First results using light level geolocators to track Red Knots in the Western Hemisphere show rapid and long intercontinental flights and new details of migration pathways

LAWRENCE J. NILES[1], JOANNA BURGER[2], RONALD R. PORTER[3], AMANDA D. DEY[4], CLIVE D.T. MINTON[5], PATRICIA M. GONZALEZ[6], ALLAN J. BAKER[7], JAMES W. FOX[8] & CALEB GORDON[9]

[1] Conserve Wildlife Foundation of NJ, 109 Market Lane, Greenwich, NJ 08323, USA. larry.niles@gmail.com
[2] Division of Life Sciences, Rutgers University, 604 Allison Road, Piscataway, NJ, USA
[3] 800 Quinard Court, Ambler, PA, 19002, USA
[4] Endangered and Nongame Program, Fish and Wildlife, New Jersey Department of Environmental Protection, 501 E. State Street, PO 420, Trenton, NJ 08625-0420, USA
[5] Victorian Wader Study Group, 165 Dalgetty Road, Beaumaris, Melbourne, Victoria 3193, Australia
[6] Global Flyway Network, Pedro Morón 385, (8520) San Antonio Oeste, Río Negro, Argentina
[7] Royal Ontario Museum, Department of Natural History, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada
[8] British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, UK
[9] Pandion Systems, Inc. 102 NE 10th Ave. Gainesville, FL. 32601, USA

Niles, L.J., Burger, J., Porter, R.R., Dey, A.D., Minton, C.D.T., Gonzalez, P.M., Baker, A.J., Fox, J.W. & Gordon, C. 2010. First results using light level geolocators to track Red Knots in the Western Hemisphere show rapid and long intercontinental flights and new details of migration pathways. *Wader Study Group Bull.* 117(2): 123–130.

Keywords: migration, migratory pathways, stopovers, wintering area, breeding area, geolocator, Red Knot, *Calidris canutus*

Geolocators affixed to Darvic leg flags were attached to the tibia of 47 Red Knots *Calidris canutus rufa* during the 2009 spring migratory stopover in Delaware Bay, New Jersey, United States. We found no difference between the behavior of birds with and without geolocators in the weeks after release and saw a greater proportion of birds with geolocators than those with inscribed leg-flags a year after release. There were no significant differences in the resighting rate in Delaware Bay in the year of attachment or in places other than Delaware Bay during the ensuing twelve months. Three individuals were re-captured in May 2010 in Delaware Bay. All three birds flew to the Arctic, only one apparently bred, and all three wintered in South America. The longest roundtrip flight was 26,700 km, which included an 8,000 km, 6-day flight from southern Brazil to the coast of North Carolina. All three wintered away from the main sites thought to be used by the subspecies. Two birds appeared to detour around weather systems. These results suggest that geolocators are likely to afford valuable new insights to our understanding of Red Knot migration strategies as well as their breeding and wintering locations, and underpin their conservation.

INTRODUCTION

Understanding the biology, constraints of migration, and the yearly movement patterns of birds is essential to conserving them, particularly in the case of long-distant migrant shorebirds that rely heavily on a limited number of stopover locations (Piersma & Baker 2000). For decades, biologists and conservationists have examined terrestrial habitat use, behavior, and the prey base of shorebirds (van de Kam *et al.* 2004). However, there is now a pressing need to understand the pattern and timing of movements as well as their spatial use of inshore and offshore migratory pathways that may intersect both coastal and offshore development, including oil drilling and wind facilities. Remarkably little information is available on the offshore movements of most birds, and of the potential risk they face during the migratory periods when they fly along coastal margins or cross oceans.

Band recoveries and sightings of color-marked shorebirds have been the main methods of determining their migration routes, stopover sites, breeding and wintering locations. Satellite transmitters used on larger shorebirds have encountered problems due to their weight (26 g) and method of attachment (Driscoll & Ueta 2002, Gill *et al.* 2005). These problems have been reduced with the use of lighter transmitters (<10 g, Watts *et al.* 2008) and surgical implantation (Gill *et al.* 2009). Light-level geolocators were originally designed for use on elephant seals (DeLong *et al.* 1992) and later the British Antarctic Survey developed 9 g geolocators for use on seabirds (Afanasyev 2004). Recent advances in their technology and miniaturization have made it possible to use them to track the movements of 50 g terrestrial birds (Stutchbury *et al.* 2009) and shorebirds (Conklin & Battley 2010, Minton *et al.* 2010). These instruments record time-stamped, periodic, ambient light-levels that can be used to determine the geographical location of birds (Conklin & Battley 2010, Minton *et al.* 2010, Stutchbury *et al.* 2009). Their advantage is that they can be used on the legs of medium-sized shorebirds; their main disadvantage is that the birds must be recaptured to access the data. Although geolocators record data for only about a year, the data are still retrievable for up to twenty years if birds are recaptured.

Red Knots *Calidris canutus* are one of the better studied migrants in the world, and a species where fundamental knowledge has often been put to good use in conservation cases (e.g. Baker *et al.* 2004, Buehler & Piersma 2008, Piersma 2007). In the Western Hemisphere, Red Knots of the subspecies *rufa* are of conservation concern because of a major population decline over the past 25 years (Baker *et al.* 2004, Morrison *et al.* 2004, Niles *et al.* 2008). It is therefore vital that conservation prescriptions are underpinned by a thorough knowledge of the birds' annual cycle, migration strategies and the sites they use. This is particularly important in the light of recent proposals for offshore drilling and the location of wind facilities on the outer continental shelf, where they might pose a danger to migrant shorebirds.

