Migration pathways, migration speeds and non-breeding areas used by northern hemisphere wintering Red Knots *Calidris canutus* of the subspecies *rufa*

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Light-level geolocators were deployed on 37 Red Knots at Monomoy National Wildlife Refuge, Cape Cod, Massachusetts, United States in Sep 2009 and eight were recovered at the same place a year later. Two of the eight geolocators failed halfway through the year, but the other six provided a full year's record of the birds' locations. All eight birds carried out the whole of their large-feather molt at Monomoy, after which they moved south to wintering areas, leaving between 29 Oct and 16 Nov. Four birds wintered on the U.S. Atlantic coast between Virginia and Florida, while four wintered in the Caribbean in areas not previously identified as important for Red Knots. During northward migration all six knots with geolocators still working stopped in the vicinity of the Nelson River estuary in the south-west corner of Hudson Bay, a site not previously identified as an important stopover for Red Knots. Migration speed (defined as the speed achieved between one stopover and the next, assuming the bird travelled along the great circle route) differed significantly between flights affected by headwinds (median 47 kph), those that took place in calm conditions (60 kph) and those affected by tailwinds (72 kph). We discuss the implications of our results for the conservation of the threatened *rufa* Red Knot population and highlight the need to investigate some of the sites the birds visited.

INTRODUCTION

In the West Atlantic Flyway, the *rufa* subspecies of the Red Knot has declined precipitously over the last 30 years (Baker *et al.* 2004, Niles *et al.* 2008). It is protected by legislation in most of the countries it visits; it is listed as endangered in Canada and is a candidate for listing as vulnerable or endangered in the United States. Effective conservation of such shorebird populations requires an understanding of all phases of their life cycles so that those factors that impinge on reproduction and survival can be determined and, if possible, managed. For those that migrate long distances, and are suffering population decline such as *rufa* knots, it is especially important to understand their migratory strategies and to identify the stopover sites they use during migration, as well as their final non-breeding destination.

Despite almost two decades of research, the migratory strategies of *rufa* knots and the range of locations they visit are not well known. They breed in the central Canadian Arctic and broadly occur in three main wintering groups: (relatively) short distance migrants that winter in the SE United States; medium distance migrants that winter on the north coast of Brazil; and long distance migrants that winter in Tierra del Fuego, at the southern tip of South America. Aerial and ground surveys have identified many important wintering and migration sites, but when individual knots were first tracked using light-level geolocators it was realized that they use many other sites and often fly very long distances without stopping (Niles *et al.* 2010).

In this study we used geolocators to determine the movements of northern hemisphere wintering *rufa* knots; i.e. birds that we anticipated would spend the winter in the SE United States. A key aim of the study was to assess the full extent of the wintering area of the population because, although knots are well known to occur on the SE United States coast, there have also been several poorly-documented reports of small groups at various locations in the Caribbean; moreover stable isotope studies indicate that the northern winterers are more numerous than known populations (Atkinson *et al.* 2005). Therefore we planned to deploy geolocators on a sample of northern-wintering *rufa* knots at a migration stopover so that the geolocator data would reveal the extent of their winter range. The data generated have already been used to evaluate a conceptual risk model for Red Knots in relation to proposals for the deployment of coastal and offshore wind turbines and the birds' use of the U.S. Atlantic coast (Burger *et al.* 2011, 2012a, b).

METHODS

We planned to deploy light-level geolocators (supplied by British Antarctic Survey (BAS); Model Mk10; assembled weight 1.4 g) on 37 *rufa* Red Knots caught by cannon-net at Monomoy National Wildlife Refuge (NWR), Cape Cod, Massachusetts (Fig. 1). Attempts were made to recapture them a year later. We used the same methods for the capture and handling of birds, geolocator attachment, and analysis of geolocator output used in our earlier studies (Niles *et al.* 2010). These methods have the approval of the Rutgers University Animal Review Board.

Our previous studies of Red Knots at Monomoy NWR show that birds from all three main wintering groups stop over there in late August and early September (Harrington *et al.* 2010). However, they are readily distinguished. Long and medium distance migrants (yielding flag resightings in South America) show no large-feather molt and are usually relatively heavy because they are laying down resources for the next stage of their migration. In contrast short distance migrants (yielding flag resightings in the SE United States) are in mid primary molt and are relatively light. Therefore we only deployed geolocators on knots that were in active primary molt; also we rejected any bird that did not appear to be in good condition or weighed <125 g. The state of the primary molt of each bird (and its molt-score) was recorded at both the time of capture and recapture according to the protocol described by Ginn & Melville (1983). In addition to a geolocator, each bird was fitted with a U.S. Fish & Wildlife Service metal band and an individually inscribed lime green flag with a 3-digit code (Clark *et al.* 2005). In this paper, we use the flag codes to refer to individual birds.

The BAS Mk10 geolocator records the maximum ambient light level every 10 minutes, and its conductivity sensor effectively records whether the bird is in contact with seawater every 10 minutes; it has enough memory to store data for at least one year. Data downloaded from recovered geolocators were processed using the free Bastrak suite of software downloaded from the BAS website. Pre-deployment calibration of geolocator output was carried out near Philadelphia; this information was used to adjust the apparent position to the true position. Post-deployment re-sightings at Monomoy NWR validated the geolocator fixes, and provided confirmation that the sensors were still calibrated properly. In general, shallow slopes of the light signal and abrupt changes of slope were interpreted as shading events, and given lower confidence.

