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MIGRATION AND OVER-WINTERING OF RED KNOTS (*CALIDRIS CANUTUS RUFA*) ALONG THE ATLANTIC COAST OF THE UNITED STATES

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Abstract. Surveys and banding records of *Calidris canutus rufa* indicate that Red Knots migrate mainly north and south through Massachusetts, Delaware Bay, and Virginia, and winter in Florida and South America. We fitted 40 adult Red Knots with geolocators at Monomoy National Wildlife Refuge, Massachusetts, during fall migration (2009), and in this paper report on the locations of migration and wintering along the Atlantic coast of the United States of eight recaptured knots. The knots' migration patterns varied: four birds wintered along the U.S. Atlantic coast, and the rest went to the Caribbean islands or the northern edge of South America. Knots spent 58 to 75 days in Monomoy Refuge before migrating south in November. Seven of the eight stopped along the U.S. Atlantic coast for relatively long periods. For the six with complete yearly cycles, the total time spent along the Atlantic coast averaged 218 days (range 121–269 days). All eight knots crossed the Atlantic outer continental shelf from two to six times. Areas of use were Monomoy, Long Island, New Jersey, Maryland, the Outer Banks of North Carolina, South Carolina, and Florida. These data indicate that Red Knots moving through Massachusetts in the fall had variable migration patterns, spent considerable periods of their life cycle along the Atlantic coast, and each knot followed a separate and distinct path, which suggests that knots can be at risk along the Atlantic coast for a substantial period of their life cycle.

Key words: Calidris canutus*, geolocator, habitat, migration, pathways, Red Knot, risk, stopovers, wintering areas.*

Riesgo durante la Migración e Invernación de *Calidris canutus rufa* a lo Largo de la Costa Atlántica de los Estados Unidos

Resumen. Muestreos y registros de anillamiento de *Calidris canutus rufa* indican que los correlimos gordos migran mayormente hacia el norte y sur através de la Bahía de Delaware, Virginia, y Massachusetts, e invernan en Florida y América del Sur. Colocamos geolocalizadores a 40 correlimos gordos adultos en el Refugio Nacional de Vida Silvestre de Monomoy, Massachussetts, durante la migración otoñal; y en esta publicación reportamos sobre sus localizaciones de migración e invernación (2009) a lo largo de la costa atlántica de los Estados Unidos, y desarrollamos un modelo de riesgo. Los correlimos tuvieron un patrón de migración variable en el cual cuatro pájaros invernaron a lo largo de la costa atlántica de Estados Unidos ($n = 8$), y el resto fueron a las islas del Caribe o al borde norte de América del Sur. Los correlimos pasaron de 58 a 75 días en Monomoy antes de migrar al sur en noviembre. Siete de ocho correlimos se detuvieron a lo largo de la costa atlántica de Estados Unidos por períodos de tiempo relativamente largos. Para seis pájaros con ciclos completos, el tiempo total a lo largo de la costa atlántica promedió 218 días/pájaro (121 a 269 días). Todos los ocho correlimos cruzaron la Plataforma Continental Exterior Atlántica de dos a seis veces. Los datos indican que las áreas usadas fueron Monomoy, Long Island, la costa de New Jersey, Maryland, los Outerbanks de North Carolina, South Carolina y Florida. Todos los ocho correlimos se detuvieron a lo largo de la costa atlántica en su migración hacia el sur o el norte. Estos datos indican que los correlimos gordos que se mueven através de Massachusetts en el otoño gastan períodos considerables de su ciclo de vida a lo largo de la costa atlántica, cada correlimos gordo tenía una ruta distintiva y separada, y los correlimos pueden estar en riesgo a lo largo de la costa atlántica debido a la pérdida de hábitat y perturbación humana, y posiblemente por el desarrollo mar afuera de facilidades petroleras o de molinos de viento.

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INTRODUCTION

Birds face different demands and stressors as a result of their yearly cycle, geographical location during these activities, social systems, competitors, predators, and habitat loss. Understanding the constraints of migration, yearly movement patterns, and wintering locations of birds is essential to protecting them, particularly for long-distant migrants that may rely heavily on stopover locations. These constraints include seasonal patterns, timing of movements, and the spatial use for migration and wintering of habitats that may intersect both coastal and offshore development, particularly beach development, offshore oil drilling, and wind farms. The process of migration and its consequences depend on strategies of arrival, residency, and departure at sites of both stopover and wintering. Loss of habitat for either stopover or wintering can have severe consequences on populations (Dolman and Sutherland 1995, Piersma and Baker 2000). Worldwide, many wintering sites and passage areas are imperiled, especially for shorebirds (Gillings et al. 2009).

The Red Knot (*Calidris canutus*) is a medium-sized shorebird with variable migration patterns. Some individuals undertake long-distance migrations from breeding grounds in the high Arctic to wintering grounds in South America (Niles et al. 2010), a round trip of up to 30 000 km. The Western Hemisphere subspecies (*Calidris canutus rufa*) migrates the greatest distance of any of the six subspecies, traveling from its arctic breeding grounds at 70° N to its wintering grounds at 53° to 66° S (Morrison et al. 2004). Other subspecies of knots occurring in North America include *C. c. islandica*, which breeds in the northeastern Canadian high Arctic and migrates to Europe, and *C. c. roselaari*, which breeds in Alaska and Wrangel Island and is thought to winter from Florida to the Caribbean, Central America, and northern South America, as well as along the Pacific coast (Morrison et al. 2004).