We present preliminary findings on the migratory pathways of three Red Knots fitted with geolocators in 2009 and recovered a year later in 2010. Our objectives were to determine: 1) whether the technology would work with Red Knots, 2) to test whether knots would suffer any immediate or long-term detrimental effects from the geolocators, and 3) the annual movement patterns of Red Knots. We detail our method of geolocator attachment, immediate behavioral responses of birds fitted with geolocators, re-sighting data on those birds with and without geolocators (but banded and flagged in the same year), and on the movements of three instrumented Red Knots.

METHODS

Overall protocol

Our experimental design was to place light-level geolocators on Red Knots during their migratory stopover in Delaware Bay in May 2009, and recapture them on their return to Delaware Bay and at other locations during migration and on the wintering grounds. The geolocators (Mk 10 design supplied by the British Antarctic Survey, Cambridge, UK) weighed 1.7 g including attachment materials. As part of our overall protocol working with shorebirds in Delaware Bay, we captured 622 Red Knots in 2009; each was provided with a uniquely coded flag (Clark *et al.* 2005) and we placed geolocators on 47. We relied on a network of observers to report sightings of geolocators during migration, on the wintering grounds, and again in Delaware Bay the following year. The protocol for this research with Red Knots, including attaching geolocators to birds, was approved by the Rutgers University Animal Review Board.

Red Knots were captured with cannon nets, removed immediately from the net, and placed in holding cages shaded from the sun. Processing occurred shortly after, and birds were then released. Geolocators were fitted (see below) on 48 birds that weighed over 125 g (Fig. 1). A sample of birds fitted with geolocators was observed in a 3 m × 5 m enclosure made of dark material for 1–2 hours after attachment of the geolocators, and behavioral data were recorded to ascertain any immediate effects. One bird seemed disturbed by the geolocator, as evidenced by continuous pecking at its leg, and this geolocator was removed. The bird walked and flew normally, and was later observed feeding with other Red Knots. Controls with flags (those without geolocators) were also observed. Behavior recorded included time spent walking, running, sitting, pecking at eggs on the sand, and pecking at their leg. An extensive network of volunteer observers searched for Red Knots with leg flags, and especially noted the behavior of birds with geolocators.

Geolocator attachment

Although we used essentially the same method of attaching geolocators to leg bands as Minton *et al.* (2010), we made two changes: we clipped the terminal pins of the instrument to reduce the likelihood that they would cause injury to the bird by chaffing and we placed a spacer ring beneath the geolocator band to prevent rubbing against the tibio–tarsal joint. All geolocators were applied with the sensor on the side facing outward away from the body when the flag is rotated forward of the leg, which is the natural position during most activities (Fig. 2).

RESULTS

Geolocator attachment

We examined whether birds were adversely affected immediately upon attachment of geolocators by observing them in pens for an hour before release and then observing them in the field before they left Delaware Bay in 2009. In the pens immediately following attachment, we could discern no behavioral differences between knots with geolocators and flags and those with flags but without geolocators. After deploying geolocators on 25 knots, efforts were made to observe all those birds in the field. It was then noticed that a few appeared to walk with a very slight limp. Further deployments were stopped to allow time to evaluate the issue. It was then found that some recently flagged birds without geolocators as well as some unmarked birds also appeared to walk with a slight limp. Later we observed two birds with geolocators that had previously appeared to limp that were no longer doing so. We therefore concluded that slight limping in a small minority of birds was probably a not uncommon but previously unnoticed short-term phenomenon; therefore geolocators were deployed on a further 22 birds. Twenty-three of the 47 knots fitted with geolocators in May 2009 were resighted in Delaware Bay a year later when none were seen to walk with a limp.

We also evaluated the effects of the geolocators by comparing resightings in 2009 and 2010 of knots with geolocators and individually-inscribed leg flags with those fitted with leg flags alone. There were no differences between the proportion of resighted birds with and without geolocators either during the May 2009 Delaware Bay stopover or during the winter elsewhere in the flyway (Table 1). However, in 2010 a greater proportion of geolocator knots (23/47, 49%) were resighted in Delaware Bay than those with only leg flags (203/622, 33%; $\chi^2 = 5.19$, $P = 0.023$).

Of the 47 Red Knots fitted with geolocators in Delaware Bay in 2009, three were recaptured in May 2010. The Red Knot with flag code "Y0U" was first captured on 11 May 2009 weighing 121 g and recaptured on 12 May 2010 weighing 107 g and recaptured again on 14 May 2010 at 128 g. The date on which this bird arrived on the Bay is unknown because the geolocator stopped working on 12 Feb 2010. The Red Knot with flag code "Y0Y" was first captured on 11 May 2009 weighing 121 g. In 2010, it arrived on the Bay on 20 May and was recaptured on 23 May 2010 weighing 158 g. The Red Knot with flag code "1VL" was originally captured on 26 May 2009 weighing 171 g. In 2010 it arrived on the Bay on 24 May and was recaptured on 25 May at 134 g. The

Fig. 1. Red Knot Y0Y with geolocator and lime flag, Delaware Bay, United States, May 2010. (Photo: Jan van de Kam.)

Fig. 2. Close-up of geolocator fitted to the tibia of a Red Knot in San Antonio Oeste, Argentina, 2009. (Photo: Jan van de Kam.)