Longitude components were the predominant indicator of changes of location, with prime importance given to intersection with coastlines, supported by re-sightings. When they are not migrating, Red Knots frequently enter saline habitats to feed and often roost standing in seawater. This is recorded by the conductivity sensor, which invariably shows that birds are rarely out of contact with seawater for more than a few hours. Google Earth was used to investigate the vicinity of each geolocator fix to identify the location of suitable Red Knot habitat, and any sources of manmade light interference. Long dry periods accompany all flights, so last and first seawater signals were used to determine maximum migration flight duration. This could be an accurate measure of flight time, and is unlikely to overestimate it by more than about four hours.

For a single fix we only assumed an accuracy of ±200 km (see Clark *et al.* 2010), but almost invariably we had many fixes for each stopover or wintering location and used them to refine our estimate of location to ±50–75 km. Further refinement was often possible based on limited availability of suitable saline habitat or because the bird was resighted.

We follow Minton *et al.* (2011) in presenting data on "migration speed", defined as the average speed achieved by a migrant shorebird between one stopover and the next, assuming the bird travels along the great circle route. Estimates of migration speed were computed by dividing the great circle distance between departure and arrival locations by the maximum possible flight duration (the interval between conductivity sensor seawater signals). This gives the minimum possible migration speed. Migration speed should be distinguished from ground speed, which is probably greater as it is unlikely that a bird can follow the great circle route exactly; moreover ground speed might be considerably greater if the bird is diverted by weather systems.

To evaluate our migration speed data and validate our location fixes, we assessed weather conditions during each flight and stopover using data from the following sources: *www.weatherspark.com* which provides free historical records of cloud cover, wind direction and speed, humidity, pressure, and temperature from thousands of airports from the arctic to South America*; www.buoyweather.com* which provides historical wind charts for all oceans of the world; and *www.hpc.ncep.noaa.gov/dailywxmap/* which provides historical North American weather maps for tracking pressure systems and fronts. Data for days (and weeks) around departures and during flights were used to assess whether the birds benefitted from wind assistance or suffered from headwinds, and to evaluate the reliability of fixes.

RESULTS

On 2 Sep 2009, we deployed geolocators on 37 Red Knots at Monomoy NWR, Cape Cod, Massachusetts, from a cannon-net catch of 136. We recaptured eight of the 37 (22%) among catches totaling 93 knots made in the same area between 19 and 22 Aug 2010. Six of the eight recovered geolocators were still recording data and provided a full year's record of the birds' movements; in the other two, the batteries had ceased to function, one on 6 Dec 2009 (042), one on 15 Feb 2010 (032).

As planned, all of the eight birds were in active primary molt when they were fitted with geolocators on 2 Sep 2009 (Table 1), seven were in mid primary molt with scores ranging from 21 to 35 (median 28); they also had active pre-basic molt of body feathers, and had varying amounts of retained breeding plumage. The remaining bird (038) had almost completed its primary molt with a score of 49 and had no breeding plumage; it was aged as a second year bird based on Harrington (2001). In 2010, the eight birds were recaptured two weeks earlier in the year than when they were first caught; six on 19 Aug 2010 and two on 22 Aug 2010. At recapture, all eight were in active primary molt with scores ranging from 10 to 29 (median 25).

Southward migration

The geolocator data show that the eight birds remained at or close to Monomoy NWR until moving south over the period 29 Oct to 16 Nov (Table 1, Figs 1–8). Five of the eight then

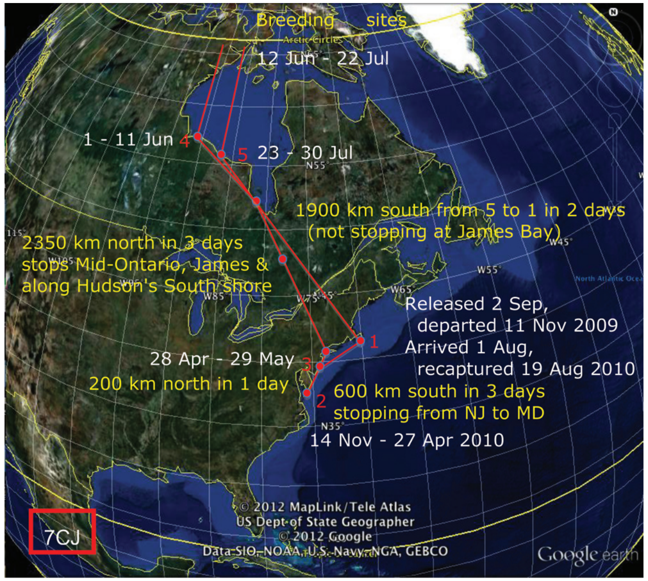

Fig. 1. Geolocator output for Red Knot 7CJ; location key:
1. Monomoy NWR, U.S.,
2. Virginia Barrier Islands, U.S.,
3. Brigantine, U.S.,
4. Nelson River, Canada,
5. Hudson Bay, Canada

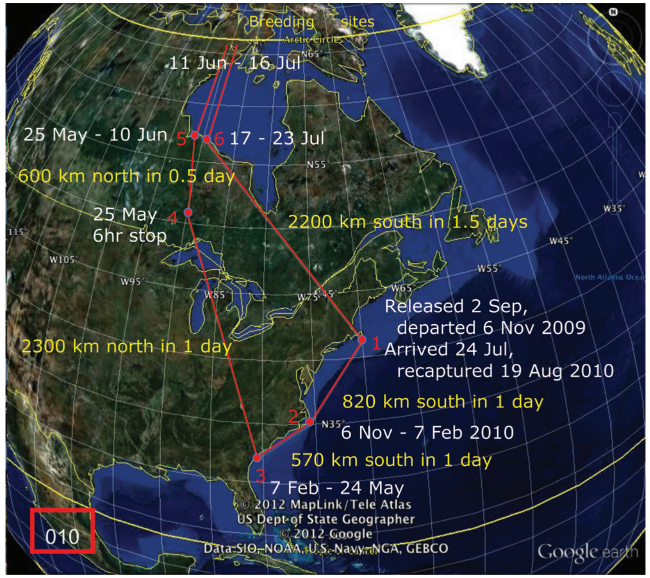

Fig. 2. Geolocator output for Red Knot 010; location key:
1. Monomoy NWR, U.S.,
2. Cape Hatteras, North Carolina, U.S.,
3. Hilton Head, SC, U.S.,
4. Uncertain location around 51°N in Canada,
5. Nelson River, Canada,
6. Pen Islands, Canada.

