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Contrasting trans-Atlantic migratory routes of Nearctic Purple Sandpipers *Calidris maritima* associated with low pressure systems in spring and winter

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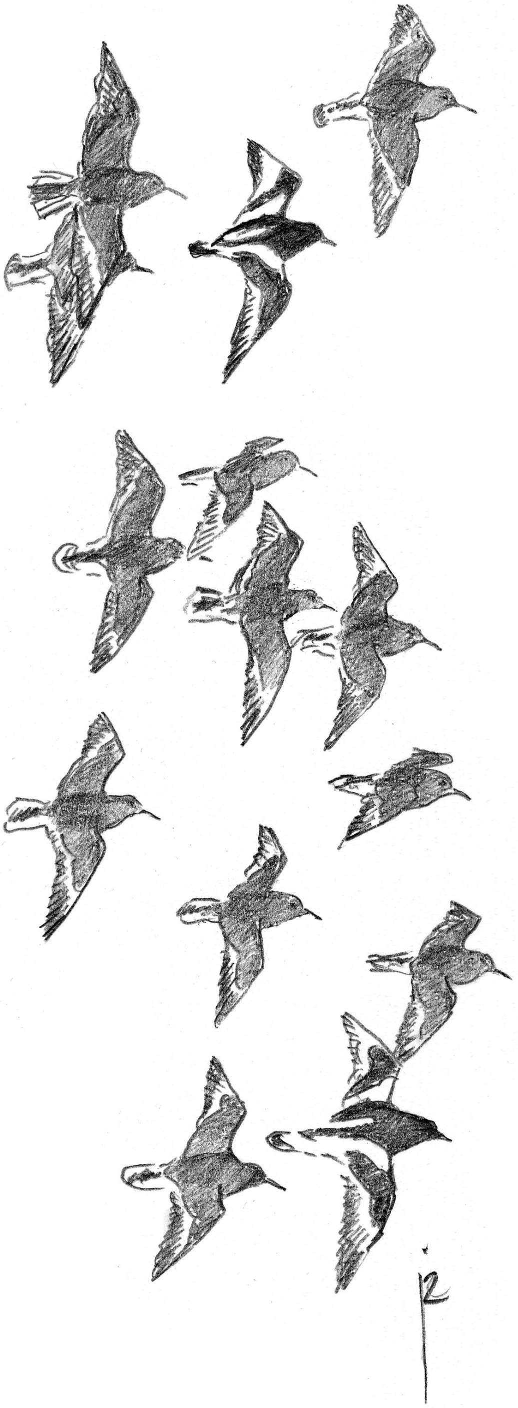

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Bird migration is generally scheduled to avoid other energetically expensive events in the annual cycle (e.g. moult) and seasons when survival can be difficult (e.g. northern winters). Purple Sandpipers winter at relatively high latitudes compared to other waders. It is suspected that the majority that winter in Britain and Ireland originate from Canada, but there is no primary evidence of their breeding grounds and migratory routes. These birds, characterised by their long bills, start to arrive in Britain and Ireland in late October/early November, after completing their post-nuptial moult at an unknown location. Fifty geolocators were attached to Purple Sandpipers in northern Scotland and southwest Ireland and we established for the first time their Canadian origin (Baffin Island and Devon Island), migration routes and post-nuptial moulting areas. Spring departure from Scotland and Ireland took place mainly in late May, followed by staging in Iceland and/or southwest Greenland before reaching the breeding grounds. Those that staged in Iceland departed earlier than those that flew directly to Greenland. Post-nuptial moulting areas were in southern Baffin Island, northern Quebec/Labrador (the Hudson Strait), and southwest Greenland. Migration from Baffin Island and Labrador took place during late October – early November, and during mid to late December from Greenland, usually in a single trans-Atlantic flight. Therefore, this migration was scheduled at a time when most other wader species are already on their wintering grounds. No birds staged in Iceland on the return trip. The flight from Baffin Island to Scotland and Ireland was accomplished in about 2.5 days at an average speed of about 1400 km per day. Freezing of coastal waters may be the reason for the eventual departure from the Hudson Strait. The more northerly route via Iceland, taken in spring by most birds, and the more southerly route in early winter were associated with seasonal shifts in the Atlantic low pressure systems (depressions) whose anti-clockwise wind-flows would have assisted flights.

Key words: Arctic, Atlantic, *Calidris maritima*, migration, synoptic charts

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Migration is an energetically costly event in the life cycle of birds that breed in areas that become untenable during the non-breeding season (Lack 1954, Alerstam 1990, Newton 2010). For long-distance migrants there is often a period of accumulation of migratory stores used as fuel during migration. There may also be a change in organ sizes, maximising those required for flight and minimising those not required (Piersma *et al.* 1999). To assist migration, birds may select favourable winds (Butler *et al.* 1997, Dokter *et al.* 2013), though species reliant on thermal soaring may show no wind selection (Thorup *et al.* 2006). Moult is an additional energetic cost (Dolnik & Gavrilov 1979) in the annual cycle and is generally scheduled in relation to breeding and migration (Holmes 1971), whilst also avoiding periods of food shortage, such as those usually experienced during northern winters (Prater 1981).

For birds that breed in the Arctic, the duration of the breeding season is short and food availability is highly seasonal, particularly for insectivorous birds. The arrival of Arctic-breeding birds is typically during May and June when the snow melts, and departure occurs during August–October prior to the first autumn snow (Freuchen & Salomonsen 1959). Arrival, and hence breeding, tends to be later and departure earlier at higher latitudes (Väisänen 1977, but see Conklin *et al.* 2010). Because of the short time between arrival and departure, breeding is often restricted to a single attempt and post-nuptial moult may be postponed until the birds reach non-breeding areas (e.g. Curlew Sandpiper *Calidris ferruginea*, Elliott *et al.* 1976), whilst others have a fast moult before leaving the Arctic (e.g. Snow Bunting *Plectrophenax nivalis*, Green & Summers 1975; Arctic geese, Owen 1980).