Table 1. Numbers of Red Knots with individually inscribed leg flags that were marked in May 2009 and later resighted with and without geolocators on the New Jersey side of Delaware Bay and elsewhere during May 2009 to May 2010.

	Geolocators and leg flags	Leg flags only	χ^2 (p)
Number of birds marked	47	622	
Resighted May 2009 in Delaware Bay	29 (62%)	342 (55%)	0.80 (ns)
Resighted elsewhere May 2009 to May 2010	4 (9%)	46 (7%)	0.06 (ns)
Resighted in Delaware Bay in 2010	23 (49%)	203 (33%)	5.19 (p = 0.023)

Fig. 3. Geolocator output for Red Knot Y0U: periods when the bird remained in the same location are shown in white; the great circle distance of movements are shown in yellow; when the bird deviated far from the great circle route, the estimated distance flown is shown in green.

Location key:
1. Delaware Bay, United States
2. James Bay, Canada
3. Southampton Island, Canada
4. Lesser Antilles
5. Maranhão-Pará border region, Brazil

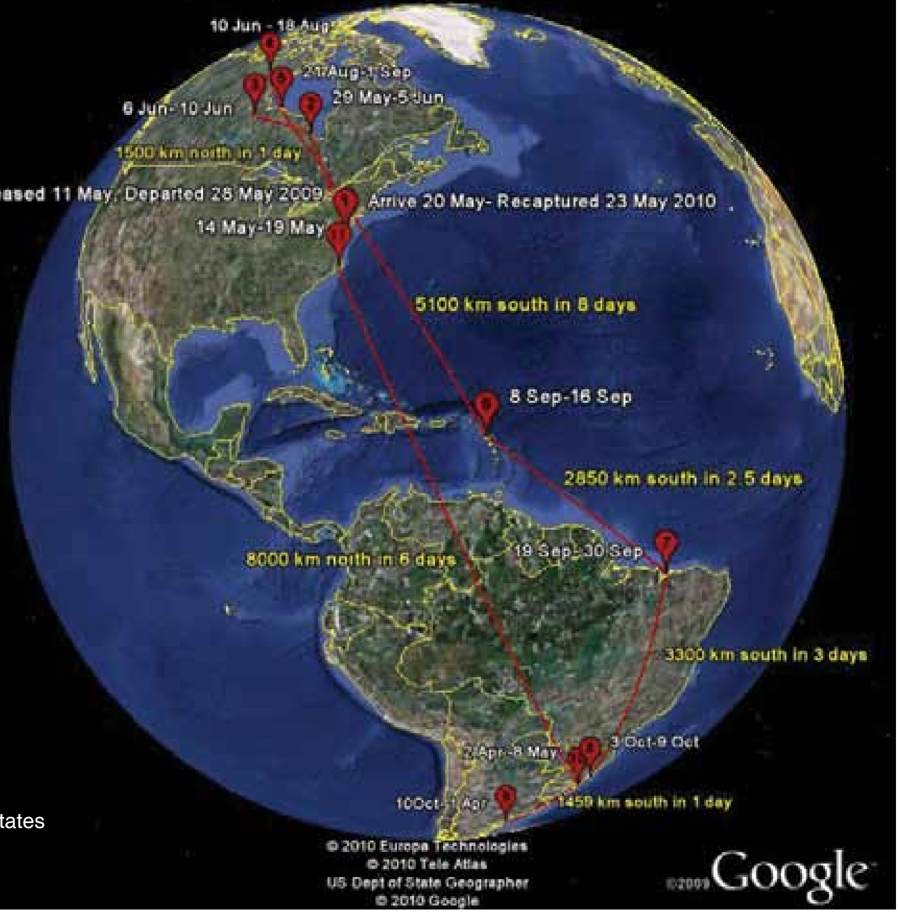

Fig. 4. Geolocator output for Red Knot Y0Y: periods when the bird remained in the same location are shown in white; the great circle distances of movements are shown in yellow.

Location key:
1. Delaware Bay, United States
2. James Bay, Canada
3. Western Hudson Bay, Canada
4. Baker Lake, Canada
5. Churchill, Canada
6. Lesser Antilles
7. Maranhão, Brazil
8. Lagoa do Peixe, Brazil
9. San Antonio Oeste, Argentina
10. Uruguay–Brazil border
11. Ocracoke, North Carolina, United States

Fig. 5. Geolocator output for Red Knot 1VL: periods when the bird remained in the same location are shown in white; the great circle distances of movements are shown in yellow; when the bird deviated far from the great circle route, the estimated distance flown is shown in green.

Location key:
1. Delaware Bay, United States
2. James Bay, Canada
3. Southampton Island, Canada
4. Pelly Bay (Kugaaruk), Canada
5. Cape Cod, United States
6. Maranhão, Brazil
7. Rio Grande do Norte, Brazil

geolocators were removed from all three birds shortly after recapture and new geolocators were attached. The legs of all three birds showed no abnormal wear or evidence of irritation suggesting that the geolocators had no adverse impact on leg morphology.

Geolocator data

Geolocator data were processed using a fixed light threshold value and edited using BASTrak TransEdit software to reject false and noisy locations caused by shading. The output was then plotted on Google Earth maps which showed considerable noise around each site at which the birds stopped. These were then simplified to a single point representing the average location, but assuming in the case of stopover and wintering sites that it was on the coast (Figs 3, 4 & 5). In most cases when a bird was migrating, the series of locations was within the expected average error of ±150 km (according to the British Antarctic Survey) from the great circle route, and in these the great circle route and distance are shown in the maps. However, in respect of three flights (one relating to Y0U and two to 1VL) it was evident that the bird deviated far from the great circle. In these three cases, the routes shown by the geolocator output are presented in the maps along with both the great circle distance between the points of departure and arrival and our estimate of the actual distance flown.