Table 1. Parameters of the annual cycle of Red Knots (dates and days) derived from geolocator output for eight birds in the West Atlantic Flyway (*Aggregate distance flown on migration in one year includes estimated flights to the Arctic Circle from the last northbound stopover and from the Arctic Circle to the first southbound stopover, but no flights within the Arctic; NR = parameter not recorded because geolocator failed).

Flag code	Molting area (Monomoy, Massachusetts)					Wintering area					Breeding area (Canadian arctic)			Migration distance (km)	
	Molt-score when captured on 2 Sep 2009	Departure date (2009)	Return date (2010)	Molt-score when recaptured on: 19 Aug 2010	Molt-score when recaptured on: 22 Aug 2010	Arrival date (2009)	Departure date (2010)	Days in wintering area	Number of wintering areas	Main wintering area	Arrival date (2009)	Departure date (2010)	Days in breeding area	Aggregate distance flown on migration during one year *	Longest flight
7CJ	26	11 Nov	1 Aug	18		14 Nov	27 Apr	165	1	Virginia (38°N)	12 Jun	22 Jul	43	7,350	2,350
010	31	6 Nov	24 Jul	26		6 Nov	24 May	198	2	S Carolina (33°N)	11 Jun	16 Jul	37	8,690	2,300
014	28	16 Nov	26 Jul		29	18 Nov	28 Mar	130	1	Cuba (20.4°N)	16 Jun	19 Jul	36	11,350	2,400
016	32	6 Nov	9 Aug	10		7 Nov	15 May	190	1	N Carolina (35°N)	10 Jun	1 Aug	52	7,520	1,500
032	21	29 Oct	NR	11		31 Oct	NR	NR	2	Cuba (22.5°N)	NR	NR	NR	NR	2,400
038	49	6 Nov	26 Jul	26		8 Nov	12 May	186	3	Florida (28°N	11 Jun	22 Jul	42	10,000	1,800
042	26	11 Nov	NR		25	23 Nov	NR	NR	NR	Venezuela (11.5°N)	NR	NR	NR	NR	2,900
058	35	5 Nov	31 Jul	25		7 Nov	21 Mar	134	1	Bahamas (21°N)	15 Jun	24 Jul	40	11,980	1,500

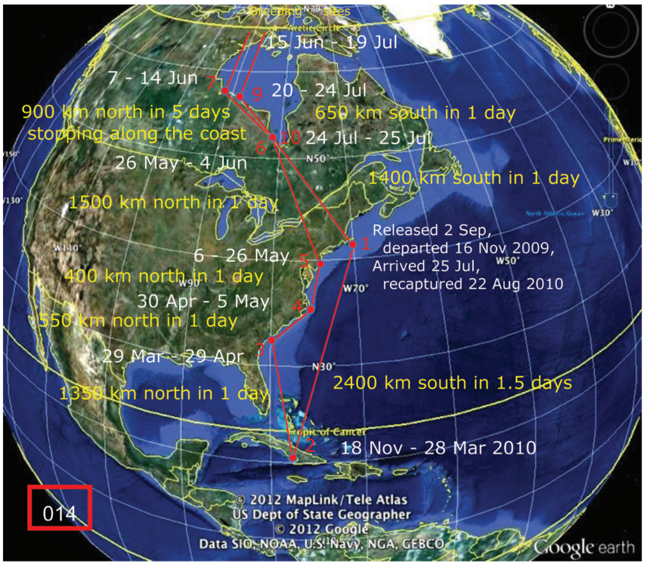

Fig. 3. Geolocator output for Red Knot 014: location key: 1. Monomoy NWR, U.S., 2. South-east Cuba, 3. Cape Island, SC, U.S., 4. Cape Hatteras U.S., 5. Brigantine, U.S., 6. and 10. James Bay, Canada, 7. Nelson River, Canada, 9. Pen Islands, Canada.

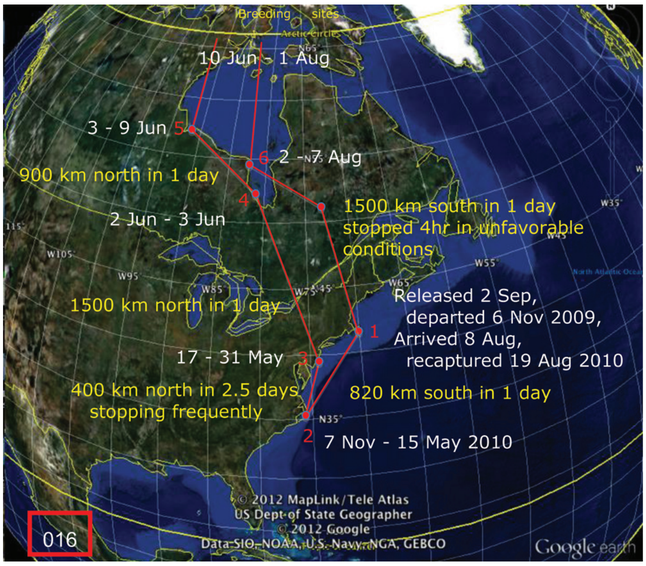

Fig. 4. Geolocator output for Red Knot 016; location key: 1. Monomoy Refuge, U.S., 2. Cape Hatteras, U.S., 3. Delaware Bay, U.S., 4. James Bay, Canada, 5. Nelson River, Canada, 6. Upper James Bay, Canada.

