. 2008. Obligatory barrier crossing and adaptive fuel management in migratory birds: The case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*). - Behav. Ecol. Sociobiol. 62: 1069–1078.

DeLuca, W. V., Woodworth, B. K., Rimmer, C. C., Marra, P. P., Taylor, P. D., McFarland, K. P., Mackenzie, S. A. and Norris, D. R. 2015. Transoceanic migration by a 12 g songbird. - Biol. Lett. 11: 1–4.

Dierschke, V., Mendel, B. and Schmaljohann, H. 2005. Differential timing of spring migration in Northern Wheatears *Oenanthe oenanthe*: Hurried males or weak females? - Behav. Ecol. Sociobiol. 57: 470–480.

Dietz, M. W., Spaans, B., Dekinga, A., Klaassen, M., Korthals, H., van Leeuwen, C. and Piersma, T. 2010. Do Red Knot (*Calidris canutus islandica*) routinely skip Iceland during southward migration? - Condor 112: 48–55.

Dunn, E. H., Brewer, A. D., Diamond, A. W., Woodsworth, E. J. and Collins, B. T. 2010. Canadian atlas of bird banding, Vol .4: shorebirds, 1921-1995. - Canadian Wildlife Service Special Publication.

Ekstrom, P. P. 2004. An advance in geolocation by light. - Mem. Natl. Inst. Polar Res. Spec. Issue 58: 210–226.

Erni, B., Liechti, F. and Bruderer, B. 2005. The role of wind in passerine autumn migration between Europe and Africa. - Behav. Ecol. 16: 732–740.

Fox, A. D., Glahder, C. M. and Walsh, A. J. 2003. Spring migration routes and timing of Greenland White-fronted Geese - results from satellite telemetry. - Oikos 103: 415–425.

Gauthreaux, S. A. J., Michi, J. E. and Belser, C. G. 2005. The temporal and spatial structure of the atmosphere and its influence on bird migration strategies. - In: Birds of Two Worlds: the ecology and evolution of migration. Johns Hopkins University Press, pp. 182–193.

Gill, R. E., Tibbitts, T. L., Douglas, D. C., Handel, C. M., Mulcahy, D. M., Gottschalck, J. C., Warnock, N., McCaffery, B. J., Battley, P. F. and Piersma, T. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? - Proc. R. Soc. B Biol. Sci. 276: 447–457.

Gill, R. E., Douglas, D. C., Handel, C. M., Tibbitts, T. L., Hufford, G. and Piersma, T. 2014. Hemisphericscale wind selection facilitates bar-tailed godwit circum-migration of the Pacific. - Anim. Behav. 90: 117–130.

Gudmundsson, G. A. and Gardarsson, A. 1993. Numbers, geographic distribution and habitat utilization of waders (Charadrii) in spring on the shores of Iceland. - Ecography. 16: 82–93.

Gudmundsson, G. A., Benvenuti, S., Alerstam, T., Papi, F., Lilliendahl, K. and Akesson, S. 1995. Examining the limits of flight and orientation performance: satellite tracking of Brent Geese migrating across the Greenland ice-cap. - Proc. R. Soc. B Biol. Sci. 261: 73–79.

Henningsson, S. S. and Alerstam, T. 2005. Barriers and distances as determinants for the evolution of bird migration links: the arctic shorebird system. - Proc. R. Soc. B 272: 2251–2258.

Hill, R. D. and Braun, M. J. 2001. Geolocation by light level. - In: Electronic tagging and tracking in marine fisheries. Springer. pp. 315–330.

Johnson, O. W., Fielding, L., Fox, J. W., Gold, R. S., Goodwill, R. H. and Johnson, P. M. 2011. Tracking the migrations of Pacific Golden-Plovers (*Pluvialis fulva*) between Hawaii and Alaska: new insight on flight performance, breeding ground destinations, and nesting from birds carrying light level geolocators. - Wader Study Gr. Bull. 118: 26–31.

Kemp, M. U., Shamoun-Baranes, J., Van Gasteren, H., Bouten, W. and Van Loon, E. E. 2010. Can wind help explain seasonal differences in avian migration speed? - J. Avian Biol. 41: 672–677.

Klaassen, R. H. G., Alerstam, T., Carlsson, P., Fox, J. W. and Lindström, Å. 2011. Great flights by great snipes: long and fast non-stop migration over benign habitats. - Biol. Lett. 7: 833–835.

Kranstauber, B., Weinzierl, R., Wikelski, M. and Safi, K. 2015. Global aerial flyways allow efficient travelling. - Ecol. Lett. 18: 1338–1345.

Kvist, A., Lindström, Å., Green, M., Piersma, T. and Visser, G. H. 2001. Carrying large fuel loads during sustained bird flight is cheaper than expected. - Nature 413: 730–732.

Lank, D. B., Butler, R. W., Ireland, J. and Ydenberg, R. C. 2003. Effects of predation danger on migration strategies of sandpipers. - Oikos 103: 303–319.

Liechti, F. 2006. Birds: Blowin' by the wind? - J. Ornithol. 147: 202–211.

