

Rufa Red Knot Ecology and Abundance

SUPPLEMENT TO

Endangered and Threatened Wildlife and Plants; Proposed Threatened Status for the

Rufa Red Knot (*Calidris canutus rufa*)

[Docket No. FWS–R5–ES–2013–0097; RIN 1018–AY17]

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BACKGROUND

SPECIES INFORMATION

Species Description

The rufa red knot (*Calidris canutus rufa*) is a medium-sized shorebird about 9 to 11 inches (in) (23 to 28 centimeters (cm)) in length. (Throughout this document, “rufa red knot,” “red knot,” and “knot” are used interchangeably to refer to the *rufa* subspecies. “*Calidris canutus*” and “*C. canutus*” are used to refer to the species as a whole or to birds of unknown subspecies. References to other particular subspecies are so indicated.) The red knot migrates annually between its breeding grounds in the Canadian Arctic and several wintering regions, including the Southeast United States (Southeast), the Northeast Gulf of Mexico, northern Brazil, and Tierra del Fuego at the southern tip of South America (figures 1 and 2). During both the northbound (spring) and southbound (fall) migrations, red knots use key staging and stopover areas to rest and feed (figure 3). This annual cycle is described in more detail below.

The red knot is easily recognized during the breeding season by its distinctive rufous (red) plumage (feathers). The face, prominent stripe above the eye, breast, and upper belly are a rich rufous-red to a brick or salmon red, sometimes with a few scattered light feathers mixed in. The feathers of the lower belly and under the tail are whitish with dark flecks. Upperparts are dark brown with white and rufous feather edges; outer primary feathers are dark brown to black (Harrington 2001, p. 2; Davis 1983, p. 372). Females are similar in color to males, though the rufous colors are typically less intense, with more buff or light gray on the dorsal (back) parts (Niles *et al.* 2008, p. 13). Subtle subspecies differences (see Taxonomy, below) in breeding plumage have been described. The intensity of rufous coloration is paler in *Calidris canutus rufa* than in other subspecies (Tomkovich 1992, p. 20). Red knots have a proportionately small head, small eyes, and short neck, and a black bill that tapers from a stout base to a relatively fine tip. The bill length is not much longer than head length. Legs are short and typically dark gray to black, but sometimes greenish in juveniles or older birds in nonbreeding plumage (Harrington 2001, p. 2). Nonbreeding plumage is dusky gray above and whitish below. Juveniles resemble nonbreeding adults, but the feathers of the scapulars (shoulders) and wing coverts (small feathers covering base of larger feathers) are edged with white and have narrow, dark bands, giving the upperparts a scalloped appearance (Davis 1983, p. 372). Body mass varies seasonally, with lowest average mass during early winter (4.4 ounces (oz); 125 grams (g)) and highest mean values during spring (7.2 oz; 205 g) and fall (6.1 oz; 172 g) migration (Harrington 2001, p. 12).

Research Methods

Best available data regarding the red knot are generated by several different research methods summarized here and referenced throughout this document and the proposed rule. For example, in many wintering and stopover areas, red knots are routinely counted by surveyors in aircraft or on the ground. In some areas, data from both ground and aerial counts are available. Although the results can be similar, data from these different methods should be compared with caution. Laursen *et al.* (2008) compared aerial and ground survey methods and found that, across all waterbird species evaluated, significantly greater numbers were identified from the ground than from aircraft. For shorebirds that were numerous and widespread and occurred in

flocks (and therefore similar to red knots), there was a moderate correspondence between the two methods—aerial surveys detected greater than 55 percent of the ground counts, and the mean bird densities derived from ground counts differed from aerial counts by less than 30 percent (Laursen *et al.* 2008, p. 165). Within the same survey type (ground or aerial), we attach greater confidence to apparent population trends when the survey team and methods have been consistent over time.