moved direct to their wintering areas in non-stop flights; one bird (042) moved first to the barrier islands of Virginia where it spent eight days before flying direct to its wintering area on the Caribbean coast of South America (Fig. 7); 058 flew from Monomoy to winter on the Bahamas, but made an eight-hour stop en route at Cape Hatteras (Fig. 8); and 7CJ moved relatively slowly taking three days to go 600 km from Monomoy to the Virginia barrier islands, stopping probably several times on the way (Fig. 1). Three of the eight birds left Monomoy on the same day, 6 Nov; two of them (010 and 016) flew to the same place, Cape Hatteras in North Carolina; the other one (038) flew to the Atlantic coast of Florida (Figs 2, 4 & 6).

Wintering areas

Four of the eight birds moved to winter on the east coast of the United States, one on the Virginia barrier islands (7CJ), two at Cape Hatteras, North Carolina, (016 and 010) and one on the Atlantic coast of Florida (038) (Figs 1, 2, 4 & 6). The other four birds moved to the Caribbean: two on Cuba (014 and 032); one on the Bahamas (058); and one on the north coast of South America close to the border between Colombia and Venezuela (042) (Figs 3, 5, 7 & 8).

During the winter, which we define as Dec–Feb, two birds moved to completely different locations: on 7 Feb, 010 left Cape Hatteras, North Carolina, and flew 600 km south to the coast of South Carolina (Fig. 2); and on 14 Feb, 032 flew from W Cuba to the Atlantic coast of Florida (Fig. 5). 038 and 058 also showed some winter movement, but they moved more slowly and the distances were less (Figs 6 & 8). Soon after it arrived in NE Florida on 8 Nov, 038 started to move south, taking 2.5 months to cover the 200 km to the Palm Beach area where it stayed from 27 Jan until 12 May. After its flight from Monomoy, 058 spent three weeks on Cat Island, Bahamas, before moving 400 km south-east to Great Inagua Island, also in the Bahamas, arriving there on 1 Dec.

Of the six knots that were monitored until they left on northward migration, the four that wintered on the Atlantic coast of the United States stayed in their wintering area(s) the longest; three of them for >6 months. The other two were birds that wintered on Cuba and the Bahamas (014 and 058) and they each stayed in their wintering areas for just over 4 months (Table 1).

Northward migration

The dates of departure on northward migration varied considerably. Possibly the movement of 032 from Cuba to Florida on 14 Feb (Fig. 5) was the beginning of its spring migration, though it may have been a movement between different wintering areas. Otherwise 058 which departed from the Bahamas on 21 Mar was the first to leave, followed by 014 from Cuba on 28 Mar. The four that wintered on the Atlantic coast of the United States all started to move north much later: 7CJ on 27 Apr, 038 on 12 May, 016 on 15 May and 010 on 24 May.

Northward migration strategies also varied although all six birds made a stopover in the vicinity of the Nelson River estuary in the south-west corner of Hudson Bay. One bird (010) flew there almost nonstop from its wintering area in South Carolina (its geolocator indicated that it might have stopped for about 6 hours at around 51°N in S Canada) (Fig. 2). Otherwise, broadly, the birds that wintered further north made fewer stopovers than those that wintered further south. 7CJ and 016 which wintered on the Virginia barrier islands and Cape Hatteras, North Carolina, respectively made three stops before reaching the Arctic (Figs 1 & 4); 038 from Florida and 058 from the Bahamas made four stops and 014 from Cuba made five stops (Figs 3, 6 & 8).

The breeding season, return to Monomoy and subsequent resightings

The arrival of the six birds in the Arctic took place over seven days, whereas their departure was spread over 14 days (Table 1). The range of departure dates is largely due to varying breeding success as discussed in relation to the current data and similar geolocator data by Burger *et al.* (2012c).

On southward migration after the breeding season, five of the six birds flew from their arctic breeding grounds to one or more stopovers in Hudson Bay (between Nelson River and James Bay) from where they returned direct to Monomoy. However, one bird (058) flew from the Arctic to Monomoy

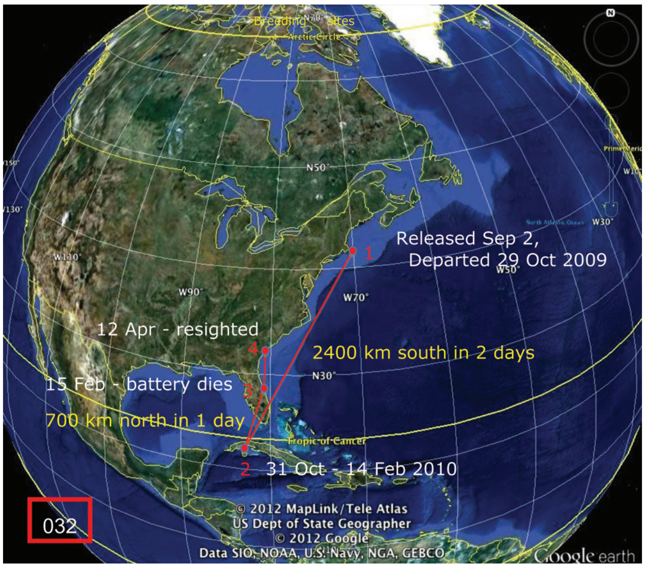

Fig. 5. Geolocator output for Red Knot 032; location key: 1. Monomoy Refuge, U.S., 2. SouthWest Cuba, 3. Cape Canaveral, U.S., 4. Kiawah Island, U.S.