Lislevand, T., Briedis, M., Heggøy, O. and Hahn, S. 2016. Seasonal migration strategies of Common Ringed Plovers *Charadrius hiaticula*. - Ibis. 159: 225–229.

Lisovski, S. and Hahn, S. 2012. GeoLight - processing and analysing light-based geolocator data in R. - Methods Ecol. Evol. 3: 1055–1059.

Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W. and Hahn, S. 2012. Geolocation by light: Accuracy and precision affected by environmental factors. - Methods Ecol. Evol. 3: 603–612.

Lisovski, S., Wotherspoon, S., Sumner, M., Bauer, S., Emmenegger, T. and Lisovski, M. S. 2015. Package 'GeoLight.' - The R Project for Statistical Computing.

Moreau, R. E. 1972. The Palaearctic-African bird migration systems. - Academic Press.

Morrison, R. I. G., Davidson, N. C. and Piersma, T. 2005. Transformations at high latitudes : why do Red Knots bring body stores to the breeding grounds? - Condor 107: 449–457.

Newton, I. 2008. The migration ecology of birds. - Elsevier Academic Press.

Pennycuick, C. J. 1975. Mechanics of flight. - In: Farner, D. S. & King, J. R. (ed), Avian Biology, vol. 5. Academic Press, pp. 1–75.

Piersma, T. 2011. Why marathon migrants get away with high metabolic ceilings: towards an ecology of physiological restraint. - J. Exp. Biol. 214: 295–302.

Piersma, T., Rogers, D. I., González, P. M., Zwarts, L., Niles, L. J., de Lima do Nascimento, I., Minton, C. D. T. and Baker, A. J. 2005. Fuel storage rates before northward flights in Red Knots worldwide. - In: Birds of Two Worlds: the ecology and evolution of migration. pp. 262–273.

Porter, R. and Smith, P. A. 2013. Techniques to improve the accuracy of location estimation using light-level geolocation to track shorebirds. - Wader Study Gr. Bull. 120: 147–158.

Richardson, W. J. 1979. Southeastward shorebird migration over Nova Scotia and New Brunswick in autumn: a radar study. - Can. J. Zool. 57: 107–124.

Salomonsen, F. 1950. Grønlands fugle: The birds of Greenland. - Munksgaard.

Salomonsen, F. 1955. The evolutionary significance of bird migration. - Biol. Meddelelser 22: 62.

Salomonsen, F. 1967. Fuglene på Grønland. - Copenhagen, DK.

Schmaljohann, H., Liechti, F. and Bruderer, B. 2009. Trans-Sahara migrants select flight altitudes to minimize energy costs rather than water loss. - Behav. Ecol. Sociobiol. 63: 1609–1619.

Serreze, M. C., Carse, F., Barry, R. G. and Rogers, J. C. 1997. Icelandic low cyclone activity: Climatological features, linkages with the NAO, and relationships with recent changes in the Northern Hemisphere circulation. - J. Clim. 10: 453–464.

Snow, D. W. 1953. The migration of the Greenland Wheatear. - Ibis. 95: 376–378.

Summers, R. W., Boland, H., Colhoun, K., Elkins, N., Etheridge, B., Foster, S., Fox, J. W., Mackie, K., Quinn, L. R. and Swann, R. L. 2014. Contrasting trans-Atlantic migratory routes of Nearctic Purple Sandpipers *Calidris maritima* associated with low pressure systems in spring and winter. - Ardea 102: 139–152.

Taylor, R. C. 1980. Migration of the Ringed Plover *Charadrius hiaticula*. - Ornis Scand. 11: 30–42.

Thorisson, B., Eyjólfsson, V., Gardarsson, A., Albertsdóttir, H. B. and Gunnarsson, T. G. 2012. The non-breeding distribution of Icelandic Common Ringed Plovers. - Wader Study Gr. Bull. 119: 97–101.

Thorup, K., Ortvad, T. E. and Rabøl, J. 2006. Do nearctic Northern Wheatears (*Oenanthe oenanthe leucorhoa*) migrate nonstop to Africa? - Condor 108: 446–451.

Tomkovich, P. S., Porter, R., Loktionov, E. Y. and Syroechkovskiy, E. E. 2017. Transcontinental pathways and seasonal movements of an Asian migrant, the Common Ringed Plover *Charadrius hiaticula tundrae*. - Wader Study Gr. Bull. 124: 175–184.

Wernham, C. 2002. The Migration Atlas: Movements of the Birds of Britain and Ireland. - British Trust for Ornithology.

Williams, T. C., Williams, J. M., Ireland, L. C. and Teal, J. M. 1977. Autumnal bird migration over the western North Atlantic Ocean. - Am. Birds 31: 251–267.

Williamson, K. 1958. Bergmann's rule and obligatory overseas migration. - Br. Birds 51: 209–232.

Wilson, J. R. 1981. The migration of High Arctic shorebirds through Iceland. - Bird Study 28: 21–32.

Supplementary material (Appendix JAV-02101 at www.avianbiology.org/readers/appendix). Appendix 1.

Figure Legend

Figure 1