Sandpipers of the genus *Calidris* form a major component of the breeding bird community in the Arctic, and are renowned for their long migrations to and from non-breeding quarters (Cramp & Simmons 1983, e.g. Red Knot *Calidris canutus*, Piersma *et al.* 2005). Many sandpipers spend the non-breeding season in the tropics, probably to minimise daily energy requirements (Piersma 1996). For many sandpiper species and populations, the migration phenology and routes are well-known (Cramp & Simmons 1983, del Hoyo *et al.* 1996). However, the Purple Sandpiper *Calidris maritima* is one species for which our understanding of its migrations is still poor (Summers 1994). Its breeding range extends from northeast Canada, eastward to Greenland, Iceland, Svalbard and Scandinavia to the Severnaya Islands north of Arctic Siberia (Cramp & Simmons 1983). The winter range encompasses the rocky sea-shores of both sides of the North Atlantic Ocean, occurring further north (up to 71°N) than any other wader species (Cramp & Simmons 1983).

Biometric studies and counts of Purple Sandpipers round Britain showed that three-quarters of the c. 19,000 wintering birds (as estimated in the 1980s) belong to a long-billed population (males with a mean bill length of 29.8 mm and females 34.5 mm) occurring mainly in northern Scotland, whilst short-billed birds (males with a mean bill length of 25.4 mm and females 29.8 mm) occur in eastern Britain (Nicoll *et al.* 1988). The most recent estimate (2006/07) for the UK population is 11,300, but the current ratio of short- to long-billed birds is unknown (Austin *et al.* 2008). Biometric studies elsewhere indicate that long-billed birds are widespread in northwest Europe: The Netherlands (Boere *et al.* 1984), Germany (Dierschke 1995), Sweden (Hake *et al.* 1997), Ireland (Foster *et al.* 2010) and France (Guyonnet *et al.* 2011). The short-billed birds originate from Norway (Rae *et al.* 1986) and arrive on their wintering grounds in eastern Britain from mid-July when they start their post-nuptial moult (Summers *et al.* 2004). The origin of the long-billed birds is unknown, though evidence indicates that they may originate from Canada (reviewed by Hallgrimsson *et al.* 2012). They arrive on the wintering grounds from late October, having carried out the post-nuptial moult elsewhere (Nicoll *et al.* 1988).

Data loggers, such as light-based geolocators, can give approximate locations (geolocations) and are now small enough to be attached to sandpipers (e.g. Fox 2010, Minton *et al.* 2010, Niles *et al.* 2010, Johnson *et al.* 2011). However, to retrieve data from the geolocators, birds have to be re-trapped. Purple Sandpipers are site faithful to their winter quarters, making this possible (Atkinson *et al.* 1981).

Thus, the aim of this project was to determine, from geolocators, the migration routes, breeding quarters and post-nuptial moulting areas of long-billed Purple Sandpipers that spend the winter and spring in northern Scotland and western Ireland. We also examined how these energetically expensive events (migration and moult) are scheduled, and if weather patterns associated with the migrations assist flight.

METHODS

Purple Sandpipers roosting or feeding at high tide at Brora (58°01'N, 3°51'W), Sutherland and Buckie (57°41'N, 2°59'W), Banffshire, Scotland and Quilty (52°49'N, 9°29'W), County Clare, Ireland, were cannonnetted during the winters of 2009/10 to 2012/13 for tagging and tag retrieval (Table 1). British Antarctic Survey Mk10(S) geolocators (18 × 9 × 6 mm, 1.1 g) were attached to 50 Purple Sandpipers using a thigh-loop harness (Rappole & Tipton 1991), so that the geolocator sat on the lower back. The loops of the harness were made of soft plastic Silastic tubing through which a thin, elasticated thread ran (R.E. Green, pers. comm.). Thus, there was scope for the thread to expand if, for example, the size of the body changed during migratory fattening. The thread was also the weakest link, so tags were not expected to last more than one year on a bird. The geolocator was glued to a 1-mm thick piece of Zoetfoam to cushion it on the bird's back. The mass of the geolocator plus harness was 1.4 g, which represented a mean of 2.0% (range 1.6–2.5%, n = 50) of the mass of the birds. The light sensor was on a 15-mm stalk and inclined at an angle of 40° to keep it clear of feathers that tended to cover much of the rest of the tag. All birds were also ringed with a numbered BTO metal ring on the tibia, maximum wing length was measured with a stopped ruler to 1 mm, bill length with dial callipers to 0.1 mm and mass (without the geolocator attached) on an electronic balance to 0.1 g.

Because geolocators determine location from the times of sunrise and sunset, we were aware of the possibility that the Purple Sandpipers may go beyond the Arctic Circle (66°32'N) and experience varying periods of continuous daylight depending how far north they bred. We therefore selected mainly males to receive geolocators because they remain with the brood after hatching whilst the female departs from the breeding grounds (Bengtson 1970, Cresswell & Summers 1988). This maximised the possibility of birds still being on the breeding grounds when the light/dark regime restarted at the birds' breeding locations. Males of the long-billed population were identified according to bill lengths; most are within 27.6–32.1 mm whilst females are generally over 32.1 mm (Nicoll *et al.* 1988). There is no difference in the return rate to non-breeding areas of birds of different bill lengths (i.e. sexes) of this population (Summers *et al.* 2012).

It was assumed that immigration would be completed in November, so attempts to recapture birds with geolocators were made after this month. Only a single catching attempt was made at a given site each year with the aim to catch the entire roosting flock at high tide. Catches were made on 23 January 2011 at Brora, 21 February 2011 at Quilty, 8 April 2012 and 27 April 2013 at Buckie when one, six, four and one geolocators were retrieved, respectively (Table 1).

The data from the geolocators were downloaded and each light/dark transition (sunset or sunrise) evaluated to remove poor transitions, for example when the change in light levels was erratic due to cloud cover. In addition, predicted locations, approximately two weeks either side of the spring and autumn equinoxes, were removed when estimates of latitude were unreliable (Fox 2010). Times between transitions allowed calculation of day and night lengths (for latitude) whilst mid-points between transitions allowed estimation of local noon and midnight to compare with GMT noon and midnight (for longitude), using BASTrak software v.18 (Fox 2010). Therefore, two estimates of location were obtained per day. A light threshold value of 10 and sun angle of –3.5° were used, because they provided geolocations that related well to the periods when the birds were at the catching sites. With only two estimates of location per day, it was not possible to obtain exact times of departure and arrival. Therefore, to estimate the duration of flights to and from non-breeding and breeding areas, start times were taken as half way between the last record at a departure site and first showing movement, whilst arrival time was taken as half way between the last record during a flight and first at a destination.