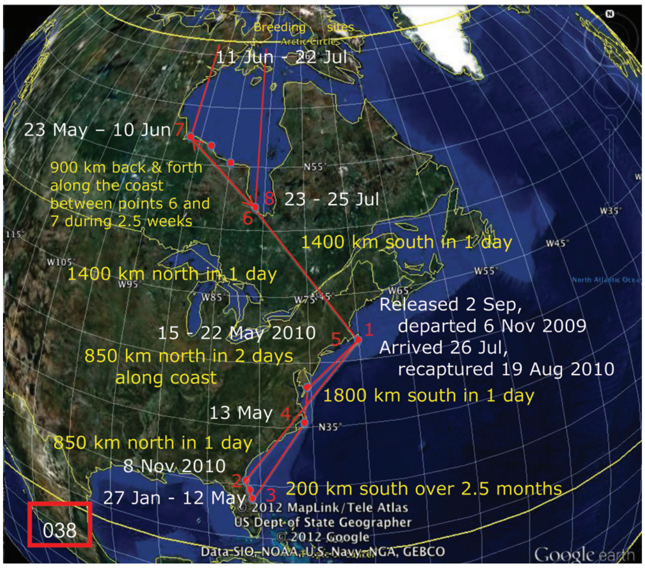

Fig. 6. Geolocator output for Red Knot 038; location key: 1. and 5. Monomoy Refuge, U.S., Jacksonville coast, U.S., 2. Palm Beach coast, U.S., 3. Cape Hatteras, U.S., 4. and 8. James Bay, Canada, 7. Nelson River, Canada.

via a six-day stop on the Mingan Archipelago in the Gulf of St Lawrence (Fig. 8).

When the geolocators were removed from the eight knots in Aug 2010, the birds were released still wearing their coded flags. Five of them were later resighted (Table 2). These show that 016, the only bird of six whose geolocator output records that it visited Delaware Bay on northward migration in 2010, also visited Delaware Bay in 2011. Moreover 014, which stopped on the New Jersey coast in 2010, stopped in Delaware Bay in both 2011 and 2012. 042 also stopped there in 2011. Another resighting of note is that 016 was seen in Feb 2011 on Bear Island, North Carolina, which is very close to its Cape Hatteras wintering site of the previous year.

Migration distance and speed

The six birds whose movements were monitored for a complete year traveled an average aggregate distance (assuming a great circle route between stops and excluding movements within the Arctic Circle that cannot be detected by geolocators) of 9,480 km on migration (range 7,350–11,980 km) (Table 1). The total distance flown on migration showed a significant negative correlation with the latitude of the wintering area ($R_S = -0.943$, $p = 0.005$, Table 1). The longest flights of all eight birds averaged 2,150 km with a range of 1,500–2,900 km (Table 1).

For all of the flights recorded in this study there was no evidence that any bird strayed significantly from the great circle route between departure and arrival locations. Geolocator output provides a fix for each bird every 12 hours that (without any other evidence of location) is subject to an error of about ±200 km (Clark *et al.* 2010). Therefore the evidence is not that all the birds followed the great circle route exactly, but that they did not stray from it by more than about 200 km. The only qualification to this is that when 042 flew south from Virginia to E Colombia the 12-hour fixes were headed directly for the place in W Venezuela at which it eventually spent the winter. However, just after it had flown over the Dominican Republic, its trajectory moved westward and it landed in E Colombia (see dashed line in Fig. 7). At the time there was a 65 kph easterly wind which may have been responsible for the change of direction. The fact that this bird only stayed in Colombia for three days after which it moved 250 km east into Venezuela would seem to lend support to the idea that Colombia was not its intended destination.

Among the geolocator output for the eight knots, there are data for 16 flights for which the great circle distance and flight duration could be determined with a reasonably high degree of accuracy (Table 3). When the migration speeds derived from these data are divided between flights subject to headwinds, flights in calm conditions (or where there was a roughly equal effect of headwinds and tail winds) and flights subject to tailwinds, the differences in the median migration speeds in these categories of 47, 60 and 72 kph respectively are statistically significant (Kruskal–Wallis test, $H = 12.39$, $p = 0.002$, Table 3); moreover flights subject to headwinds (median 47 kph) were significantly slower than flights in calm conditions (60 kph; Mann–Whitney test, $W = 6.0$, $p = 0.0133$) and flights in calm conditions (60 kph) were significantly slower than flights with tailwinds (72 kph; Mann–Whitney test, $W = 22.0$, $p = 0.0135$).

It is noteworthy that virtually all of the migration departure times were in the latter third of the day, between 1600 and 2300 GMT–5 hours with only one after midnight; in contrast arrival times were at all times of the day (Table 3).

DISCUSSION

To date, all studies of shorebirds using geolocators have changed our conceptions about their migration strategies and the sites they use. This study is no exception. It has revealed previously unknown stopover and wintering sites and a surprising lack of commonality between the eight focal birds in their migration pathways.