In addition, an international team of scientists have marked tens of thousands of shorebirds since the mid-1990s, including red knots (BandedBirds.org 2012). About 1,000 red knots per year are trapped for scientific study in Delaware Bay, and about 300 in South America (Niles *et al.* 2008, p. 100). Additional birds are trapped in some years in other parts of the range. The legs of the trapped birds are marked with bands and with individually numbered, color-coded flags (one color per country). By tracking where the marked birds are observed in future seasons and years, researchers can draw inferences about wintering and migration areas, migration routes and timing, life history, regional population sizes, and survival rates.

Through 2008, about 50 of the birds caught in Delaware Bay each year were the subject of radio-telemetry studies in which a radio transmitter was glued to the back of each bird (Niles *et al.* 2008, p. 100). Relative to resighting of marked birds, radio tracking allows for more direct observations of bird movements within the area. However, because the radio tags drop off after 1 to 2 months (Niles *et al.* 2008, p. 100), birds can be observed only during the same season that the transmitter was attached. Satellite transmitters that can remotely send locational data over long distances and time frames are too heavy for use on red knots (J. Cohen and B. Watts pers. comm. October 4, 2012). Information on where migrant red knots spent the previous winter can also be discerned from chemical analysis that produces a stable isotope “signature” from the feathers, which reflects the geographic region in which the birds were feeding when those feathers were grown.

Since 2009, researchers have gained many new insights into red knot migration and life history using light-sensitive geolocators, a small device attached to the bird’s leg. These instruments record periodic, time-stamped, ambient light levels that can be used to determine geographic location. Geolocators are small enough to be used on the legs of medium-sized shorebirds such as red knots. However, the birds must be recaptured to access the data, so return rates are low. Although geolocators record data for only about a year, the data are still retrievable for up to 20 years if birds are recaptured (Niles *et al.* 2010a, pp. 123–124). Based on light-dark periods indicating day length, the latitude, longitude, and duration of stopovers can be estimated. Flight segments connecting the stopovers can be inferred based on the time between stops and general knowledge of shorebird migration (e.g., Alerstam *et al.* 2001, entire). The precision of the flight segments is limited, as they must be inferred based on points where birds remained in one place for at least an entire day (Normandeau Associates, Inc. 2011, p. 77). Even at such stopping points, the amount of geospatial imprecision ranges from 31 to 186 miles (mi) (50 to 300 kilometers (km)) depending on the latitude (higher latitudes render more precise readings, except at very high latitudes where there are not 24-hour light-dark cycles) and other conditions (e.g., shading of the geocator) (Normandeau Associates, Inc. 2011, p. 77).

Taxonomy

Calidris canutus is classified in the Class Aves, Order Charadriiformes, Family Scolopacidae, Subfamily Scolopacinae (American Ornithologists Union (AOU) 2012a). Six subspecies are recognized, each with distinctive morphological traits (i.e., body size and plumage characteristics), migration routes, and annual cycles. Each subspecies is believed to occupy a distinct breeding area in various parts of the Arctic (Buehler and Baker 2005, pp. 498–499; Tomkovich 2001, pp. 259–262; Piersma and Baker 2000, p. 109; Piersma and Davidson 1992, p. 191; Tomkovich 1992, pp. 20–22), but some subspecies overlap in certain wintering and migration areas (Conservation of Arctic Flora and Fauna (CAFF) 2010, p. 33).

Birds in the Order Charadriiformes are commonly called shorebirds, and include the plovers (Family Charadriidae). Birds in the Family Scolopacidae are commonly known as sandpipers or snipes. Roosevelt (1866, pp. 91–93) reported considerable confusion around the names of commonly hunted shorebirds, which he referred to generally as bay-snipe. Many different scientific and common names have been used for the rufa red knot since the early 1800s. Scientific names for the rufa red knot appearing in the historic literature include *Tringa canutus*, *T. islandica*, *T. cinerea*, *Canutus canutus*, and *C. canutus rufus*. The following common names for the rufa red knot have been used by scientists, naturalists, and hunters, although many of these names have also been used to refer to a variety of other shorebird species: red-breasted sandpiper, ash-colored sandpiper, robin snipe, robin-breasted snipe, red-breasted snipe, beach robin, gray snipe, white robin snipe, red-breasted plover, blue plover, silver plover, red-breast, buff-breast, gray-back, silverback, knot, red knot, American knot, and Western Atlantic knot (AOU 2012b; Harrington *et al.* 2010a, p. 191; Urner and Storer 1949, p. 185; Hellmayr and Conover 1948, p. 166; Stone 1937, p. 456; Bent 1927, pp. 131–132; Ridgway 1919, p. 231; Forbush 1912, p. 262; Eaton 1910, p. 307; Shriner 1897, p. 94; Dixon 1895 in Barnes and Truitt 1997, pp. 113–114; Mackay 1893, p. 25; Stearns and Coues 1883, p. 229; Hallock 1877, p. 168; Coues 1868, p. 293; Roosevelt 1866, p. 151; Herbert 1853, p. 160; Audubon 1844, plate 328; Giraud 1844, p. 224; Wilson 1829, p. 140).