Each May to early June, Red Knots and other northbound shorebirds stop over at Delaware Bay (bordered by New Jersey and Delaware) to feed on the eggs of spawning horseshoe crabs (*Limulus polyphemus*) (Clark et al. 1993, Tsipoura and Burger 1999). During about two weeks in Delaware Bay, Red Knots gain sufficient body reserves for their final flight to arctic breeding grounds (Morrison and Harrington 1992, Harrington 2001), and the body reserves gained in Delaware Bay are critical for both migration and successful breeding in the Arctic (Baker et al. 2004, Morrison and Hobson 2004, Morrison et al. 2007).

Because of the Red Knot's rapid population decline (Baker et al. 2004, Niles et al. 2008, Cohen et al. 2009), its long migratory paths, and the declines in horseshoe crab eggs (Niles et al. 2010), it is critical to gain some understanding of the routes the species follows on its northward and southward journeys. While considerable focus has been placed on understanding its ecology in northward migration, there has been much less focus on the southward migration (Harrington et al. 2010).

The development of geolocators (global location sensors) has enabled researchers to obtain continuous accounts of the movements of birds, such as seabirds (Phillips et al. 2004, Landers et al. 2011) and raptors (Rodriguez et al. 2009a,b, Bachler et al. 2010). Recently, more light-weight geolocators have allowed researchers to track movements of smaller seabirds (Nisbet et al. 2011) and shorebirds (Conklin and Battley 2010, Conklin et al. 2010, Minton et al. 2010, Niles et al. 2010, Klaassen et al. 2011). These devices add to our information about the life cycle of birds and allow assessment of risks faced, management options, and conservation needs.

In the spring of 2009, we placed 47 geolocators on knots captured at Delaware Bay (Niles et al. 2010). There were no significant differences in the rate of resighting of these knots and of 622 knots fitted with only leg flags during the following year. All three recaptured knots flew to the Arctic and all three wintered in South America in areas where wintering was previously unknown (Niles et al. 2010). The longest round-trip flight was 26 738 km, which included an 8000-km, 6-day flight from southern Brazil to the coast of North Carolina. Two birds detoured around weather systems, indicating that storms can force birds away from straight-line flights.

Prior to the use of geolocators on the Red Knot, it was believed that subspecies *rufa* had two migration strategies: (1) long-distance migration directly to southern South America and (2) shorter-distance migration to a winter range in Florida (Niles et al. 2010). Delaware Bay has long been a known major spring stopover area during northbound migration, and Monomoy National Wildlife Refuge in Massachusetts is a major staging area where birds spend several weeks during southbound migration (Harrington et al. 2010). Because the short-distance migrants need less flight time than knots migrating to the southern tip of South America, they can spend more time at Monomoy, undergoing molt while they forage (Harrington et al. 2010). A full understanding of the migratory behavior and strategies of *Calidris canutus rufa* must include information on all its patterns of migration and wintering, not just those on Delaware Bay and in South America.

In this study we examined the migratory behavior, stopover times, and winter residency of eight adult Red Knots (subspecies *rufa*) that were short-distance migrants and recaptured at Monomoy Refuge one year later. We addressed the following questions: (1) where were the primary stopover areas along the U.S. Atlantic coast during migration, (2) what were the residency times at these stopovers, (3) where did knots overwinter in the United States, and (4) what were the patterns of movement. We focused on the U.S. Atlantic coast because the U.S. Fish and Wildlife Service has undertaken a two-year review of the status of the Red Knot (*rufa*) to determine whether it should be listed as endangered or threatened. Our objective was to understand the importance of Atlantic coastal habitats to migrating and overwintering knots. The data we report here are only part of the picture, as additional information needs to be gained from knots marked at other stopover areas along the U.S. Atlantic coast.

METHODS FOR GEOLOCATOR STUDY

OVERALL PROTOCOL

Our overall design was to place between 40 and 60 geolocators on Red Knots (subspecies *rufa*) at each of the main known areas of stopover and wintering, including New Jersey (Delaware Bay), Massachusetts (Monomoy Refuge), and Florida. In 2009 we placed geolocators on adult knots that we believed were short-distance migrants from their molt (short-distance migrants molt in Monomoy Refuge, whereas long-distance migrants molt in South America, Niles et al. 2008). Geolocators are small devices for detecting and locating position by recording changes in ambient light levels. These data can be used to estimate the times of sunrise and sunset, from which latitude and longitude can be calculated (Nisbet et al. 2011).

In Massachusetts in 2009, we placed geolocators and leg flags on 40 knots and leg flags only on 89 knots. We relied on a network of paid and volunteer observers to report sightings of GL and flagged birds during migration, on the wintering grounds, and again in Massachusetts the following year (where birds were retrapped). The protocol for this research with Red Knots, including attaching geolocators to birds, was approved by the Rutgers University Animal Review Board.