Monomoy National Wildlife Reserve as a location for large-feather molt

The capture/recapture site, Monomoy NWR near Cape Cod, was clearly of key importance for all eight geolocator birds as a molting site. We do not know exactly how long any of them spent there in any one autumn, but if it is assumed that the

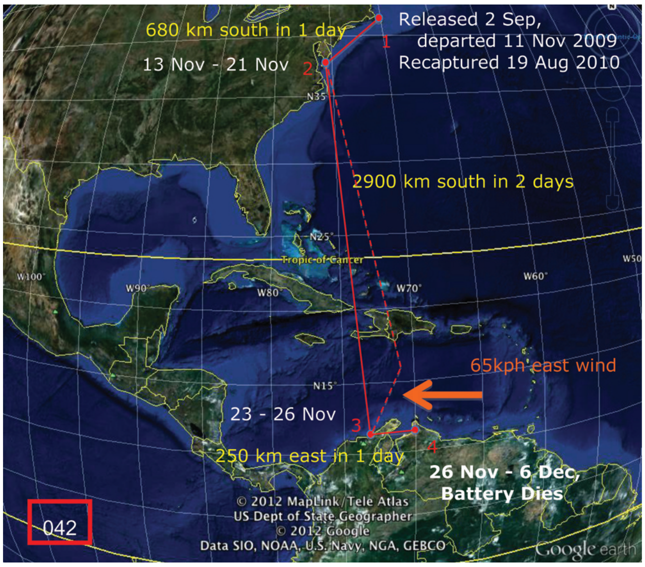

Fig. 7. Geolocator output for Red Knot 042; location key: 1. Monomoy Refuge, U.S., 2. Virginia Barrier Islands, U.S., 3. West of Riohacha, Columbia, 4. Bay South of Puenta Fijo, Venezuela.

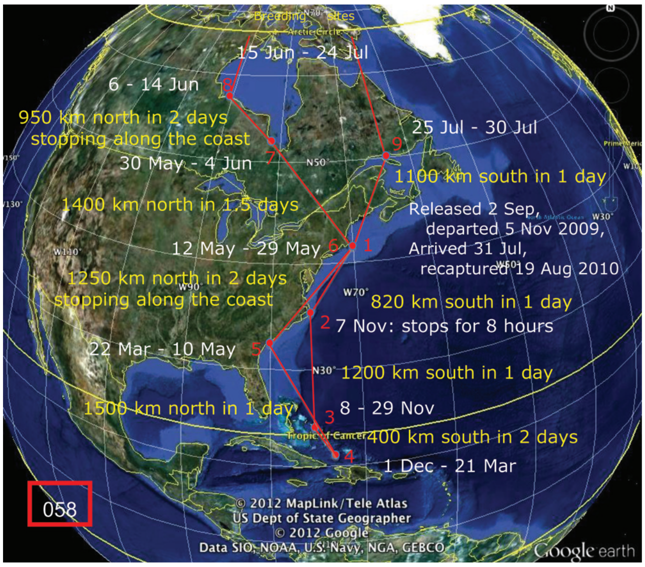

Fig. 8. Geolocator output for Red Knot 058; location key: 1. and 6. Monomoy Refuge, U.S., 2. Cape Hatteras, U.S., 3. Cat Island, Bahamas, 4. Great Inagua, Bahamas, 5. Cape Island, SC, 6. James Bay, Canada, 7. Nelson River, Canada, 8. Mingan Archipelago, Canada.

Monomoy departure and arrival dates of the six birds whose geolocators lasted the whole year are typical of every year, the duration of their stays ranged from 89 to 113 days (89, 97, 102, 103, 105 and 113 days; Table 1). The duration of primary molt has not yet been measured in any population of the *rufa* subspecies of the Red Knot, but in the *islandica* subspecies in Scotland it averages 77 days and in the *canutus* subspecies in South Africa it averages 95 days (Summers *et al.* 2010). Therefore, as it is unlikely that any shorebird would migrate with inefficient wings during primary molt, and in view of the state of the molt of the focal birds at the time of capture and recapture and the likely duration of their stay at Monomoy, it would seem virtually certain that all eight completed the whole of their primary molt at that location in both 2009 and 2010. It is also likely that they remained at Monomoy after completion of primary molt for the 1–2 weeks it would take to lay down resources for their next southward flights.

Molting sites need to be safe from predators (because the wing-gap means that birds are less maneuverable and less able to take evasive action) and provide sufficient food resources for a three month stopover (because onward migration with less efficient wings is not a good option). The adult Red Knot molting population in the vicinity of Monomoy has been around 500 individuals during Aug–Oct in recent years (B. Harrington, unpublished information). This is >1% of the entire *rufa* population and a much greater proportion of the northern wintering population. Therefore Monomoy should be considered to be of particular value for Red Knots, not only because of the numbers that occur there but also because good molting sites are of key importance in the annual cycle.

Table 2. Resightings of the focal Red Knots between Aug 2010 when their geolocators were removed and Jun 2012 (we have no record that birds 7CJ, 032 and 058 were resighted during this time).

Flag code	Date(s)	Location	Coordinates
010	8–15 Nov 2011	Avalon, New Jersey	39°06'N, 74°42'W
014	19 May 2011	Delaware Bay, New Jersey	39°06'N, 74°54'W
	25 Apr 2012	North Core Banks, Portsmouth, N Carolina	34°57'N, 76°12'W
	21 May 2012	Delaware Bay, New Jersey	39°06'N, 74°54'W
016	2 Feb 2011	Bear Is., N Carolina	34°38'N, 77°09'W
	13 May 2011	Delaware Bay, New Jersey	39°06'N, 74°54'W
038	29 Mar 2012	Bay Point Island, S Carolina	32°16'N, 80°38'W
042	22–29 May 2011	Delaware Bay, Delaware & New Jersey	39°N, 75°W

Winter locations and movements

Although it is a small sample, the fact that four of the eight geolocator knots wintered in the Caribbean is an indication that the Caribbean might be a more important wintering area for knots than previously thought. In a review of important wintering habitat for *rufa* knots throughout the West Atlantic Flyway, many sites were identified along the south-east coast of the United States, especially in Florida, and on the north coast of Brazil but none in the Caribbean (Niles *et al.* 2008). Therefore, as there appears to be a distinct possibility that substantial numbers of northern-wintering *rufa* occur in the Caribbean and as the subspecies has undergone a dramatic decline (Niles *et al.* 2008), a conservation priority is to identify the sites used by knots in the Caribbean and to determine whether they face any threats in those places. Up to 10,000 Red Knots wintered on the west coast of Florida in the 1980s, but numbers using that area have since undergone a steep decline, possibly a result of loss of beach habitat to development and excessive use of the beaches for recreation (Harrington *et al.* 1988, Niles *et al.* 2006). Therefore the discovery of birds wintering in previously unknown locations in the Caribbean raises the possibility that the population in W Florida did not decline but dispersed to other wintering areas.