The geolocator output for each bird is summarized as follows and in the maps (Figs 3, 4 & 5).

Y0U: After geolocator attachment on 11 May 2009, Red Knot Y0U stayed in Delaware Bay until 27 May, and then flew in one day to James Bay, Ontario, where it stopped for 12 days (Fig. 3). After flying a further two days it arrived at Southampton Island, Nunavut, Canada, on 11 Jun, where it stayed for 63 days, presumably to nest. Y0U left Southampton Island on 13 Aug and flew in one day to James Bay, staying for 12 days. On 27 Aug, it flew to the Atlantic Coast of New Jersey, USA, in one day (possibly Stone Harbor, a known Red Knot stopover site) and stayed for two days. After leaving New Jersey, it flew north along the US east coast to Cape Cod where it flew east out into the Atlantic, then south to arrive in the Lesser Antilles on 3 Sep. On 10 Sep, the bird flew for three days to the north coast of Brazil close to the border between the states of Maranhão and Pará, where it wintered. The geolocator on Y0U recorded location for 152 days before failing from saltwater intrusion, but it flew back to Delaware Bay where it was recaptured on14 May 2010.

Y0Y: The Red Knot with inscribed flag Y0Y departed Delaware Bay on 28 May 2009 and flew for one day to James Bay, Ontario, where it stayed for 7 days (Fig. 4). On 6 Jun 2009, it flew to an inland area ~300 km south-west of Churchill, Manitoba, on Hudson Bay and stopped for 4 days. Y0Y then wandered across an area east of Victoria Island, south of King William Island, west of Southampton Island, and north of Baker Lake for 69 days, apparently not nesting because of its continuing movement. On 20 Aug, it left this area and stopped for 11 days just south of Churchill on Hudson Bay. Y0Y left Hudson Bay on 1 Sep and, like Y0U, flew to the Lesser Antilles, crossing Cape Cod, Massachusetts, in a non-stop, 8-day flight of 5,100 km. After 7 days in the Lesser Antilles, it flew to the eastern coast of the state of Maranhão, Brazil, arriving on 19 Sep and staying for 11 days. On 30 Sep, it left Maranhão, flew for 3 days, and stopped around the southern end of Lagoa dos Patos, Rio Grande do Sul, S Brazil, for 6 days. On 9 Oct, Y0Y moved to its wintering site probably on the shores near the mouth of the Río Negro estuary in northern Patagonia, Argentina, arriving on 10 Oct. It stayed in approximately the same area for 173 days, though it was observed at San Antonio Oeste, 100 km west, on 13 Mar 2010 by PMG and AJB. It left the area on 1 Apr 2010; flew for just one day to the shore close to the border between Uruguay and Brazil. It was seen by Joaquín Aldabe and Pablo Rocca on 10 Apr 2010 at Barra del Chui in Uruguay, and on 11 and 12 Apr on the Brazilian side of Barra del Chui. Y0Y remained around the Uruguay–Brazil border for 36 days. On 8 May, Y0Y flew 8,000 km in 6 days to the United States east coast, stopping for 6 days at Ocracoke, North Carolina; then it flew in one day to Delaware Bay, arriving on 20 May.

1VL: The Red Knot with inscribed flag 1VL left Delaware Bay on 29 May and stopped in James Bay, Ontario, where it stayed for 9 days; on 8 Jun it flew on to Southampton Island, arriving on 10 June (Fig. 5). On 30 Jun it moved to an area NNW of Southampton Island, centered near Pelly Bay, Nunavut, north of the Arctic Circle, where the lack of nighttime signals made location uncertain. It arrived again on Southampton Island on 14 Aug, stayed for 6 days; then it flew 3 days to Cape Cod, Massachusetts, where it stayed for 18 days. On 8 Sep, 1VL made a direct flight of 6 days and 5,400 km to an area 80 km northwest of Sao Luis, Maranhão, Brazil. On the way, it apparently encountered a weather system that caused it to detour nearly 1,000 km to the north-east. It stayed in Maranhão for 7 days, left on 22 Sep, and flew one day to winter in an area just north of Natal, Rio Grande do Norte, Brazil, close to the north-easternmost point of South America, where it stayed for 8 months. It left Brazil on 18 May 2010, flying 6 days and 6,700 km, crossing the Lesser Antilles and the Virginia coastal islands, and arriving in Delaware Bay on 24 May. 1VL was recaptured the next day at 134 g, one day short of a year after it was first caught.

Flight range

For each flight, we measured the great circle distance between departure and arrival sites and these data are presented on the maps (Figs 3, 4 & 5) in yellow. However, we emphasize that these represent the absolute minimum distances flown, if the birds deviated from the great circle route at all (which is very likely) the distances flown will be greater. In those cases in which the geolocator output makes it clear that the route flown was substantially different from the great circle, we have added our estimate of the actual distance flown to the maps (in pale green).

Y0Y, which wintered in Argentina, flew the longest aggregate distance, based on the great circle route between each stop, of 26,700 km and also made the longest single flight of 8,000 km. 1VL, which wintered in NE Brazil, flew an aggregate of 21,150 km on migration including two flights when it clearly deviated from the great circle. Y0U was recorded as having travelled about 12,200 km before its geolocator failed when it was on its wintering grounds in N Brazil. If it is assumed that it flew direct from there to Delaware Bay, it would have covered about 17,500 km in the year.