SITE DESCRIPTION

Monomoy Refuge is located in southeastern Cape Cod, Massachusetts. The refuge encompasses over 3000 ha, and most land above mean low tide is federally designated wilderness. This dynamic wind- and tidal-driven system of shifting sands creates approximately 100 ha of saltmarsh dominated by *Spartina alterniflora* and 900 ha of intertidal mudflat on the northern portion of the refuge. Semidiurnal tides generally expose mudflats twice daily, with mean tidal amplitude usually <1.5 m, but tidal fluctuations are often influenced by prevailing winds.

FIGURE 1. Structure and attachment of a geolocator on a Red Knot.

CAPTURE AND GEOLOCATOR PLACEMENT PROTOCOL

We deployed cannon nets where Red Knots concentrated on Monomoy. Once Red Knots were netted, they were removed from the net, placed in holding cages shaded from the sun, processed, and immediately released. Processing included examining fat condition and molt, recording weights and other measurements, banding, and attaching geolocators and/or flags. Geolocators were fitted on adult knots that weighed over 125 g. Knots fitted with geolocators in Delaware Bay showed no significant differences in behavior from knots handled the same way and fitted only with leg flags (Niles et al. 2010). The dimensions of the numbered flag that extended from the band were 7 mm × 14 mm.

We used the same basic method of attaching geolocators to leg bands discussed by Minton et al. (2010) for the Ruddy Turnstone (*Arenaria interpres*) with two variations. One variation included clipped terminal pins and a spacer ring beneath the geolocator band to prevent rubbing, and the second variation was to include two rings. The geolocator was tied and glued to a PVC flag on the tibia above the heel joint. To allow free rotation, the diameter of the plastic ring was slightly larger than the USFWS metal ring. The pin was clipped short, and the ring spaced it away from the joint (Fig. 1). The position was farther from the leg than when a simple ring mount was used, and the increased height of the flag distributed the torque over a much wider area. Torque varied with the center of gravity, which increased only slightly. The advantages are greater surface area of glue and projection out of the feathers. After attachment, geolocators naturally rotate to hang forward, with the sensor facing outward. Detailed construction information is available from the authors. All geolocators were British Antarctic Survey (BAS) Model MK10, and all assemblies weighed less than 1.4 g. The MK10 records the maximum light level every 10 min and whether it is wet or dry every 3 sec, with memory storage of more than one year. When the geolocator gets wet from salt water, it records a signal.

CALIBRATION AND INTERPRETATION OF LOCATIONS

Red Knots proved to be excellent subjects for geolocation because they inhabit only beach areas (as recorded by the saltwater sensor in the BAS Mk10 geolocator) with few shading shrubs and flat terrain. The leg mounts are seldom obscured by feathers, and the birds are active enough during sunrise and sunset that light sampling was not impeded by roosting or orientation. Knots wandered over only relatively small territories between major flights, seldom (if ever) sat outside of incubation, and the eight birds we consider in this study remained at Monomoy for weeks at a time, where they were sighted frequently. These characteristics aided greatly the production of good results.

Pre-deployment calibration was carried out near Philadelphia, with confirmation in the field via resightings at Monomoy (40.6° N, 70.0° W). Prior to deployment, geolocators were exposed to weather and sun, and we carefully noted weather and cloud cover at sunrise and sunset. We used this calibration to adjust the apparent position to the true position. The sun angle that placed the geolocator on the calibration location on a very clear day ranged from 5.2° to 5.7° (flag numbers 7CJ, 010, 014, 032, and 042 = 5.2°; 058 = –5.2°; 016 = –5.1°; 038 = –5.7°). Further adjustment was made to balance the track so that the edge of the fix cluster was placed on Monomoy, where the subject birds were resighted many times.

A single outlying fix that jumped more than 2° longitude, and then immediately returned to the previous location, was discarded from our data set. It represented fewer than 1% of all fixes. Eighty-seven resightings at Monomoy Refuge validated the geolocator positions (number of resightings: 7CJ = 8, 010 = 16, 014 = 16, 016 = 11, 032 = 7, 038 = 11, 042 = 9, 058 = 9, spread over many weeks). The resightings that followed deployment indicated that the sensors were still calibrated properly and drift was negligible. Three additional resightings (of 016 at Delaware Bay; 032 at Kiawah Island, South Carolina; 058 at Mingan, Canada) confirmed that locations had been correctly assigned.

We assembled the geolocators to project forward (the most common position), the light sensor faced outward (rather than under the bird). Excellent light signals with little apparent shading were recorded both on land and in flight. Signals that the device was wet were also clear, with frequent detections every day except during flights. We processed the data with the free Bastrak suite of software downloaded from www.birdtracker.co.uk. The software provides a method for calibration of latitude. Longitude is not calibrated.

We used a Bastrak threshold value of 16 (total scale 64). Changing this value had little effect, because the signal for Red Knots with leg mounts proved to be reliably symmetrical, and changing the threshold moved the transit times little. The Red Knots typically spent weeks in the same location, subjecting the geolocators to many varied weather conditions and orientations. Longitude averages for the sites are shown in Table 1, and for the number of samples. The information on longitude presented in this table has not been presented in other papers based on geolocator technology but gives a picture of the database upon which our conclusions are drawn.

We identified latitude primarily with information supplemental to the geolocator: the geolocators signaled contact with salt water daily, and away from their breeding range knots are well known to use coastal habitat only. So we gave prime importance to intersection of longitude with coastlines, supported by occasional resightings. We used Google Earth to investigate the sites and identify those with possible man-made light interference. Because the geolocator is dry during migration flights, we confirmed these flights with last and first wet signals as well as changes of location. On Long Island, the north and south coasts have the same longitude, so the shore is indeterminate from geolocation.