Geolocators provide locations that can have a mean error of 186 km (SD = 114 km) for birds in flight and 85 km (SD = 47 km) for static loggers (Phillips *et al.* 2004), thereby providing a scatter of fixes even when a bird is stationary. To obtain further information on errors in geolocations, we calculated the median latitude and longitude for geolocations for each bird during 8–30 April from Scotland and Ireland prior to departure and compared these with the locations of the marking sites. The data prior to departure were typified by a scatter of geolocations that showed no trend, whilst departure was noted as a major shift in geolocation. A similar procedure was carried out for January geolocations when the birds were back at their winter quarters. For birds that were at staging and moulting areas, median latitudes and longitudes (plus inter-quartile ranges; IQRs) were calculated to provide estimates of locations. Kernel densities were calculated in the Spatial Analyst Tools in ArcToolbox for time spent resident in areas, with the deeper blue colours representing more frequently used areas.

To relate timing and routes of flights to weather, an assessment of meteorological variables was made along the trajectory of each bird. Data were sourced from professional meteorological websites. Daily Meteorological Office surface synoptic charts were obtained from www.wetterzentrale.de/topkarten/tkfaxbraar.htm.

Other meteorological data, e.g. surface and upper level wind directions and speed, and cloud cover, were obtained from www.ogimet.com/index.phtml.en, supplemented by upper level charts from www.wetterzentrale.de/topkarten/fsrea2eur.html.

Cloud cover was also sourced from polar orbiter and geostationary satellite data via www.sat.dundee.ac.uk. These data allowed potential effects of the weather on tracks of individual birds to be determined. Interpolation of data was necessary over most of the data-sparse tracks and it was also assumed that migratory flights were at altitudes of 500–1000 m, equivalent to the level of winds measured from isobars on synoptic charts (Elkins 2004). Most bird migration is below 1500–2000 m (Alerstam 1990). Wind directions refer to the direction from which the wind is blowing.

Incubation and brood attendance by Arctic-breeding Purple Sandpipers takes place from mid-June to the end of July (Summers & Nicoll 2004), though failed breeders may leave the breeding grounds earlier. Therefore, only geolocations obtained during mid-June to mid-July were regarded as indicative of breeding areas. The post-nuptial moulting period of Purple Sandpipers can occur between July and November depending on the origin of the population (Summers *et al.* 2004). Those that breed at lower latitudes in Norway and Iceland moult during late July to late September, whilst those in Russia are thought to moult from late August to early November. There is little known about the period of post-nuptial moult for Nearctic Purple Sandpipers. The only data are from Sutton & Parmelee (1955), who recorded early stages of primary moult during early August for three females in southern Baffin Island. Therefore, the moult period was taken as during August and September.

Purple Sandpiper geolocations were mapped on North Pole Lambert Azimuthal Equal Area projections in ArcGIS v. 9.3 (Gudmundsson & Alerstam 1998). To convert degrees to distance, one degree of latitude was taken as 111.4 km and one degree of longitude calculated from π/180 × radius of the Earth × cosine of the latitude.

RESULTS

The effect of the geolocators on the birds

We re-trapped 12 (24%) of 50 birds that were fitted with geolocators in groups of captured birds that also had birds that were not tagged (Table 1). We also re-trapped 27 (26%) of the 104 ringed birds that did not receive geolocators from the same groups. There was no evidence of a significantly lower return rate to non-breeding areas by the birds with geolocators (Yates' corrected $\chi^2_1 = 0.004$, $P = 0.95$). The only visible effect of the tags when the birds were in the hand was some feather loss around the thighs, perhaps due to the leg loops. For free-living birds, the upper legs are usually covered by body feathers, minimising any additional heat loss that the birds may have experienced. The mean percentage change in mass of the birds with geolocators was a 1.2% decline, compared to a mean 1.5% increase in mass for those birds that did not receive a geolocator. The difference in mass between the two groups was statistically significant ($t_{19} = -3.1$, $P = 0.006$), indicating a potential tag effect. The birds with geolocators were not treated separately during the recording of biometrics, so the difference cannot be accounted for by, for example, later weighing of those with geolocators. The data for the late-April catch were

Table 1. Summary of catches and recaptures of Purple Sandpipers. For each site, data on masses (g) are shown at initial capture, and recapture in the line below for those birds that were subsequently recaptured. The changes in masses between 8 and 27 April (in italics) were influenced by deposition of fat and protein for migration. A catch of four untagged re-traps is not shown.

Place	Date	Number captured (tagged)	Number recaptured		Mean mass at ringing and recapture of those recaptured	
			With tag	Without tag	With tag	Without tag
Brora	2 Mar 2010	14 (7)	0	0	67.0	71.0
Brora	23 Jan 2011	21	1	3	64.0	72.3
Quilty	1 Apr 2010	84 (24)	0	0	68.2	63.8
Quilty	21 Feb 2011	75	6	7	67.5	64.7
Buckie	21 Mar 2011	9 (9)	0	0	72.3	–
Buckie	8 Apr 2012	47 (10)	4	0	71.8, *69.0*	–, *71.5*
Buckie	27 Apr 2013	28	1	13	*69.0*	*77.9*

Table 2. The timing of migration by individual Purple Sandpipers marked in southwest Ireland (I#) and northern Scotland (S#). Sex (M = male, F = female). Dashes indicate that a site was not used. Blank spaces indicate that data were not obtained because the bird entered continuous day-light or the tag stopped recording (dates in brackets). Medians were based on different sample sizes.