Four genetically distinct groups of *Calidris canutus* have been identified. Three of the groups correspond to recognized subspecies: *C. canutus canutus*, *C.c. piersma*, *C.c. rogersi*. The fourth is a North American group containing the other three recognized subspecies (*C.c. rufa*, *C.c. roselaari* and *C.c. islandica*), which are not fully distinct at the genetic level based on analyses conducted to date (discussed further below) (Buehler and Baker 2005, p. 502). Based on low overall genetic variability, *C. canutus* is thought to have recently survived a genetic bottleneck. On the scale of evolutionary time, the subspecies groups are estimated to have diverged very recently, within the past 20,000 years. The North American group is estimated to have diverged from a Siberian ancestor about 12,000 years ago, then split into the three recognized North American subspecies within the past 5,500 years (Buehler and Baker 2005, p. 505). Buehler *et al.* (2006, p. 485) estimated that populations of the three North American breeding subspecies may have diverged even more recently, within about the last 1,000 years.

Because of the recent divergence times and low overall genetic variability, genetic distances among subspecies are small and not fully distinct. However, it is important to consider morphological and ecological differences along with the genetic evidence, particularly when taxa have only recently diverged (Committee on the Status of Endangered Wildlife in Canada

(COSEWIC) 2007, p. 9; Buehler and Baker 2005, pp. 507–508). In addition, the results of the genetic analysis conducted by Buehler and Baker (2005) may have been affected by these authors' attribution of birds in the Southeast United States to *Calidris canutus roselaari* (Buehler and Baker 2005, p. 498), as was widely believed at the time. In that study, all the birds sampled as the *roselaari* subspecies were from the Southeast (Buehler and Baker 2005, p. 511). As discussed further below, newer evidence now suggests that birds in the Southeast are *C.c. rufa* (U.S. Fish and Wildlife Service (USFWS) 2011a, p. 305; Niles *et al.* 2008, p. 132). The Service and our partners are investigating *C. canutus* genetics to better assess the relationship between the *rufa* and *roselaari* subspecies and population structure within *rufa*; results are expected within the next few years.

Calidris canutus canutus, *C.c. piersma*, and *C.c. rogersi* do not occur in North America. The subspecies *C.c. islandica* breeds in the northeastern Canadian High Arctic and Greenland, migrates through Iceland and Norway, and winters in western Europe (COSEWIC 2007, p. 4). *Calidris c. rufa* breeds in the central Canadian Arctic (just south of the *C.c. islandica* breeding grounds) and winters along the Atlantic coast and the Gulf of Mexico coast (Gulf coast) of North America, in the Caribbean, and along the north and southeast coasts of South America including the island of Tierra del Fuego at the southern tip of Argentina and Chile (figures 1 and 2); detailed information on the distribution of *rufa* red knots is provided in the sections that follow. *Calidris c. islandica* breeds just north of *C.c. rufa*; the southern limit of the *C.c. islandica* breeding range and the northern limit of the *C.c. rufa* breeding range (and thus the potential for any overlap) are poorly known (CAFF 2010, p. 33; COSEWIC 2007, p. 12; Morrison and Harrington 1992, p. 73) (see Breeding Distribution, below). Resightings of three marked birds have documented infrequent movements between the *C.c. islandica* and *C.c. rufa* migratory flyways. It is unknown if any of the three birds permanently changed flyway or breeding area. However, these were clearly atypical movements, probably of vagrant individuals (Wilson *et al.* 2010, entire).