RESULTS

CONDITION OF GEOLOCATORS

The recovered geolocators were missing parts of the Kevlar attachment thread, had the surface glue chipped, and had their encapsulation milky. This may be due to sand blasting typical of knot habitats, although the encapsulation is known to become cloudy from sun exposure. Retention of the geolocator was due mainly to the glue bond at the edges and to sticky mounting tape beneath it. All nooks and crannies contained fine sand, and occasionally algae. The batteries of two of eight geolocators died before retrieval, but many months of data were recovered when those units were returned to BAS. Hereafter GL refers to knots with geolocators attached.

SURVIVAL AND OBSERVATION RATE OF RED KNOTS FITTED WITH GEOLOCATORS

We used the wet/dry data to indicate whether the GL birds appeared to change behavior following attachment, by comparing the wet/dry signal in the ten falling tide periods for the first five days following deployment (knots actively feed on a falling tide). Seven of the eight knots showed typical wet activity during the first falling tide after attachment. Thereafter,

TABLE 1. Longitudes (°W) of Red Knots fitted with geolocators at Monomoy, Massachusetts, in 2009. Values are mean (range), total number of fixes/number of outliers omitted.

	Monomoy								
	Fall 2009	Spring 2010	Fall 2010	Long I.	New Jersey coast	Maryland coast	North Carolina (outer banks)	South Carolina	Florida (Atlantic coast)
Wintered in U.S.									
7CJ	69.9 (63.2–76.6) 135/2			73.5 (70.4–76.3) 57/0	73.5 (70.4–76.3) 57/0	75.4 (70.8–79.1) 324/5			
010	70.0 (67.8–72.3) 126/0						75.4 (72.1–78.0) 184/0	81.0 (79.0–83.4) 211/0	
016	69.9 (66.7–77.0) 124/1				74.5 (72.1–78.3) 35/3		75.7 (72.0–79.0) 372/3		
038	70.0 (67.4–74.2) 137/4	69.9 (67.0–71.5) 16/1	70.4 (68.5–73.6) 46/0						80.9 (77.2–82.9) 366/3
Wintered outside U.S.									
014	69.8 (67.9–72.3) 146/0				73.4 (70.8–76.2) 39/0		75.6 (74.1–76.5) 11/0	79.4 (78.0–81.0) 62/0	
032	70.0 (66.3–72.0) 100/1							80.6 (78.7–82.9) 21/0	80.0 (78.6–82.1) 27/0
042	70.0 (66–82.6) 136/3					75.5 (74.2–76.9) 14/0			
058	69.6 (65.7–72.8) 128/0	69.4 (67.6–71.4) 34/1	70.2 (65.7–73.6) 37/0					78.8 (77.2–80.3) 80/0	

between five and eight knots showed a clear pattern of wet signals during each falling tide (and those that missed the falling tide often showed this pattern on the alternate tide). We found no apparent immediate negative effect on feeding as indicated by wet/dry data from the geolocators.

There were no significant differences in the rates of resighting of GL knots and those with only leg flags during the year after marking or in their rate of recapture in 2010 (Table 2). Although the former data rely on presence of observers in particular locations, the bias should be the same for each treatment. GL knots recaptured in 2010 were in good condition, none showed any sign of leg wear or damage when the geolocators were removed, and there was no difference in weights when they were captured in 2009 and 2010 (Table 2). Furthermore, in 2010 the mean weights of the knots with geolocators and those with flags only were not different (Table 2).

LOCATIONAL DATA

Longitudinal data for the eight knots initially fitted with geolocators at Monomoy are shown in Table 1. The average longitudinal error from all three seasons (which includes some brief visits) at Monomoy was ±0.2° (±18 km). The average longitudinal error of Monomoy in fall 2009, when the sample size was >100 fixes for each bird, was ±0.1° (±9 km).

STOPOVER BEHAVIOR IN MONOMOY REFUGE

The eight GL knots remained at Monomoy Refuge for the same period as those given only leg flags; all birds departed Monomoy in late October or early November. Knots spent considerable time at Monomoy after attachment of geolocators (58–70 days; Table 3). Duration of their stay was not related to the distance to their first stopping place. Two stopped at Monomoy Refuge on their northward migration in 2010.

MIGRATORY ROUTES, BEHAVIOR, AND WINTERING AREAS ALONG THE U.S. ATLANTIC COAST

The migratory routes, stopover areas, and wintering areas of the eight Red Knots were highly variable (Table 3, Fig. 2). All knots spent some time along the Atlantic coast (either on stopovers or while wintering). Only two of the eight stopped

TABLE 2. Observations of Red Knots individually marked with inscribed leg flags, with and without geolocators, for the first time in September 2009 at Monomoy National Wildlife Refuge, Massachusetts, and later resighted along the Atlantic coast. Means are given ± standard deviation.