DISCUSSION

Hitherto, everything we have discovered about the migration of Red Knots in the Western Hemisphere, including the location of their wintering, stopover and breeding sites has been based on direct observations of birds, and the absence of birds. These data are inextricably bound to our choice of survey location and their value is hampered by our inability to make observations simultaneously everywhere in the flyway. Thus they provide us with only a limited understanding. But now, with their ability to track birds throughout their annual cycle, it seems that geolocators are poised to greatly improve our comprehension of shorebird migration. However, until the impact of these instruments on the birds has been fully evaluated, the interpretation of results should always take account of the possibility that they were influenced by the method.

Our results substantiate some of what we already knew or suspected about Red Knots in the West Atlantic Flyway, but also reveal new aspects that had not been expected.

Effect of geolocators on Red Knots

The geolocators mounted on Darvic flags did not appear to have any effect on the behavior, survival or leg morphology of Red Knots in this study. The devices weigh only 1.7 g (1.3% of the birds' average fat-free mass (Atkinson *et al.* 2007)), but as with most location devices, the method of attachment presents the greater problem. In a similar project on Ruddy Turnstones *Arenaria interpres* in Australia, eight birds were fitted with geolocators and four recaptured after round-trips of up to 27,000 km to the Arctic and back (Minton *et al.* 2010), which also suggests that geolocators attached to flags are virtually no impediment to medium-size shorebirds. The fact that proportionately more knots with geolocators were resighted in May 2010, compared with knots with only flags appears to be evidence that geolocators have little or no effect on annual survival, but this should be treated with caution because there are clear reasons for this result that do not relate to survival. The high resighting rate of geolocator birds probably arises partly because a bird with a geolocator is more conspicuous to an observer and partly because an effort was being made to find birds with geolocators for recapture. Therefore if a geolocator bird was seen, an observer would persist in following it until the flag could be read, but flagged birds without geolocators might be ignored if they proved too difficult to observe. In principle the high resighting rate could arise because the geolocator birds had a longer residence time in Delaware Bay, but we have no reason to believe that this is the case.

A potential impact of geolocators that we have not been able evaluate is that they could cause damage to eggs during incubation. We are aware of current breeding-ground based studies of Red Knots, Dunlins *Calidris alpina* and Hudsonian Godwits *Limosa haemastica* using geolocators, so whether this is a matter of concern should soon become clear.

Migration routes

All three birds wintered in South America, providing us with the first direct evidence of the pathways Red Knots take between their arctic breeding grounds and South America. Three is a small sample from which to generalize, but there was some commonality among the birds in the routes they took that might be applicable to a substantial proportion of the knot population.

First, all three departed from Delaware Bay heading inland in a NNW direction, which is consistent with all observed departures of knots from the Bay (Harrington & Flowers 1996, authors' unpublished observations). They then flew to James Bay and on to Southampton Island and other breeding areas.

Second, flying south after the breeding season, they all either stopped at, or crossed, the US mid-Atlantic Coast, and all stopped on or crossed the Lesser Antilles before reaching Brazil.

Y0U wintered on the north coast of Brazil on the border between Maranhão and Pará, 1VL made landfall in Maranhão but then wintered about 1,100 km to the east, while Y0Y stopped in Maranhão for 12 days before moving on to winter in Argentina. Only Y0Y went to southern South America and flew overland going both south and north. Its northbound path took it across the Pantanal region of Brazil, where 10 knots were seen in Sep 1989 (Niles *et al.* 2008 citing CEMAVE unpub. data). Therefore, although the evidence is sparse, it would seem quite likely that the Red Knots that winter in Patagonia can traverse the Brazilian interior in both spring and fall.

Stopovers and wintering sites

After leaving Delaware Bay, all three birds stopped at James Bay before moving on to the Arctic. This is surprising because James Bay was not thought to be a major spring stopover though large numbers have been seen over-flying the area, presumably en route between Delaware Bay and the breeding grounds (Niles *et al.* 2008). James Bay is only 1,500 km from Delaware Bay, which is a relatively short distance for the birds that leave Delaware Bay heavily laden with fuel. We do not think it likely that the three birds stopped in James Bay because they were hampered by the geolocators as they all made much longer non-stop flights later in the year. Probably the number of knots stopping in James Bay in 2009 was greater than usual because of a large area of persistent low temperatures and spring snow that forced the birds to delay their flight to the breeding areas (Paul Smith, pers. comm.). Therefore although James Bay may not be a key stopover under normal spring conditions, in 2009 and in similar years it may support a substantial proportion of the population.

Two birds, Y0U and Y0Y, stopped in the Lesser Antilles arriving on 3 and 8 Sep respectively. The geolocator locations suggest that both were in the area of Guadeloupe, Martinique and Barbados. However, so far as we know there are no previous observations of substantial numbers of knots stopping in this area, though small numbers occur during both north and south migration (Anthony Levesque, pers. comm., Holland & Williams 1978, Steadman *et al.* 1997). Two tropical storms were active in the region at the time (Erika, 1–3 Sep and Fred, 7–12 Sep), so it may be that the birds stopped in the Lesser Antilles on account of the weather conditions.