Subspecies *Calidris canutus roselaari* breeds in western Alaska and on Wrangel Island, Russia (Carmona *et al.* in press; Buehler and Baker 2005, p. 498). Wintering areas for *C.c. roselaari* are poorly known (Harrington 2001, p. 5). In the past, *C. canutus* wintering along the northern coast of Brazil, the Gulf coasts of Texas and Florida, and the southeast Atlantic coast of the United States have sometimes been attributed to the *roselaari* subspecies. However, based on new morphological evidence, resightings of marked birds, and results from geolocators, *C.c. roselaari* is now thought to be largely or wholly confined to the Pacific coast of the Americas during migration and in winter (Carmona *et al.* in press; Buchanan *et al.* 2011, p. 97; USFWS 2011a, pp. 305–306; Buchanan *et al.* 2010, p. 41; Soto-Montoya *et al.* 2009, p. 1; Niles *et al.* 2008, pp. 131–133; Tomkovich and Dondua 2008, p. 1). Although *C.c. roselaari* is generally considered to occur on the Pacific coast, a few *C. canutus* movements have recently been documented between Texas and the Pacific coast during spring migration (Carmona *et al.* in press). Despite a number of population-wide morphological differences (USFWS 2011a, p. 305), the *rufa* and *roselaari* subspecies cannot be distinguished in the field due to physical variability among individuals, necessitating the use of other methods (e.g., mark-resighting efforts, stable isotope analysis, genetics) to delineate the distributions of these two subspecies (D. Newstead pers. comm. September 14, 2012).

In some years, small numbers of *Calidris canutus roselaari* winter at Golfo de Santa Clara (State of Sonora) in the northern Gulf of California (Soto-Montoya *et al.* 2009, p. 192), and an important wintering aggregation of *C.c. roselaari* has been documented in western Mexico at Guerrero Negro (State of Baja California Sur) (Carmona *et al.* in press). North of Guerrero Negro, *C. canutus* (presumed but not confirmed *roselaari*) have been reported between December and February in the Mexican State of Baja California and along the coast of California (especially around San Francisco Bay), with small numbers as far north as northern Washington State and southern British Columbia, Canada (eBird.org 2012). *Calidris c. roselaari* probably also winters south of Guerrero Negro, but no other sites have been confirmed for this subspecies (Carmona *et al.* in press; USFWS 2011a, p. 306; Soto-Montoya *et al.* 2009, p. 1; Carmona *et al.* 2008, p. 10).

Further south on Mexico's Pacific coast, *Calidris canutus* has been documented wintering in considerable numbers at two sites in the Gulf of California, Ensenada Pabellones and Bahía Santa Maria (State of Sinaloa); at Las Garzas (State of Nayarit); and at Laguna Superior (State of Oaxaca) (Carmona *et al.* in press). Small numbers of *C. canutus* have been reported along the Pacific coasts of Central and South America from Guatemala south to the Los Lagos Region of Chile (Carmona *et al.* in press; eBird.org 2012; Ruiz-Guerra 2011, entire; Hughes 1979, p. 52). The subspecies composition of Pacific-wintering *C. canutus* from central Mexico to Chile is unknown. We have no evidence to suggest that *C. canutus* in the Mexican States of Sinaloa or Nayarit are the *rufa* subspecies, and Carmona *et al.* (in press) suspect that further mark-resighting efforts will likely link these areas to *C. canutus roselaari*; thus, these birds are not addressed in the proposed rule. Because a few birds have been documented moving from *C.c. rufa* areas to parts of Central America (State of Oaxaca, Mexico, and Panama), this region is addressed in the proposed rule, and these movements are detailed in subsequent sections of this document. We recently learned that a few birds have been documented moving between *C.c. rufa* areas and the Pacific coast of Chile (Chiloé Island in the Los Lagos Region) (Niles pers. comm. March 15, 2013; Newstead and Parvin pers. comm. March 12, 2013), suggesting that at least some of the Pacific-wintering *C. canutus* from Colombia to Chile may be *rufa* red knots. However, these movements and this region are not addressed in the proposed rule because we have only preliminary information regarding the marking and resighting of these birds.