	Leg flags only	Leg flag and geolocators
Number of birds marked in 2009	89	40
Number recaptured in 2010	13 (14%)	8 (20%)
Resightings along the Atlantic coast in 2009 and 2010	42%	48%
Mean weight in 2009	122.8 ± 6.3	135.7 ± 8.8
Mean weight when recaptured in 2010	136.8 ± 21.4 (*n* = 13)	135.4 ± 5.8 (*n* = 8)

again along the U.S. Atlantic coast on their southward migration, while six stopped along the Atlantic coast while migrating north. The variability in time at stopovers was greatest for birds moving north in the spring, from ≥12 days for 042 (time was surely longer because its battery died during its northward migration) to 59 days for 014 (Table 3).

Four knots wintered along the Atlantic coast in Maryland (7CJ), North and South Carolina (010, 016), and the Atlantic coast of Florida (038, Table 3). The remaining four wintered south of Florida (Table 3).

The longest flight between places along the Atlantic coast varied from 280 km (7CJ) to 1700 km (038, Table 3). Individual knots generally made two or three stops along the Atlantic coast during their southward or northward migrations;

TABLE 3. Summary of locations and times Red Knots spent along the Atlantic coast of North America in migration and winter. One juvenile (7HN) that was fitted with a geolocator at Brigantine, New Jersey, and not otherwise considered in this paper, flew directly to the west coast of Florida (1440 km in 1 day, 60 km hr^{-1}).

Individual	Time in Massachusetts	Number crossings of outer continental shelf[a]	Longest flight in U.S. waters (km)	Time and location at stop-overs during southward migration (days)[b]	Time and location in areas of apparent wintering (days)	Time and location at stopovers during northward migration	Days along Atlantic coast[e], other than at Monomoy (days at Monomoy); percent of year
7CJ	70	2	280: Monomoy to New Jersey (7 hr)[a]	3: New Jersey	166: Maryland	27: New Jersey 3: Long Island, New York	199 (269) 74%
010	65	2	280: Monomoy to North Carolina (14 hr)		92: North Carolina 107: South Carolina		199 (264) 72%
014	75	4	400: North Carolina to New Jersey (8.5 hr)		(none in U.S., wintered in Cuba)	33: South Carolina 5: North Carolina 21: New Jersey	61 (136) 37%
016	58	3	800: Monomoy to North Carolina (1 day)		189: North Carolina	16: New Jersey	205 (263) 72%
032	58	4	430: Florida to South Carolina (7–9 hr).		(none in U.S., wintered in Cuba)	43: Florida ≥12: South Carolina[c]	≥55 (≥113) (31%)[e]
038	65	6	1700: Monomoy to Florida (2 days)		185: Florida (Atlantic coast)	8: Monomoy	193 (258) 71%
042	70	3	Coastal hopping (3 hr)	9: Maryland	(none in US, wintered in northern South America)	Unknown[d]	≥12 (≥82) (23%)[e]
058	64	4	850: SC to Monomoy (2 days)		(none in US, wintered in Haiti)	50: South Carolina 17: Monomoy	57 (121) 33%

[a]Number of times the bird was clearly over the Atlantic outer continental shelf while making a long-distance flight. Actual number is likely larger because of shorter-distance flights.
[b]After leaving Monomoy. Time at Monomoy is along the Atlantic coast but is not considered in this column.
[c]Battery died 10 April, but bird resighted 2 days later still in South Carolina.
[d]Unknown; battery died 6 December (but bird sighted a few days later; additional interval added to time).
[e]Geolocator recorded <1 year of data.