Bird code/ Sex	Last date Ireland/ Scotland	First date Iceland	Last date Iceland	First date Greenland	Last date Greenland	First date Canada	Continuous daylight	Last date Canada	First date Greenland	Last date Greenland	First date Ireland/ Scotland
I48/M	2 Jun	–	–	4 Jun	12 Jun	12 Jun	17 Jun – 16 Jul	8 Nov	–	–	12 Nov
I49/F	31 May	–	–	1 Jun	5 Jun	5 Jun	9 Jun – 18 Jul	1 Nov	–	–	5 Nov
I51/M	27 May	28 May					2 Jun – 10 Aug	9 Nov	–	–	12 Nov
I55/M	21 May	22 May	31 May	1 Jun			4 Jun – 17 Jul	26 Oct	–	–	28 Oct
I57/M	21 May	22 May	28 May	29 May			3 Jun – 24 Jul	26 Oct	–	–	29 Oct
I62/M	1 Jun	–	–	4 Jun	10 Jun	11 Jun	–	20 Nov	23 Nov	13 Dec	16 Dec
S1/F	19 May	20 May	24 May	25 May			3 Jun – 20 Aug	24 Aug	25 Aug	26 Dec	29 Dec
S41/M	18 May	–	–	19 May	29 May	31 May	11 Jun – 21 Jul	4 Nov	–	–	7 Nov
S53/F	1 May	2 May	18 May	19 May	23 May	24 May	12 Jun – 12 Jul	5 Nov	–	–	8 Nov
S58/F	5 May	6 May	29 May	30 May	3 Jun	3 Jun	15 Jun – 26 Jul	8 Nov	–	–	11 Nov
S48/M	25 Apr	26 Apr	(21 May)								
S04/M	7May	8 May	(18 May)								
Median	20 May	14 May	28May	30 May	4 Jun	4 Jun		5 Nov			10 Nov

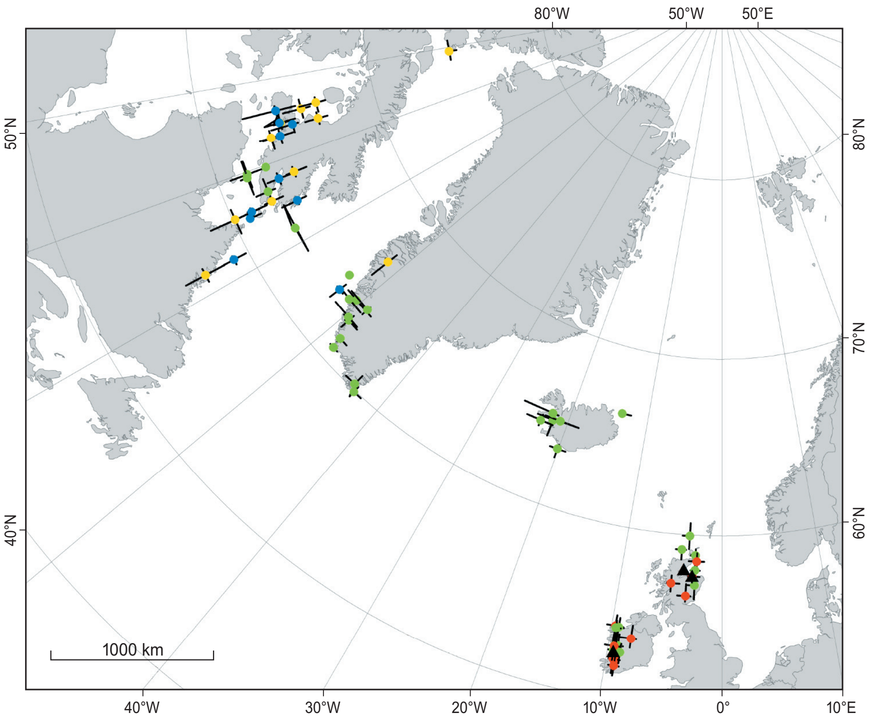

Figure 1. Median latitudes and longitudes (with interquartile ranges) of Purple Sandpipers prior to departure from Scotland and Ireland, whilst staging in Iceland and Greenland, and during moulting and prior to departure from Canada and Greenland. Green symbols: spring records, yellow: postnuptial and prior to the autumn equinox, blue: after the autumn equinox and prior to winter migration, red: winter, triangles: marking localities.

excluded from this comparison because masses were changing rapidly due to fat and protein deposition for migration, making a comparison unreliable. The recaptured bird with a geolocator on 27 April had not changed mass (69 g) whereas the average mass of untagged birds had risen from 71.5 to 77.9 g (Table 1). These included two birds that had also not changed mass.

The accuracy of geolocations

In April, the mean difference in longitude between median geolocations for the birds and marking sites was 0.71° (SD = 0.29) east, equivalent to 40 km. There was a similar difference in January; 0.76° (SD = 0.65), 48 km east. There was no significant difference between the two months ($t_{19} = 0.24$, $P = 0.82$), and the combined mean was 0.73° (SD = 0.48), 41 km east of the marking sites. Although these errors were small, they were consistent, and the April value was more than 1.96 SDs from the longitudes of the marking sites. Consequently, the longitudes for all geolocations were shifted west by 0.73° to account for this error.

The mean differences in latitude between median geolocations for the birds and marking sites were 0.63° (SD = 0.97), 70 km north for April and 0.05° (SD = 0.89), 6 km south for January. However, there was no significant difference between months ($t_{19} = 1.67$, $P = 0.11$), and the combined mean was 0.31° (SD = 0.97), 34 km north of the marking sites. These errors were also small and as neither was more than 1.96 SDs from the latitudes for marking sites, no adjustments were made for latitude.

The timing of migration

The median last day in Scotland and Ireland prior to departure was 20 May (range 25 April – 2 June; Table 2). Birds leaving from Scotland, did so significantly earlier (median last date = 6 May, $n = 6$) than those from Ireland (29 May, $n = 6$; Mann–Whitney U-test = 36, $P = 0.004$). This difference was associated with whether birds staged first in Iceland or Greenland. The median last date for those that headed to Iceland was 13 May ($n = 8$), whereas those that headed to Greenland departed later (median = 1 June, $n = 4$) (Mann–Whitney U-test = 4, $P = 0.041$), and a higher proportion of Scottish birds staged in Iceland (5 out 6) than Irish birds (3 out of 6).