Y0Y stopped at the southern end of Lagoa dos Patos, Rio Grande do Sul, Brazil, on its southbound flight but in an area about 250 km to the south on the Brazil–Uruguay border for 36 days on its way north. This is at the southern end of the Rio Grande do Sul coast where in the 1980s researchers concluded that Red Knots move in short flights during April from south to north while feeding on the clam *Donax haleyanus* and the mole crab *Emerita brasiliensis* (Harrington *et al.* 1986, Vooren & Chiaradia 1990) coincident with the late summer peak of abundance of juveniles of these species (Gianuca 1983). Thus the fact that Y0Y stayed in the same area around the Brazil–Uruguay border from which it launched on an 8,000 km flight suggests that the local food supply is currently good enough to support major refueling for Red Knots, but was passed through continuously by the larger population that existed in the 1980s.

The main *rufa* wintering sites are thought to be the southeast United States coast (mainly Florida), the coast of Maranhão, N Brazil, between São Luís and Baía de Turiaçu and Isla Grande, and Tierra del Fuego (Niles *et al.* 2008). However, all of the geolocator birds wintered elsewhere. This is not particularly surprising because counts of knots stopping over on the US east coast are sometimes greater than numbers estimated to be wintering in the main sites (A.D. Dey, unpub. information). Nevertheless this result highlights the need for more extensive surveys before we can claim to have a thorough knowledge of the winter distribution of *rufa*.

Non-stop flight range

South American wintering knots have long been thought to make very long non-stop flights during their northbound migration. In May 1984, for example, individually-marked knots were last seen at Lagoa do Peixe, S Brazil, and first seen in Delaware Bay 13 days apart, a great circle distance of 8,170 km (Harrington & Flowers 1996). At the time it was thought that the birds might have stopped en route; and there would have been time to do so because total flying time was estimated at about 6 days. However, subsequent discovery that long-distance migrants ingest much of their digestive apparatus before departure, and this has to re-grow before they can feed efficiently again (Piersma & Gill 1998) means that a refueling stop would be unlikely. Two similar instances of probable long non-stop flights occurred in 2010 when one individually marked knot was last seen at San Antonio Oeste, Argentina, and next seen in NE Florida 9 days later, a great circle distance of 8,050 km (PMG & P. Leary), while another was last seen at San Antonio Oeste and next seen in Delaware Bay 11 days later, a great circle distance of 8,900 km (PMG & AJB). The 8,000 km flight of Y0Y from the Brazil–Uruguay border to North Carolina provides the final proof that such long flights do indeed take place.

Although Y0Y and probably the other birds mentioned above flew from at least southern Brazil to the United States without stopping on the north coast of South America, count data and band resightings show that many other Patagonia-wintering knots do make a stopover there (Antas & Nascimento 1996, González *et al.* 2006, Morrison & Harrington 1992, Piersma *et al.* 2005, Rodrigues 2000, Wilson *et al.* 1998). We do not know why some knots overfly the north coast while others stop, but it would seem to be an analogous situation to that of the *canutus* knots that winter on Banc d'Arguin, W Africa, and fly direct to the Wadden Sea in NW Europe if the weather is favorable, but stop in W France if they encounter adverse wind conditions (Leyrer *et al.* 2009). Although there are several reasons why migrant shorebirds may choose to stop in one place and not in another (van de Kam *et al.* 2004), a reason why at least some knots may avoid stopping on the north coast of South America is the prevalence of ectoparasites in that area (D'Amico *et al.* 2008).

In a review of the northward migration of Red Knots worldwide, Piersma *et al.* (2005) assumed that all Patagonian *rufa* stop on the north coast of Brazil and that their longest non-stop flight is the 5,200 km from there to Delaware Bay. Among other knot subspecies, the longest flight they describe is that of *canutus*, some of which fly 6,900 km from South Africa to Mauritania. Possibly therefore those *rufa* that winter in southern South America and fly from at least S Brazil to the United States make the longest non-stop flights of any population of Red Knots worldwide, but that remains to be confirmed.

1VL arrived in Delaware Bay on 24 May having just flown 6,700 km from NE Brazil. It was caught the next day at what seems, in the circumstances, the relatively high mass of 134 g, just above the average fat-free mass of *rufa* knots (Atkinson *et al.* 2007). It is unlikely that it had gained significant mass between arrival and capture in view of its need to re-grow its digestive apparatus (Piersma & Gill 1998). Though many low mass knots are caught in Delaware Bay at the beginning of the stopover, it is normally impossible to know how long the birds have been present. Therefore more observations like this will give a useful insight into actual arrival mass.

Influence of adverse weather

Adverse weather probably influenced the track of two birds, IVL and Y0U. When Y0U departed from New Jersey on southward migration, it first flew north to Cape Cod, then east out into the Atlantic, and ultimately south to the Lesser Antilles (Fig. 3). The initial northward flight may have been a response to strong southerly winds during the dying phase of tropical storm Danny and the landfall on the Lesser Antilles may have been caused by storm Erika which was traversing that area at the time (Fig. 3). We estimate the distance flown by Y0U to be around 4,000 km compared with the great circle distance between departure and arrival sites of 2,970 km. Similarly 1VL made a detour over the sea during its southward migration from Cape Cod to Brazil, probably in response to strong adverse winds recorded by weather buoys in the area at the time (*www.buoyweather.com*), flying at least 6,800 km as opposed to the great circle distance of 5,400 km. That two of the three birds encountered stormy weather in the early hurricane season in the Atlantic is not surprising, but the birds' responses to such weather events was not previously known. The extra flying represents substantial additional energy expenditure, which on some occasions might lead to mortality.