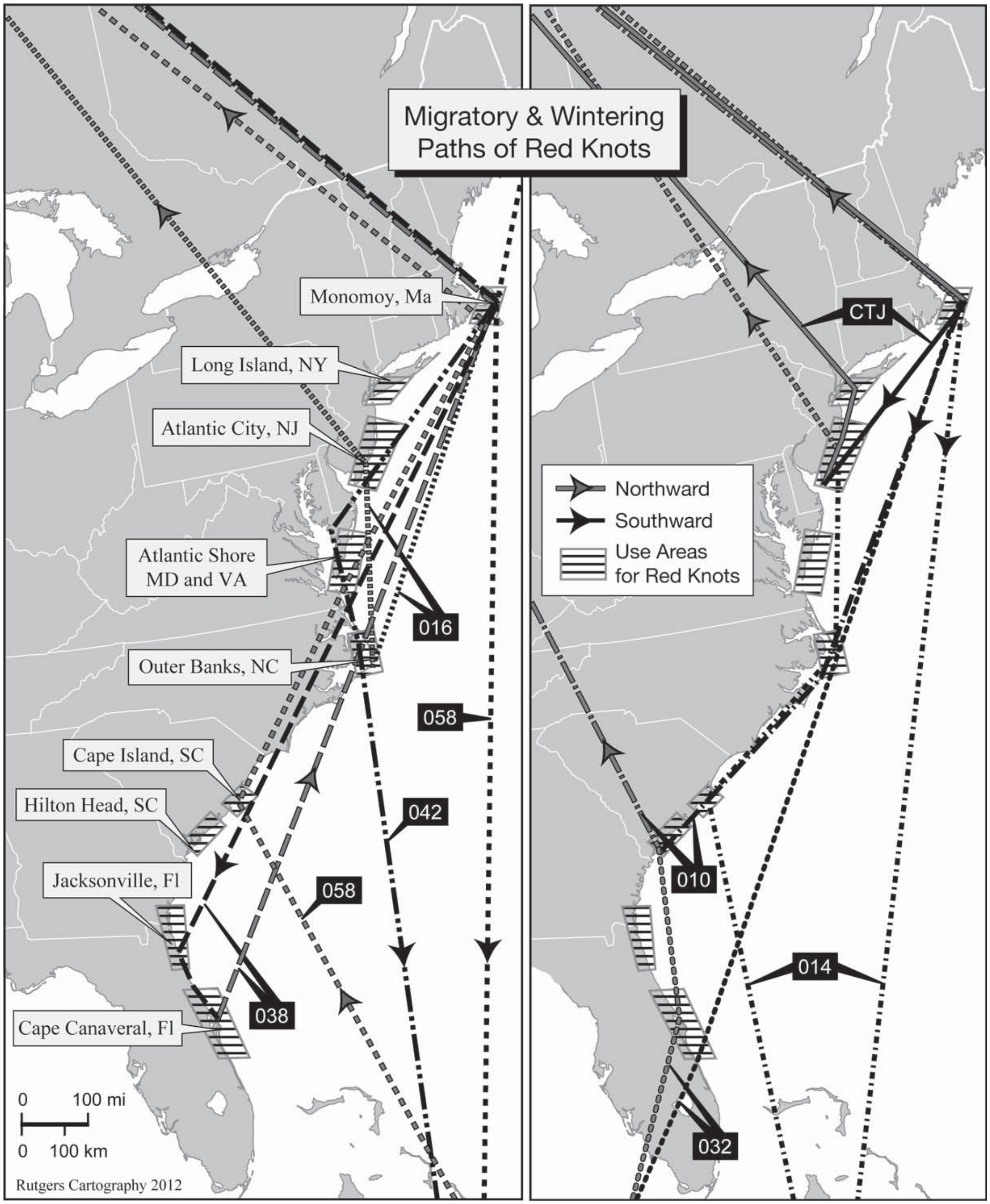

FIGURE 2. Map of the Atlantic coast of North America indicating the northbound and southbound flights (arrows), and high-use areas (checked) of eight adult Red Knots fitted with geolocators at Monomoy National Wildlife Refuge in 2009. The data reflect complete yearly cycles for six knots and partial cycles for two knots. Results are divided between the two panels for clarity; knots 014, 032, 042, and 058 wintered south of the U.S., while the others remained in the U.S. Different symbols represent each of the eight individuals.

the only bird from which we recorded a complete cycle that did not do so was 010, which flew directly from Monomoy to North Carolina, where it spent 92 days, before moving on to South Carolina. In most cases, there were several wet signals every day, except during the long periods of flight (up to 2 days along the Atlantic coast).

One relevant measure of potential exposure and risk is the total time spent along the Atlantic coast (Table 3). The six birds with complete cycles (032 and 042 excluded) spent from 57 to 205 days along the Atlantic coast after leaving Monomoy Refuge. When Monomoy is added, the six knots spent an average of 233 (range 136–269) days along the Atlantic coast, which is 64% of their yearly cycle. During migration, only one knot stopped on Long Island, three stopped in New Jersey, two stopped in Maryland, three stopped on the Outer Banks of North Carolina, two stopped on Cape Island in South Carolina, two stopped on Hilton Head in South Carolina, on stopped in Jacksonville, Florida, and two stopped at Cape Canaveral (Table 4). This indicates that some Red Knots wintered from Maryland south to Florida (Table 4).

The spots of high activity along the Atlantic coast of North America are shown in Fig. 2. Birds moved several kilometers within these sites, actually forming a matrix or cluster of points (shown as checked areas on Fig. 2). For example, knot 016's geolocator position was centered on the Atlantic coast of New Jersey, but it was reported by reliable observers on Reeds Beach and adjacent beaches between 15 and 29 May, suggesting that it was moving back and forth between the Atlantic coast and Delaware Bay shore.

Field observers reported Red Knots fitted only with leg flags at Monomoy Refuge (fall 2009) in Delaware (Delaware Bay shore), New Jersey (mainly Delaware Bay, but also Atlantic coast), Virginia, North Carolina, South Carolina, Georgia, and Florida (both Atlantic and Gulf coasts; www.bandedbirds.org). However, the majority of reports were from Delaware Bay in the spring of 2010 (82%).

DISCUSSION

MIGRATION ROUTES

The outstanding feature of these results is the unexpected finding that the southbound short-distance knots (subspecies *rufa*) captured at Monomoy did not migrate to the west coast of Florida but showed highly variable migratory pathways and use of the U.S. Atlantic coast. They exhibited several patterns: (1) some flew directly to wintering areas in the Caribbean (L. Niles, unpubl. data) but stopped along the Atlantic coast on their way north, (2) some flew to stopover places along the Atlantic coast before reaching wintering grounds also along the Atlantic coast, and then flew north, stopping along the Atlantic coast, and (3) some flew directly to wintering areas along the Atlantic coast, then stopped at other places along the coast on their way north. Evidently, there are many places along the Atlantic coast where some Red Knots stop to forage and later to overwinter.