The median arrival date in Iceland was 14 May (range 26 April – 28 May, $n = 8$), mainly on the west coast (Figure 1, Table 2). One bird (S1) arriving in east Iceland moved to the west coast of Iceland before departing, thereby minimising the distance for the next sea-crossing (Figure 2A). The subsequent movements of three birds were not determined because two tags failed in Iceland and one bird entered continuous daylight. However, for those whose departure times were deter-

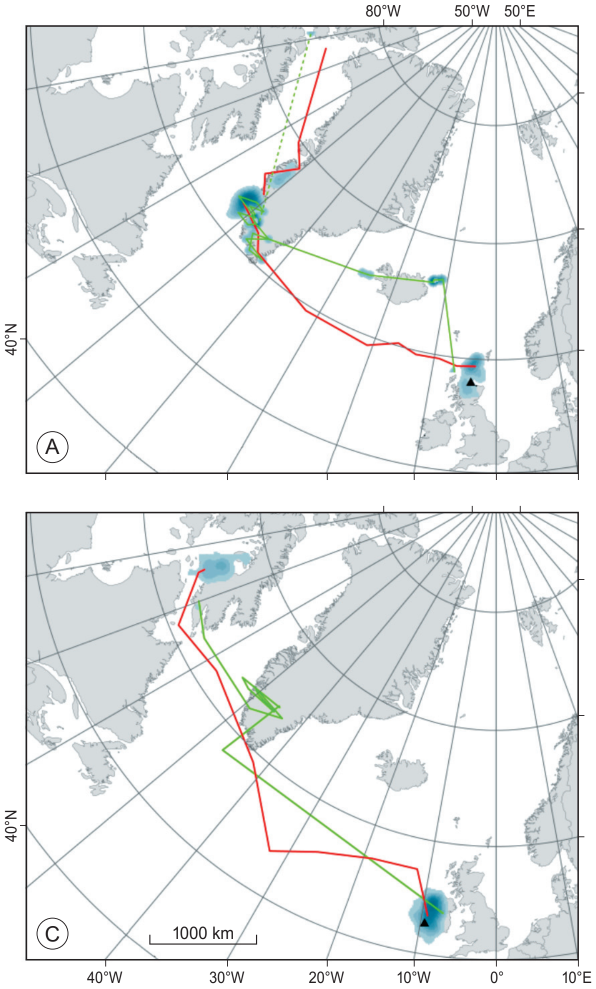

Figure 2. Geolocations and tracks of individual Purple Sandpipers with contrasting migration patterns (A = S1, B = I62, C = I49 and D = S53). Triangles show marking sites, the green lines show spring migration routes and red lines winter routes. The dashed green line for (A) indicates an unknown route to the High Arctic due to loss of data during continuous daylight.

mined, the median length of stay was 10 days (range 5–23 days, *n* = 5) and median last date prior to departure date was 28 May (range 18–31 May). After these five birds departed from Iceland, there was a further stop-over in southern or southwest Greenland.

Four birds did not stage in Iceland but flew directly to Greenland from Ireland or Scotland (Figure 2B, C). The median first date in Greenland was 30 May (range 19 May – 4 June, *n* = 9), including those that staged in Iceland (Table 2). There was no significant difference between arrival times for those that flew directly from Scotland/Ireland and those that staged in Iceland (Mann–Whitney U-test = 15, *P* = 0.22). For six of these birds, the median stop-over time in Greenland was 6 days (range 4.5–11 days) before they left (median last date = 4 June, range 23 May – 12 June) and travelled to Baffin Island, where they arrived approximately half a day later (median first date = 4 June, range 24 May – 12 June; Figure 1). Their spring migration had taken between 6 and 30 days (median = 12 days, *n* = 6), with longer times taken by those that had staged in Iceland as well as Greenland.

The movements between northern Scotland/southwest Ireland and southwest Iceland (1100/1500 km), southwest Iceland to southern Greenland (1200 km) and southern Greenland to southern Baffin Island (1100 km) were each accomplished in about a day. The migration via Iceland and Greenland required changes in headings, whereas the flight to Baffin Island via Greenland alone was direct.

Ignoring the two tags that failed in Iceland, nine of the 10 birds were in continuous daylight (light levels

> 0 lux) during the latter half of June and first half of July when they would have been breeding (Table 2). The remaining bird was in southern Baffin Island during this period.

The first geolocations when the light/dark regime resumed (between 12 July and 20 August) were from the east coast of Devon Island, the west (Foxe Basin) and south coasts of Baffin Island, and the north coast of Quebec and Labrador (Hudson Strait; Figures 1 and 2). The bird on Devon Island then travelled to southwest Greenland on 25 August and presumably carried out the post-nuptial moult in this region (Figure 2A). The other birds remained in southern Baffin Island and the Hudson Strait, presumably to moult, and most were in similar locations after the autumn equinox, or had moved further south. One bird, though, moved north to the Foxe Basin (Figure 1).

The median last day that the birds were in Baffin Island and the Hudson Strait was 5 November (range 26 October – 20 November, $n = 9$; Table 2). Eight made a direct crossing of the Atlantic to Ireland and Scotland (Figure 2). One bird had a stop-over of 20 days in southwest Greenland before heading across the Atlantic to Ireland on 13 December (Figure 2B). The bird that moulted in southwest Greenland did not depart from Greenland until 26 December and arrived in Scotland on 29 December. No birds staged in Iceland on the return migration to Scotland and Ireland. The median first date for all birds in Ireland and Scotland was 10 November (range 28 October – 29 December). Those that crossed the Atlantic directly from Baffin Island to Scotland and Ireland, did so in a median flight time of 2.5 days (range 2.5–3.5 days), thereby covering the 3500 km at an average speed of approximately 1400 km per day (Table 2).

The weather during the migrations

Those birds departing Scotland in spring had winds that were favourable for migration, whilst several Irish birds faced head-wind components; i.e. wind from the

Table 3. Wind directions and strengths during spring migration from Scotland and Ireland (dates in Table 2). For columns for arrival and departure, conditions for arrival are given in normal text and departure in italics.

Bird code	**Wind direction and strength**					**Comments**
	Ireland/ Scotland departure	*En route*	Iceland arrival/ *departure*	Greenland arrival/ *departure*	Canada arrival	
I48	Moderate WSW	Moderate SE		Fresh N–NE		Circumnavigated N flank of depression
				Light E	Light N	Flew through weak depression
I49	Light N			Light variable		Circumnavigated N flank of depression
				Light variable	Light variable	Flew through ridge of high pressure
I51	Light NW	Light N		Light variable		Flew through slack pressure distribution
I55	Light variable	Light S	Light SE			Crossed weak front
			Light variable	Light variable		Circumnavigated N flank of depression
I57	Light variable	Light S	Light SE			Crossed weak front
			Light NE	Light variable		
I62	Moderate S–SW	Moderate SE		Strong NE		Circumnavigated N flank of depression
				Light E	Moderate N	Crossed weak front
S1	Light SE	Moderate S	Moderate S			
			Light variable	Light variable		Flew through ridge of high pressure
S41	Strong SSE	Light variable		Fresh NW		Flew through depressions
				Light NW	Light NW	Flew through a weak ridge of high pressure
S48	Light variable	Fresh SW	Strong WSW			Departure in ridge of high pressure
S53	Light E	Light SE	Moderate SE			Flew through ridge of high pressure
			Moderate NE	Light NNW		Circumnavigated N flank of depressions
				Light variable	Light SE	Circumnavigated NE flank of depressions
S58	Light SE	Fresh E	Moderate E			Circumnavigated N flank of depressions
			Strong NE	Light variable		
				Light SE	Light SE	Flew through high pressure