That two of the geolocator knots moved significant distances during winter is not easy to explain. Winter movements might occur to avoid cold weather, if food supplies become insufficient, if the risk of predation increases or if human disturbance does not allow birds time to feed or rest, but none of

Table 3. Migration speed parameters of those flights by the focal Red Knots (for which the great circle distance could be determined to within ±100 km and the flight duration as shown by the geolocators' salt-water sensors was unlikely to be overestimated by >10%) divided between those flights that were mainly subject to headwinds, those that took place in calm conditions or subject to a roughly equal mixture of headwinds and tailwinds and those that were mainly subject to tailwinds. The data on wind strength and direction given in the last column are for ground level so they might not necessarily reflect the conditions that the birds experienced at the altitude at which they were flying. Where wind conditions changed during a flight, the conditions considered to be the most important (e.g. because of wind strength or duration) are underlined. The times of departure and arrival are given in Greenwich Mean Time minus 5 hours which is equivalent to the eastern North American time zone in winter (Eastern Standard Time). It should be noted that some departures and arrivals were at places in other time zones. Estimated departure and arrival times are last and first contacts with seawater (according to the geolocators' conductivity sensors). Therefore flight durations may be overestimated (and therefore migration speed underestimated).

Flag code	Direction	Departure			Arrival			Great circle distance (km)	Flight duration (hours)	Minimum migration speed (kph)	Median (mean) migration speed (kph)	Wind strength (kph) and direction during flight
		Site	Date	Time (GMT–5 h)	Site	Date	Time (GMT–5 h)					
Flights mainly subject to headwinds												
058	S	Mingan, Quebec	29 Jul	22:53	Cape Cod	30 Jul	23:53	1,100	25.0	44		12–20 Headwind
032	N	West Cuba	14 Feb	17:42	Florida Atlantic coast	15 Feb	08:42	700	15.0	47		16 Headwind
010	S	Hudson Bay	22 Jul	18:32	Cape Cod	24 Jul	13:02	2,200	42.5	52	47 (48.4)	Calm / <u>8–32 Headwind</u> / 0–8 Tailwind
016	N	New Jersey Atlantic coast	31 May	17:32	James Bay	1 Jun	20:41	1,500	27.2	55		0–8 Tailwind / <u>0–16 Headwind</u>
058	N	Cape Cod	28 May	20:04	James Bay	30 May	04:04	1,400	32.0	44		0–16 Tailwind /<u>16–24 Headwind</u>
Flights in calm conditions or subject to a roughly equal mixture of headwinds and tailwinds												
032	S	Cape Cod	29 Oct	16:02	West Cuba	31 Oct	12:42	2,400	44.7	54		8–24 Tailwind / <u>8–16 Beam</u>
038	N	Florida Atlantic coast	12 May	18:07	Cape Hatteras	13 May	09:17	850	15.1	56		16 Tailwind / 16 Headwind
7CJ	S	Hudson Bay	30 Jul	18:46	Cape Cod	1 Aug	02:06	1,900	31.5	60	60 (59.7)	<u>8–16 Beam</u> /8–16 Headwind
010	N	S. Carolina	23 May	22:52	Hudson Bay	25 May	14:12	2,900	48.2	60		Calm
042	S	Maryland	21 Nov	17:26	Columbia S.A.	23 Nov	17:06	2,900	47.8	61		Calm/ 8–16 Beam /60–70 Beam
014	N	New Jersey Atlantic coast	25 May	20:30	James Bay	26 May	19:01	1,500	22.5	67		Light & variable
Flights mainly with tailwinds												
038	N	Cape Cod	22 May	18:47	James Bay	23 May	16:37	1,400	21.8	64		8–16 Tailwind
058	S	Cape Hatteras	7 Nov	16:07	Bahamas	8 Nov	08:57	1,200	16.8	71		<u>16 Tailwind</u> / 28–32 Beam
014	S	Cape Cod	16 Nov	17:21	Cuba	18 Nov	02:41	2,400	33.3	72	72 (72.6)	28 Tailwind
016	N	James Bay	2 Jun	21:31	Hudson Bay	3 Jun	09:11	900	11.7	77		8–16 Tailwind
014	S	James Bay	25 Jul	00:50	Cape Cod	25 Jul	18:40	1,400	17.8	79		16–24 Tailwind

the observed movements can be attributed to any one of these factors with any degree of certainty. A southward movement in February, such as the 600 km flight by 010 from North Carolina to South Carolina, might have been prompted by cold weather; however, we have looked at the weather data and they show no change that could have had this effect. The northward movement of 032 from Cuba to Florida in mid-February is similarly difficult to explain. Perhaps it was the first flight of northward migration, but if so it was a month earlier than the other Caribbean-wintering birds moved north. The gradual 200 km southward movement along the Atlantic coast of Florida by 038 between November and January might have resulted from the high degree of human disturbance that affects Florida beaches in winter. More information about local conditions is needed before conclusions can be drawn about the reasons for such winter movements.