The variability in migration routes, stopover locations, and wintering areas along the Atlantic coast and the Caribbean was unexpected. While we have assumed that these birds are *Calidris canutus rufa*, the possibility exists that information from more knots fitted with geolocators in Delaware Bay, Texas, Florida, and elsewhere will reveal additional subspecies. Geolocators are revolutionizing our understanding of shorebird migration, providing more concrete information on all the birds' locations, and could lead to firmer discrimination of the winter ranges and places of overlap of the various subspecies.

HIGH-USE AREAS ALONG THE ATLANTIC COAST

Plotting the areas of high use, and of migration routes along the Atlantic coast, was relatively easy for Red Knots because they remained along the coast, as indicated not only by their position but by the signals indicating contact with salt water. Furthermore, the longitudinal information was critical given the coastline. Pinpointing the location might be difficult for species not limited to coasts (at least along the Atlantic). The knot's exclusive use of the coast, along with longitude and latitude data, made possible only a small error in these estimations. Such small error would be more difficult in an examination of the knot's high-use areas and migration routes in South America and in interior North America where longitudinal information is not as useful.

Protection of habitats of the Red Knot and other species using coastal habitats depends upon identification of areas of high use where the birds are at risk from habitat loss due to natural (erosion of beaches, sea-level rise) and anthropogenic (development on and off shore, high recreational use, human disturbance) factors (Burger et al. 2004, 2007, 2011). Since habitat loss and degradation are the most direct threats to migrating shorebirds (Burger et al. 1997, 2012, Piersma and Baker 2000, Galbraith et al. 2002, Warnock et al. 2002), it is critical to identify the places where knots concentrate. In combination with survey data, the information from the GL knots focuses our attention on conservation, protection of habitat, high-density areas, human disturbance, and avoidance of offshore development that might provide a risk.

Although our sample is small, the data indicate a pattern of places along the Atlantic coast that the birds were clearly using during migration and winter. Furthermore, the knots were not simply stopping over for a few days but remained for several months. All eight spent considerable time (around 2 months) at Monomoy and surrounding suitable habitat before migrating farther south, indicating the clear importance of this site to the Red Knot. Once they left Monomoy Refuge, all eight stopped along the U.S. Atlantic

TABLE 4. Overlap in use of specific stopover and wintering areas by Red Knots along the Atlantic coast. All birds spent about 2 months at Monomoy before migrating south (September–early November). Symbols: AC = Atlantic Coast, S = southward migration, W = wintering, N = northward migration.

Bird	NY: Long Island	NJ: Atlantic-coast	MD: eastern shore	NC: Outer Banks	SC: Cape Island	SC: Hilton Head	FL: Jacksonville	FL: Cape Canaveral
7CJ	N: 28–30 May	S: 14–17 Nov N: 28 Apr–27 May	W:17 Nov–27 Apr					
010				W: 6 Nov–7 Feb		W: 7 Feb–24 May		
014		N:6–26 May		N: 30 Apr–5 May	N: 9–29 Mar			
016		N:15–31 May		W: 7 Nov–15 May				
032						N: 1–12 Apr[a]		N: 15 Feb–1 Apr
038							W:8 Nov–29 Dec.	W: 29 Dec–12 May[b]
042			S:13–21 Nov[c]					
058					N: 21 Mar–10 May[d]			
Total in days[e]	3	67	161+[e]	287	72+[e]	121+[e]	52	149

[a]Battery died shortly thereafter.
[b]Stopped on northbound flight at Monomoy from 15 to 22 May
[c]Battery died in December.
[d]Stopped on northbound flight at Monomoy 12–29 May.
[e]Incomplete because of battery failures.

coast on their northward or southbound migration, and four wintered there. The variability among the eight in timing, residency in different locations, and wintering areas along the Atlantic coast suggests a much more flexible strategy for migration and wintering than previously believed (Niles et al. 2008, 2010).

Additionally, the majority of observer reports came from Delaware Bay, and not from along the Atlantic coast, even though knots spent much more time there than in Delaware Bay. This indicates the limitation of relying on observer reports to determine distribution patterns, especially with uneven distribution of observer effort. Thus a combination of observations and data from geolocators provides the best information on use of space.

Finally, it should be mentioned that there are some assumptions in the interpretation of data from the geolocators (see Methods). While these do not affect the location of routes of migration or sites of wintering, they may affect the size of the high-use areas we indicate.

RISK AND MANAGEMENT TO PROTECT RED KNOTS IN THE U.S.

The data from the eight short-distance migrants fitted with geolocators in Massachusetts suggest that some knots (subspecies *rufa*) spend considerable time along the Atlantic coast of the U.S. during both migration and winter. The six birds with complete cycles (a full year) spent an average of 64% of their yearly cycle in places along the U.S. Atlantic coast. This new information broadens our understanding of the temporal and spatial use of the Atlantic coast, and supports the conclusion that the Atlantic coast is important to wintering Red Knots, since half of the GL birds remained along this coast throughout the winter. Furthermore, it provides evidence that managers and conservationists in the United States can have a direct and positive effect on Red Knot populations by protecting and managing areas where knots stop and overwinter.