north through to west (Table 3). In the flights to either Iceland or Greenland, most birds circumnavigated the northern flanks of low pressure systems (hereafter called depressions), thereby receiving assistance from anti-clockwise wind-flow. One exception was a bird (S48) that departed Scotland in fine weather in late April but encountered a strong southwest airstream *en route* to Iceland. Departure from Greenland also took place in light winds, with only one bird encountering head-wind components. Light winds also characterised arrival in Canada.

All birds experienced stronger winds during the winter migration, but these usually had tail-wind components (Table 4). Notably, three birds circumnavigated the southern flank of depressions, thereby being assisted by the anti-clockwise wind-flow. However, other birds flew through depressions and others encountered head-winds in the later stages of the flight. For example, the latest migrant (S1), flying east from Greenland in late December, was slowed by head-winds in its final stages northwest of Scotland (Figure 2A). Two birds (S41 and S53, Figure 2D) departed from Canada one day apart in November, the first following an occluded front southeast-wards and the second later became embedded in a much stronger northwest wind-flow of over 90 km per hour. Their separation south of Greenland was approximately 800 km, but only 400 km when northwest of Ireland. At this point, at midnight on 7 November 2010, both crossed a strong SSW wind-flow, but the first (S41) then moved southeast to make landfall. The second (S53), somewhat further northwest, reached northwest Scotland directly. Although most flights were across the ocean, the most northerly track involved one bird (I57) in late October crossing the southern part of the Greenland icecap in moderate westerly winds. The midday geolocation suggested that this bird climbed to an altitude of 2500 m to clear the icecap, with an air temperature of –18°C.

One bird (I62) crossed the Labrador Sea through a vigorous depression with strong crosswinds, which perhaps forced the staging in Greenland for three weeks before departing for Ireland. It is notable that it took two days to cross to Greenland, perhaps back-tracking (Figure 2B). Its eventual trans-Atlantic track took it through a large anticyclone with little wind assistance, before being assisted by a strong northwest airflow in its final stages.

DISCUSSION

This study showed that the long-billed Purple Sandpipers that spend the winter in north Scotland, western Ireland and presumably other countries in northwest Europe originate from Canada and use Iceland and Greenland as staging sites. As such, the Purple Sandpiper joins the list of other Nearctic waders that winter in or migrate through northwest Europe:

Table 4. Wind directions and strengths during winter migration from Canada and Greenland to Scotland and Ireland (dates in Table 2). All birds departed from Baffin Island except S1 which departed from Greenland, and I62 which staged in Greenland.

Bird code	Wind direction and strength			Comments
	Labrador Sea	Mid Atlantic	East Atlantic	
I48	Light SSW	Strong NW	SW–W gale	Circumnavigated S flank of depression
I49	Moderate NW	Light variable	Moderate W	Flew through weak depression, E Atlantic
I51	NW gale	WNW gale	WNW gale/storm	Circumnavigated S flank of depression
I55	Moderate N	Moderate N	Moderate SW	Flew through depression, E Atlantic
I57	Moderate NW	Moderate N	Fresh NW becoming SW	Circumnavigated S flank of depression in E Atlantic
I62	SE–E gale			Flew through deep depression to stage in Greenland
		Light NW becoming light variable	Strong NW	Flew through extensive anticyclone
S1		Light NW	Moderate SE	Delayed by depression, E Atlantic
S41	Strong NNW	Strong W	Strong SSW	Crossed frontal zones
S53	Strong NNW	Strong W	Strong SSW	Crossed frontal zones
S58	Light WNW	Light NW	Moderate SSE	Flew through weak depression, E Atlantic

Red Knot, Sanderling *Calidris alba*, Dunlin *Calidris alpina*, Ringed Plover *Charadrius hiaticula* and Turnstone *Arenaria interpres* (Cramp & Simmons 1983). Prior to our study, there had been only five European ringing recoveries of Purple Sandpipers west of Iceland. Two ringed in northwest and northeast England were recovered in southern Greenland on 27 October and 9 June, respectively (Lyngs 2003). They were probably Canadian breeders recovered whilst staging during autumn and spring migration, respectively. A third bird ringed in southwest Iceland on 20 May 1942, and presumably staging there, was recovered in southern Baffin Island (Foxe Peninsula) in April of the following year (Peters 1944). While the recovery location is consistent with our results, the recovery in late April (no date was given) is substantially earlier than our results (24 May to 12 June for the range of first dates). A fourth bird was ringed in Iceland on 11 October and recovered in southern Greenland one year later, also in October (20th; Lyngs 2003), indicating that some Canadian birds do occur in Iceland in autumn. This is supported by a study indicating that many Canadian Purple Sandpipers winter in Iceland (Hallgrimsson *et al.* 2012). The fifth bird was also ringed in southwest Iceland, on 17 May and recovered in Newfoundland on 25 December (Morrison 1984). This bird had perhaps switched wintering grounds and remained in the Nearctic.

When using an unconventional marking method, there is concern that it affects the welfare and behaviour of the birds. Although we found no discernible reduction in return rate to Ireland and Scotland of tagged birds, they were however lighter relative to birds that were only metal-ringed. The mean difference in mass between marking and recapture was 0.9 g (a decline of 1.2%), which is less than the 3–4% decline in mass lost during a single high tide roosting period when Purple Sandpipers are not feeding (Summers *et al.* 1990). Therefore, if the geolocator and harness were having a negative effect on the birds, it appeared to be minor. The weakest link of the harness was the elasticated thread which eventually perishes, so the harness plus geolocator will fall off those birds which we were unable to recapture.