Risk of collision with wind turbines

One focus of this work was to assess the potential risk to Red Knots of wind turbines that may be sited 3–20 miles (5–32 km) off the US Atlantic coast. The Bureau of Ocean Energy Management Regulation and Enforcement has identified three primary questions that need to be addressed to characterize the risk to knots from offshore wind development on the Atlantic Outer Continental Shelf (AOCS): 1) do knots fly within the 3–20 mile area?, 2) do they fly 40–150 m above sea level, the span of turbine rotors?, and 3) can they avoid the rotors if they do fly within this zone? Geolocator data can only answer the first of these questions, but there are concerns over the low resolution of the locations. Currently, the resolution for their geolocators is estimated by the British Antarctic Survey at around 150 km, but this is greatly affected by local factors, especially shading and weather. Minton *et al.* (2010) found errors as high as 250–300 km when comparing several known resightings to geolocator derived locations. However, both newer software and further interpretation of locations, based partly on weather information and repeated locations in the same place, can narrow this error in geospatial position calculation. Nevertheless, with current analytical techniques, resolution was sufficient for the three birds to indicate that the area of the AOCS from North Carolina to Cape Cod, Massachusetts, and particularly the vicinity of Delaware Bay may be critical for migrant Red Knots.

Future research directions

In addition to the 47 geolocators attached to Red Knots in Delaware Bay discussed in this paper, we have since deployed a further 200 on Red Knots trapped between May 2009 and May 2010 on the Mingan Archipelago, Canada, the Atlantic coast of New Jersey and Massachusetts, the Gulf coast of Florida and Texas and at San Antonio Oeste, Argentina. We plan to continue efforts to recapture the knots already carrying geolocators and, subject to sufficient funding, intend to attach more geolocators to enable us to build up a comprehensive understanding of the birds' migration strategies, wintering and breeding locations. Such data will underpin conservation prescriptions for this vulnerable population and help assess the implications of coastal developments, including the placement of offshore wind facilities and drilling operations.

ACKNOWLEDGEMENTS

This study was funded by BOEMRE (formerly MMS, USDOI) contract M08PC20060 to Pandion Systems, Natural Land Trust of NJ, Rutgers University, and the Conserve Wildlife Foundation of NJ. We thank Jeannine Parvin and Dick Veitch for helping sort out geolocator and banding data and the NJ Delaware Bay shorebird team for helping to catch birds with geolocators. We are grateful to Joaquín Aldabe and Pablo Rocca for providing details of their observations of Y0Y around the Brazil–Uruguay border. We are also most grateful to Nigel Clark and Theunis Piersma for reviewing our draft paper and making many constructive comments.

REFERENCES

Afanasyev, V. 2004. A miniature daylight level and activity data recorder for tracking animals over long periods. *Mem. Natl Inst. Polar Res., Spec. Issue* 58: 227–233.

Antas, T.Z.P. & I.L.S. Nascimento. 1996. Analysis of Red Knot *Calidris canutus rufa* banding data in Brazil. *Int. Wader Studies* 8: 63–70.

Atkinson, P.W., A.J. Baker, K.A. Bennet, N.A. Clark, J.A. Clark, K.B. Cole, A. Dekinga, A. Dey, S. Gillings, P.M. Gonzalez, K. Kalasz, C. Minton, J. Newton, T. Piersma, R.A. Robinson & H.P. Sitters. 2007. Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent. *J. Appl. Ecol.* 44: 885–895.

Baker, A.J., T. Piersma & A.D. Greenslade. 1999. Molecular versus phenotypic sexing in Red Knots. *Condor* 101: 887–893.

Baker, A.J., P.M. Gonzalez, T. Piersma, L.J. Niles, I. de Lima S.do Nascimento, P.W. Atkinson, P. Collins, N.A. Clark, C.D.T. Minton, M.K. Peck & G. Aarts. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London B* 271: 875–882.

Buehler, D.M. & T. Piersma. 2008. Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Philosophical Transactions of the Royal Society of London, B*, 363**,** 247–266.

Clark, K., L. Niles & J. Burger. 1993. Abundance and distribution of shorebirds migrating on Delaware Bay, 1986–1992. *Condor* 95: 694–705.

Clark, N.A., S. Gillings, A.J. Baker, P.M. González & R.R. Porter. 2005. The production and use of permanently inscribed leg flags for waders. *Wader Study Group Bull.* 108: 38–41.

Conklin, J.R. & P.F. Battley. 2010. Attachment of geolocators to Bar-tailed Godwits: a tibia-mounted method with no survival effects or loss of units. *Wader Study Group Bull.* 117: 56–58.

D'Amico, V.L., M.N. Bertellotti, A.J. Baker, W.R.T. Júnior & P.M. González. 2008. Migration strategies of wintering populations of red knots *Calidris canutus rufa* in South America: the role of parasite pressure. *Ardeola* 55: 193–202.

DeLong, R.L., B.S. Stewart & R.D. Hill. 1992. Documenting migrations of northern elephant seals using day length. *Marine Mammal Science* 8: 155–159.

Driscoll, P.V. & M. Ueta. 2002. The migration route and behaviour of Eastern Curlews *Numenius madagascariensis*. *Ibis* 144: E119–130. (online)

Gianuca, N.M. 1983. A preliminary account of the ecology of sandy beaches in southern Brazil. *In*: McLachlan, A. & T. Erasmus (eds). *Sandy Beaches as Ecosystems*. W. Junk, The Hague, the Netherlands.