The high dependence of these birds on the Atlantic coast suggests a need for (1) more information about the use of this coast by knots captured elsewhere, (2) an understanding of the level of protection of these high-use areas, (3) an understanding of human disturbance in high-use areas (regardless of protection status), and (4) data on the use by long-distance migrants along the Atlantic coast. To form a complete picture of knot use of the Atlantic coast, data are also needed on short-distance migrants captured elsewhere (e.g., Delaware Bay, Virginia, Florida) and on long-distance migrants from any locations. Long-distance migrants depart earlier from Monomoy in the fall (Harrington et al. 2010), may stop at few or no places along the Atlantic coast in fall migration (Niles et al. 2010), or may stop at a few places along the Atlantic coast in both fall and spring migration (Cohen et al. 2009). We suggest that the locations where knots stop over or winter along the U.S. Atlantic coast also need to be examined with respect to relative population size, population trends, and use in spring and fall migration.

It is encouraging that some areas that the knots used for stopover or wintering are refuges (e.g., Monomoy) protected by regulations and conservation efforts (e.g., Delaware Bay), or are of low human use (e.g., Outer Banks of North Carolina). However, knot use of other places suggests the importance of obtaining more information on the areas used by knots, the level of habitat preservation, and the degree of protection from human disturbance. Furthermore, knots may stop at the protected areas because they have little human disturbance, not because of a preference.

While shorebird biologists often focus conservation efforts on coastal habitats, we suggest that some attention should be focused on knot presence and behavior off shore, particularly in regions that may be developed for wind power (Burger et al. 2011, 2012) or oil drilling. The GL knots crossed the outer continental shelf from at least 2 to 6 times, and short-distance flights from one place to another may also occur in these regions.

EFFECT OF GEOLOCATORS ON RED KNOTS AND SCIENCE

Geolocators were initially used on relatively large and heavy birds that could carry the weight, and they have since been used on medium to large seabirds, providing invaluable information (González-Solís et al., 2007, Bost et al., 2009, Barron et al. 2010, Ismar et al. 2011). Geolocators are now sufficiently light to be placed on small songbirds (Stutchbury et al. 2009) and shorebirds (Minton et al. 2010, Nisbet et al. 2011, Egevang et al. 2010), although possible effects are often not reported. In a study of Common Terns (*Sterna hirundo*) breeding at a colony in Massachusetts, Nisbet et al. (2011) reported no effect of geolocators on survival but did find several adverse effects, such as injury or body-mass loss. They concluded that the unique value of the data justified the geolocators' use, even if it entailed some risks of injury or even death.

Until our study, the information available on the behavior of Red Knots migrating and wintering along the Atlantic coast was based on site-based observations of the presence and absence of birds, yielding data dependent on the methods, timing, and spatial extent of surveys. Even though there are annual aerial surveys and sporadic ground surveys of the Red Knot along the Atlantic coast,, the full extent of stopovers and wintering are inadequately understood. Observational data led us to believe that Red Knots moving through Monomoy migrated primarily either to the west coast of Florida, or to the Caribbean or South America, with few wintering along the Atlantic coast of the southern U.S. (Niles et al. 2008, 2010). Existing sight records did not reveal the degree to which knots used the Atlantic coast, other than Delaware Bay and Monomoy. Thus geolocators are a time and cost-effective method of providing data on movements and patterns of use of space.

The results from this study of eight GL Red Knots have provided us with a different picture of the species' migration and overwintering, especially along the U.S. Atlantic coast. The knots spent considerable time in Monomoy Refuge, and were not merely migrating straight to Florida or farther south to overwinter, but stopped along the way. Half of the birds wintered entirely along the U.S. Atlantic coast. While these data represent only eight individuals, and we selected adults of sufficient weight that were molting (indicating short-distance migrants), the biases introduced do not negate the conclusion that they used the Atlantic coast extensively. Although the geolocator batteries last only about a year, the data encoded are retrievable for at least up to 5 years. Thus, over the next several years, additional knots can be caught, adding to our knowledge of movements along the Atlantic coast.

Possible adverse effects on Red Knots fitted with geolocators include leg injury, difficulty in walking or flying, weight loss, or egg breakage during incubation (noted for some species of terns that burst from the nest when disturbed). We can not evaluate the latter problem because we did not observe the knots on the breeding grounds. Knots usually get up quietly from the nest and skulk away furtively, making egg breakage unlikely. Preliminary analysis of the light signals (as well as wet/dry) indicated that three of the six birds whose batteries lasted for a full year incubated for over 19 days, another incubated for 13 days (which may indicate failed breeding), and that two did not incubate. Although we cannot assume that these GL knots did not damage their eggs, at least 11 of 19 knots examined (Burger et al., unpubl. data) incubating to full term (18–24 days) suggests successful hatching of some eggs.

Immediately after deployment of geolocators on Red Knots in Delaware Bay, Niles et al. (2010) found no significant differences in locomotion or foraging, and birds with geolocators were as likely to be reported on Delaware Bay and elsewhere as birds fitted in the same year with leg flags only. Knots captured the following year at both Delaware Bay and Monomoy Refuge (this study) showed no leg injuries, and their mean weights did not differ from their weight in the previous year (2009) or from that of other knots captured in 2010. Thus we detected no effects of the geolocators while the birds were foraging, migrating, or at stopover locations.

Our observations, and the return of Red Knots fitted with geolocators in good condition, suggest there are no ill effects, although the breeding season has not been investigated. On balance, the increase in our knowledge of the Red Knot's stopover and wintering areas, which may allow for their increased protection, seems to greatly outweigh any as yet unidentified disadvantages of geolocators.

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