Purple Sandpipers depart Orkney in northern Scotland with migratory fuel that would be sufficient for a flight of 2600 km (Corse & Summers 1999). The distances from northern Scotland and southwest Ireland to Iceland are 1100 and 1500 km, respectively, so the short period that some birds spent in Iceland in late May (as little as five days) indicates that some only ‘top-up’ migratory fuel before continuing migration.

The assumption that most migration altitudes were below 2000 m (Alerstam 1990) was supported by changes in higher level wind directions that were often less favourable to migrants. This is different to radar studies of the altitude of southward wader migration from northeast North America (Richardson 1976, 1979) where departing birds climbed to between 1000 m and 3500 m, with a few as high as 7000 m, to reach favourable winds. However, such passage occurred mainly in September and in warmer air-masses (Elkins 1988).

In spring, most birds took a track north of 60°N, staging in Iceland and Greenland, or just Greenland. This route benefits from the weakening Icelandic mean low pressure area lying to the south (Figure 3). This creates a wind-flow along the migration track from the southeast backing northeast, giving favourable tail winds over the whole route. Direct flights to Greenland in spring were made more frequently from Ireland than from Scotland (only one of five Scottish birds compared to three of six Irish birds). This may have been due to a more southerly departure point for the Irish birds. Despite their more southerly departure point, it was notable that the Irish birds could still make use of tailwinds on the northern flank of individual depressions (Table 3).

By November, when birds departed for winter quarters, the mean Icelandic low pressure area is centred north of 60°N and is much deeper, more extensive and has stronger winds (Figure 3). This enables migrants to choose favourable W–NW winds in the early stages, hastening migration along the southern flanks, so that one single overwater journey could be undertaken, although active weather fronts had to be traversed. For most birds, passage began in fine weather and with northwest (tail) winds over northeast Canada. These were mostly associated with Arctic air-masses to the rear of eastward moving depressions where, at these late dates, surface air temperatures were below 0°C. Passage through frontal cloud was necessary at some stage of their trans-Atlantic flights and many were constrained to move through strong southwest windflows on reaching the northeast Atlantic ahead of decelerating depressions. The mean pressure distributions shown in Figure 3 mask considerable daily and sometimes even hourly variation in the actual situation as successions of frontal depressions cross the North Atlantic. Stochastic events towards the end of the migration cannot be predicted, and may lead to flights of longer duration if unfavourable weather is encountered. By crossing the Atlantic at 55–60°N, the Purple Sandpipers do not have the possibility of short-stopping

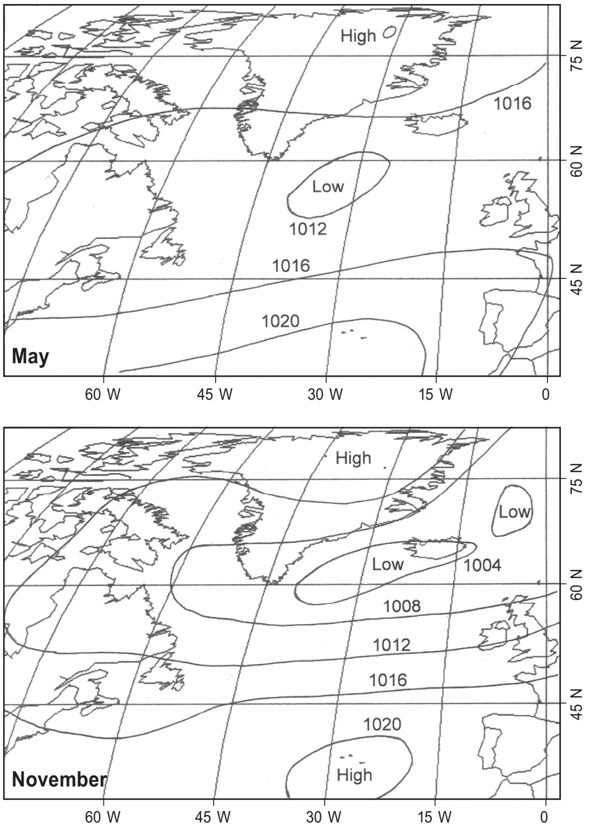

Figure 3. Long-term mean sea level pressure distribution over the North Atlantic in May and November (values in hectopascals). Courtesy of the Meteorological Office.

to rest, which was possible in spring (in Iceland and potentially the Faeroe Islands), and by waders that migrate along the coast (e.g. Red Knots; Shamoun-Baranes *et al.* 2010). A similar Atlantic crossing from Baffin Island, Canada, to the western British Isles has been shown for Wheatears *Oenanthe oenanthe* (Bairlein *et al.* 2012).

One bird migrated to Iceland in late April, well before other tagged individuals and before Purple Sandpipers in Britain accumulate migratory stores. This usually occurs in May, as it does for many Arctic-breeding waders (Johnson 1985, Summers *et al.* 1992, Corse & Summers 1999). Perhaps some individuals accumulate stores at an earlier date or accumulate only moderate stores for the relatively short distance to Iceland, thereby adopting a different migratory strategy than their conspecifics. Having different strategies within a population has been shown for other migratory birds (Dias *et al.* 2012). This Purple Sandpiper remained in Iceland for at least 25 days before its tag failed, longer than the other tagged birds that staged in Iceland.

Purple Sandpipers have only a moderate gain in mass during May in Iceland (attaining 33–42% of the lean mass at a rate of 0.9% per day, Summers *et al.* 2009), perhaps because they have the additional stopover in south and southwest Greenland to acquire additional food stores before reaching the breeding grounds. By contrast, the High Arctic waders that use Iceland as a staging site have a different migration strategy. Red Knots, Sanderlings and Turnstones increase mass to 53–54% of lean mass at a rate of 2.3–3.6% of the lean mass per day (Gudmundsson *et al.* 1991). For these waders, Iceland is the last staging site before they fly directly to northwest Greenland or Ellesmere Island, Canada, after crossing the Greenland icecap (Alerstam *et al.* 1986). Weather conditions in the High Arctic can be poor when waders arrive (Morrison 1975), so any residual stores would be important for survival.

The Purple Sandpipers that flew directly from Ireland to southern Greenland had a flight of 2300 km, so would have used the bulk of their migratory fuel. Greenland would therefore be an important re-fuelling site prior to reaching the breeding grounds in Canada, though the stop-over period was relatively short (median of 6 days).