Gill, R.E., T. Piersma, G. Hufford, R. Servranckx & A. Riegen. 2005. Crossing the ultimate ecological barrier: Evidence for an 11,000-km-long nonstop flight from Alaska to New Zealand and eastern Australia by Bar-tailed Godwits. *Condor* 107: 1–20.

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

González, P.M., A.J. Baker & M.E. Echave. 2006. Annual survival of Red Knots (*Calidris canutus rufa*) using the San Antonio Oeste stopover site is reduced by domino effects involving late arrival and food depletion in Delaware Bay. *Hornero* 21(2): 109–117.

Harrington, B.A., P. de T.Z. Antas & F. Silva. 1986. Northward shorebird migration on the Atlantic coast of southern Brazil. *Vida Silvestre Neotropical* 1: 45–54.

Harrington, B. & C. Flowers. 1996. *The Flight of the Red Knot.* Norton, New York.

Holland C.S. & J.M. Williams. 1978. Observation of birds of Antigua. *North American Birds* 32: 6.

Leyrer, J., P. Bocher, F. Robin, P. Delaporte, C. Goulevent, E. Joyeux, F. Meunier & T. Piersma. 2009. Northward migration of Afro–Siberian Knots *Calidris canutus canutus*: high variability in Red Knot numbers visiting staging sites on the French Atlantic coast, 1979–2009. *Wader Study Group Bull.* 116: 145–151.

Minton, C., K. Gosbell, P. Johns, J.W. Fox & V. Afanasyev. 2010. Initial results from light level geolocator trials on Ruddy Turnstone *Arenaria interpres* reveal unexpected migration route. *Wader Study Group Bull.* 117: 9–14.

Morrison, R.I.G. & R.K. Ross. 1989. *Atlas of Nearctic Shorebirds on the Coast of South America.* Canadian Wildlife Service. 2 vols. Special Publication, 325 pp.

Morrison, R.I.G. & B.A. Harrington. 1992. The migration system of the Red Knot *Calidris canutus rufa* in the New World. *Wader Study Group Bull.* 64, Suppl.: 71–84.

Morrison, R.I.G., R.K. Ross & L.J. Niles. 2004. Declines in wintering populations of Red Knots in southern South America. *Condor* 106: 60–70.

Niles, L.J., H.P. Sitters, A.D. Dey, P.W. Atkinson, A.J. Baker, K.A. Bennett, R. Carmona, K.E. Clark, N.A. Clark, C. Espoz, P.M. González, B.A. Harrington, D.E. Hernández, K.S. Kalasz, R.G. Lathrop, R.N. Matus, C.D.T. Minton, R.I.G. Morrison, M.K. Peck, W. Pitts, R.A. Robinson & I.L. Serrano. 2008. Status of the Red Knot, *Calidris canutus rufa*, in the Western Hemisphere. *Studies Avian Biol.* 36: 1–185.

Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *J. Ornithol.* 148 (Suppl. 1): S45–S59.

Piersma, T. & A.J. Baker. 2000. Life history characteristics and the conservation of migratory shorebirds. *In:* Gosling, L.M. & W.J. Sutherland (eds). *Behaviour and Conservation.* pp. 105–124. Cambridge University Press, Cambridge.

Piersma, T. & R.E. Gill. 1998. Guts don't fly: small digestive organs in obese Bar-tailed Godwits. *Auk* 115: 196–203.

Piersma, T., D.I. Rogers, P.M. Gonzalez, L. Zwarts, L.J. Niles, I. de Lima S.do Nascimento, C.D.T. Minton & A.J. Baker. 2005. Fuel storage rates before northward flights in red knots worldwide: facing the severest ecological constraint in tropical intertidal environments? *In:* Greenberg, R. & P.P. Marra (eds). *Birds of Two Worlds: Ecology and Evolution of Migration*. Johns Hopkins University Press, Baltimore. pp. 262–273.

Rodrigues, A.A.F. 2000. Seasonal abundance of Neartic shorebirds in the Gulf of Maranhão, Brazil. *J. Field Ornith*. 71: 665–675.

Steadman, D.W., R.L. Norton, M.R. Browning & W.J. Arendt. 1997. The birds of St Kitts, Lesser Antilles. *Carib. J. Sci.* 33: 1–20.

Stutchbury, B.M., S.A. Tarof, T. Done, M. Gow, P.M. Kramer, J. Tautin, J.W. Fox & V. Afanasyev, V. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323: 896.

Vooren, C.M. & A. Chiaradia. 1990. Seasonal abundance and behavior of coastal birds on Cassino Beach, Brazil. *Ornitologia Neotropical* 1: 9–2.

van de Kam, J., B.J. Ens, T. Piersma & L. Zwarts. 2004. *Shorebirds. An illustrated Behavioural Ecology*. KNNV Publishers, Utrecht.

Watts, B.D., Truitt, B.R., Smith, F.M., Mojica, E.K., Paxton, B.J., Wilke, A.L. & Duerr, A.E. 2008. Whimbrel tracked with satellite transmitter on migratory flight across North America. *Wader Study Group Bull.* 115: 119–121.

Wilson, J.R., A.A.F. Rodrigues & D.M. Graham. 1998. Red Knots *Calidris canutus rufa* and other shorebirds on the north-central coast of Brazil in April and May 1997. *Wader Study Group Bull.* 85: 41–45.