Northward migration

By far the most important stopover for *rufa* knots during northward migration along the Atlantic coast of the United States is Delaware Bay (Clark *et al.* 1993, Niles *et al.* 2008, Tsipoura & Burger 1999), yet only one of the Monomoy birds (016) stopped there in the spring of 2010. The same bird stopped there in 2011; and another bird, 014, stopped there in 2011 and 2012 and as did 042 in 2011 (Table 2). These data show, albeit for just three birds, that an individual may stop in Delaware Bay in some years but not in others. This is probably also reflected by quite substantial year-to-year variation in the total number of Red Knots stopping in Delaware Bay (Niles *et al.* 2008). The opportunity of feeding on Horseshoe Crab *Limulus polyphemus* eggs in Delaware Bay may be more important to medium- and long-distance migrant knots from South America. Those birds have probably flown 5,000–8,000 km nonstop, arriving in Delaware Bay with under-developed digestive apparatus (Niles *et al.* 2008, 2010, Piersma & Gill 1998). Therefore they may benefit most from the soft, easily digested eggs (Niles *et al.* 2009). In contrast the northern winterers make much shorter flights and might retain the ability to feed on shellfish. Thus they have many more feeding options and may be less reliant on Delaware Bay eggs and therefore less likely to stop there every year.

Red Knots leaving Delaware Bay in late May have far more stored energy resources than are needed for the flight to the breeding grounds (Baker *et al.* 2004, Niles *et al.* 2008), and the same is presumably true of knots that stop over at other sites on the U.S. east coast (e.g. in Virginia, Maryland or New Jersey). It has therefore been assumed that, although some have been recorded as stopping in James Bay in the south-east corner of Hudson Bay, most fly direct from Delaware Bay to the breeding grounds without stopping and that the surplus resources are needed to sustain them in the period after arrival when arctic food resources are in short supply (Baker *et al.* 2004, Morrison & Hobson 2004, Morrison *et al.* 2007, Niles *et al.* 2008). However, neither the results of the present study relating to six knots nor those of Niles *et al.* (2010) relating to three knots support that assumption; all nine birds stopped in Hudson Bay for periods ranging from 8 to 19 days (mean 12 days). With data for only nine birds in two years, it is impossible to know whether all *rufa* knots always make a stopover in Hudson Bay before flying on to their breeding grounds, but it seems quite possible. Why they should do this is not readily apparent. One reason might be that, despite the resources they are already carrying, they need more to ensure their survival once they reach the breeding grounds. Another possibility might be that when they reach southern Hudson Bay they are already close enough to the breeding grounds to be aware of the conditions they are likely to encounter if they go straight there; for example if the south coast of Hudson Bay is still snowbound, it is likely that the breeding areas will be as well. Therefore they may choose to stop short of the breeding areas in a place that affords an adequate food supply until conditions improve.

All six of the geolocator knots that were monitored during their northward migration stopped in the vicinity of the Nelson River estuary in south-west Hudson Bay. This is an area that has not previously been recognized as important for Red Knots (Niles *et al.* 2008) and we have no detailed information about the habitats or food resources that are available there. It is therefore a conservation priority to study the use of this area by knots in late May and early June.

Migration speed

The famous satellite-tagged Bar-tailed Godwit *Limosa lapponica*, E7, flew from the Yukon-Kuskokwim delta in Alaska to the Piako River Mouth, North Island, New Zealand, a tracked distance (using the satellite fixes) of 11,680 km in 8.1 days (Gill *et al.* 2009), which is 60.0 kph. The errors associated with geolocator data mean that migration paths cannot be tracked with accuracy; therefore in estimating migration speed we have to assume that the bird travelled along the great circle route between departure and arrival locations. The great circle route of E7's flight was 10,950 km, so its migration speed according to our definition would have been 56.3 kph.

It is possible that our measures of migration speed in Table 3 are underestimates because the measurement of duration depends on last and first contacts with seawater and we cannot tell how they relate to actual departure and arrival times. Nevertheless – and acknowledging that there may be differences between flight speeds attained by Red Knots and Bar-tailed Godwits – the fact that our estimates are close to E7's satellite-monitored migration speed suggests that they are probably quite accurate. This is also suggested by the fact that the different categories of wind conditions have statistically significant effects on migration speed.

An advantage of being a short-distance migrant *rufa* Red Knot

Quite apart from the obvious advantages of short as opposed to long distance migration (e.g. less energetic costs, less risks associated with migration, less requirement for food to fuel migration), the results of this study indicate that in *rufa* knots a short distance migration strategy has another benefit: avoiding risks associated with migration through the Caribbean – W Atlantic hurricane belt. Two of the three *rufa* knots with middle/long distance migration strategies reported by Niles *et al.* (2010) were apparently diverted by tropical storms in late August and early September so that the routes they took were in each case at least 1,000 km longer than the great circle distance between departure and arrival locations. In contrast none of the flights by the eight geolocator knots in the present study were significantly diverted by adverse weather.

The Atlantic Hurricane Season 'officially' lasts from 1 Jun to 30 Nov; however 78% of all storm days, 87% of minor hurricanes and 96% of major hurricanes occur during August to October (Hurricane Research Division, National Oceanic & Atmospheric Administration, *www.aoml.noaa.gov/hrd/tcfaq/G1.html*). Therefore when the middle/long distance migrants traverse the tropical cyclone zone in August and September, the short-distance migrants, or at least the Monomoy molters, are well out of the way far to the north and do not enter the zone until the hurricane season is nearly over.

Conclusions

These results are the latest output from a sustained effort by ourselves and many others to reach a better understanding of the natural history of *rufa* knots in the West Atlantic Flyway, and thereby underpin their conservation. They show that despite two decades of research we have a long way to go before we can claim to have a full understanding of these great travelers. In particular they show that there are new places, especially around the Caribbean and the Nelson River area of Hudson Bay, that need to be investigated. Moreover they show that eight birds can exhibit such a diversity of migration strategies that it will be very difficult to reach firm conclusions about the strategies of the whole population without a lot more data.

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