Only one set of geolocations was obtained during late June – early July, indicating that this bird was breeding in southern Baffin Island. Geolocation errors during the Arctic summer are larger than other times of the year because the light/dark transitions are less abrupt, leading to uncertainty about its actual location in southern Baffin Island. However, it was clear that this and the other birds belonged to the Canadian breeding population; all were either on Devon Island, Baffin Island or in the Hudson Strait when relocated after being in continuous daylight. The light/dark regime is already apparent in early July in southern Baffin Island (D. Hussell, pers. comm.), so it is likely that the birds bred further north, and they became detectable only when they moved south after breeding.

Holmes (1971) found that distance of migration could be one of the factors determining when postnuptial moult takes place in relation to migration. Thus, waders that migrate long distances to non-breeding areas in the southern hemisphere (Little Stint *Calidris minuta*, Pectoral Sandpiper *C. melanotos*, Semipalmated Sandpiper *C. pusilla*, Baird's Sandpiper *C. bairdii* and Curlew Sandpiper) moult after migrating (Holmes 1971, Elliott *et al.* 1976). By contrast, Dunlins *C. alpina pacifica* in north Alaska moult on the breeding grounds, even overlapping moult with incubation so that moult is complete before their migration. Holmes

(1966) argued that by remaining on the tundra to moult after other sandpipers had left, Dunlins were able to capitalise on a still abundant food supply in the absence of competitors. Dunlin of this subspecies could adopt this strategy because they had a short migration to temperate latitudes, though other subspecies have longer migrations (e.g. *C. alpina arctica* migrates from northeast Greenland to West Africa, Clark in Wernham *et al.* 2002). The Purple Sandpipers that moult on Baffin Island are therefore another example of a population adopting this strategy of moulting prior to migration.

Even though the tundra food supplies (insects) would have disappeared during the first snow in September, Purple Sandpipers are able to utilise invertebrates in the inter-tidal zone in the Arctic (e.g. in Svalbard, Leinaas & Ambrose 1992), a feature shared with the closely related Rock Sandpiper *Calidris ptilocnemis* (Ruthrauff *et al.* 2013). It is probably this food resource that allows them to remain in the Hudson Strait until early winter. Potentially, they would be able to remain for the entire winter like Purple Sandpipers in southwest Greenland and north Norway, consuming small molluscs (Salomonsen 1950, Strann & Summers 1990). However, declining temperatures and formation of sea-ice, usually by mid-November/early December in the Hudson Strait (Canadian Ice Service), eventually makes the inter-tidal zone untenable, despite the large tidal range of 10 m which would break ice near to the shore (M. Mallory, pers. comm.). On leaving Canada, it is not clear why some Purple Sandpipers should cross the Atlantic rather than join resident populations of Purple Sandpipers in southwest Greenland and Iceland where other birds from Canada have chosen to winter (Summers 2007, Hallgrimsson *et al.* 2012). Perhaps the prior occupancy by the resident birds precludes additional immigrants that could potentially compete for resources through the winter (Holmgren & Lundberg 1993).

Conclusion

The study established for the first time the Canadian origin of the bulk of the wintering Purple Sandpipers in Britain, Ireland and perhaps other countries in northwest Europe. It has also described the contrasting migration routes in relation to the North Atlantic depressions, and the importance of southwest Iceland and southwest Greenland as staging sites in spring. In particular, the Hudson Strait region of Canada is a key area in the annual cycle as a post-nuptial moulting area and where birds prepare for the flight across the Atlantic in early winter.

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SAMENVATTING

De jaarlijkse trek van vogels valt meestal niet samen met andere energetisch dure activiteiten (zoals de rui) en leidt doorgaans tot het vermijden van seizoenen met een verlaagde overlevingskans (zoals noordelijke winters). Paarse Strandlopers *Calidris maritima* zijn hierop een uitzondering. Zij overwinteren op relatief hoge breedtegraden (zelfs vergeleken met andere steltlopersoorten). De rui vindt plaats vóór de aankomst in de wintergebieden. Veel Paarse Strandlopers die in Groot-Brittannië en Ierland overwinteren, worden gekarakteriseerd door lange snavels en zouden Canadese broedvogels kunnen betreffen. Zij arriveren hier eind oktober/begin november. Hun najaarsrui, die op een tot dusver onbekende locatie plaatsvindt, is dan al voltooid. De auteurs van dit artikel hebben in het noorden van Schotland en het zuidwesten van Ierland 50 Paarse Strandlopers uitgerust met geolocators. Daarmee hebben zij voor het eerst kunnen vaststellen dat deze lokale wintervogels inderdaad van Canadese origine zijn (Baffin Island en Devon Island). Ook werden de trekroutes en de gebieden waarin de najaarsrui plaatsvindt vastgesteld. De terugtrek naar de broedgebieden vond grotendeels eind mei plaats. De terugtrek werd onderbroken met een tussenstop op IJsland en/of in het zuidwesten van Groenland. De vogels die een tussenstop op IJsland maakten, vertrokken gemiddeld vroeger dan de vogels die rechtstreeks naar Groenland vlogen. De najaarsrui werd hoogstwaarschijnlijk uitgevoerd in het zuiden van Baffin Island, in het noorden van Quebec en Labrador (langs de Hudson Straat) en in het zuidwesten van Groenland. De wegtrek vanuit Baffin Island en Labrador vond plaats van eind oktober tot begin november, die vanuit Groenland tussen medio en eind december. Dit betekent dat deze Paarse Strandlopers pas aan de najaarstrek beginnen als andere steltlopersoorten al in de overwinteringsgebieden zijn. Geen van de vogels verbleef op de najaarstrek op IJsland. De vlucht van Baffin Island naar Schotland en Ierland duurde ca. 2,5 dag en vond plaats met een gemiddelde snelheid van ca. 1400 km per dag. Het dichtvriezen van de kustwateren in Canada is waarschijnlijk de reden voor het uiteindelijke vertrek uit de Hudson Straat. De meer noordelijke route via IJsland, gebruikt door veel vogels in het voorjaar, en de meer zuidelijke route in het begin van de winter waren geassocieerd met seizoensgebonden veranderingen in het Atlantische systeem van lagedrukgebieden (depressies), waarbij de gangbare (tegen de klok in) windrichtingen de vluchten vergemakkelijken. (YIV)

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