In 6 to 7 years of banding and resighting efforts on the west coast of North America involving over 1,000 birds, there had been only 5 documented movements of *Calidris canutus* between the Gulf and Pacific coasts as of January 2013: (1) one bird banded in Mexico and one in Washington were later sighted in Texas in April 2012, and (2) three birds banded in Texas in April 2010 were sighted at the Laguna Superior (State of Oaxaca) in February 2012 (Carmona *et al.* in press; J. Buchanan pers. comm. January 9, 2013; D. Newstead pers. comm. September 14, 2012). Other than these three Texas-banded birds at Laguna Superior, no *C. canutus* banded on the Atlantic or Gulf coasts have been observed on the Pacific coast of North America. In Washington and northwestern Mexico, researchers have regularly seen *C. canutus roselaari* marked as part of small-scale banding operations in Russia, on the Alaskan breeding grounds near Nome, and at the Yukon River delta, but have not seen any birds that were banded on the Texas coast, despite there being more birds banded at North Padre Island, Texas than at these three northern (Alaska-Russia) *C.c. roselaari* areas combined (J. Buchanan pers. comm. January

9, 2013). Likewise, aside from the 2 birds seen in Texas in April 2012, none of the 1,088 birds banded on the Pacific coast (Carmona *et al.* in press) have been resighted on the Atlantic or Gulf coasts. These findings support the current understanding that *C.c. roselaari* is generally restricted to the Pacific coast.

Pursuant to the definitions in section 3 of the Act, “the term species includes any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature.” Based on the information described above, the Service accepts the characterization of *Calidris canutus rufa* as a subspecies because each recognized subspecies is believed to occupy separate breeding areas, in addition to having morphological and behavioral character differences. Therefore, we find that *C.c. rufa* is a valid taxon that qualifies as a listable entity under the Act.

Longevity and Survival

The oldest *Calidris canutus* of any subspecies recorded worldwide was estimated to be 25 years old when recaptured (Niles *et al.* 2008, p. 28). The oldest recorded *rufa* red knot was at least 20 years old when last resighted in spring 2013 (Bauers 2013a). Although these records indicate that the potential lifespan of a *C. canutus* is considerable, the average life span is thought to be much less. Based on estimated survival rates for a stable population, few red knots live for more than about 7 years (Niles *et al.* 2008, p. 28). Age of first breeding is uncertain but for most birds is probably at least 2 years (Harrington 2001, p. 21).

From resightings of marked birds, survival estimates have been calculated for several particular *Calidris canutus rufa* wintering and stopover areas. For birds stopping in Delaware Bay in spring, Atkinson *et al.* (2001, p. 4) estimated survival at 80.5 percent for the period 1997 to 2001, although the 95 percent confidence interval was large (44.4 to 95.5 percent). Baker *et al.* (2004, pp. 878–897) estimated adult survival rates for Delaware Bay at 84.6 percent from 1994 to 1998, but only 56.4 percent from 1998 to 2001. With a longer data set, 1997 to 2008, McGowan *et al.* (2011a, p. 13) calculated a survival rate of about 92 percent for Delaware Bay.

For birds wintering in Florida, Schwarzer *et al.* (2012, p. 729) found an average annual adult survival rate of 89 percent, with the 95 percent confidence interval overlapping the 92 percent survival estimate from McGowan *et al.* (2011a). Given that similar survival rates have been calculated for Delaware Bay migrants, most of which winter in South America (P. Atkinson pers. comm. November 8, 2012), as for Florida-wintering birds, Schwarzer *et al.* (2012, p. 729) concluded that factors influencing adult survival likely do so where populations of red knots from different wintering regions co-occur, such as along the Atlantic migratory flyway or on the breeding grounds (i.e., important survival factors operating in the wintering areas would be expected to produce differential survival rates among different wintering regions).

Breeding

Breeding Distribution

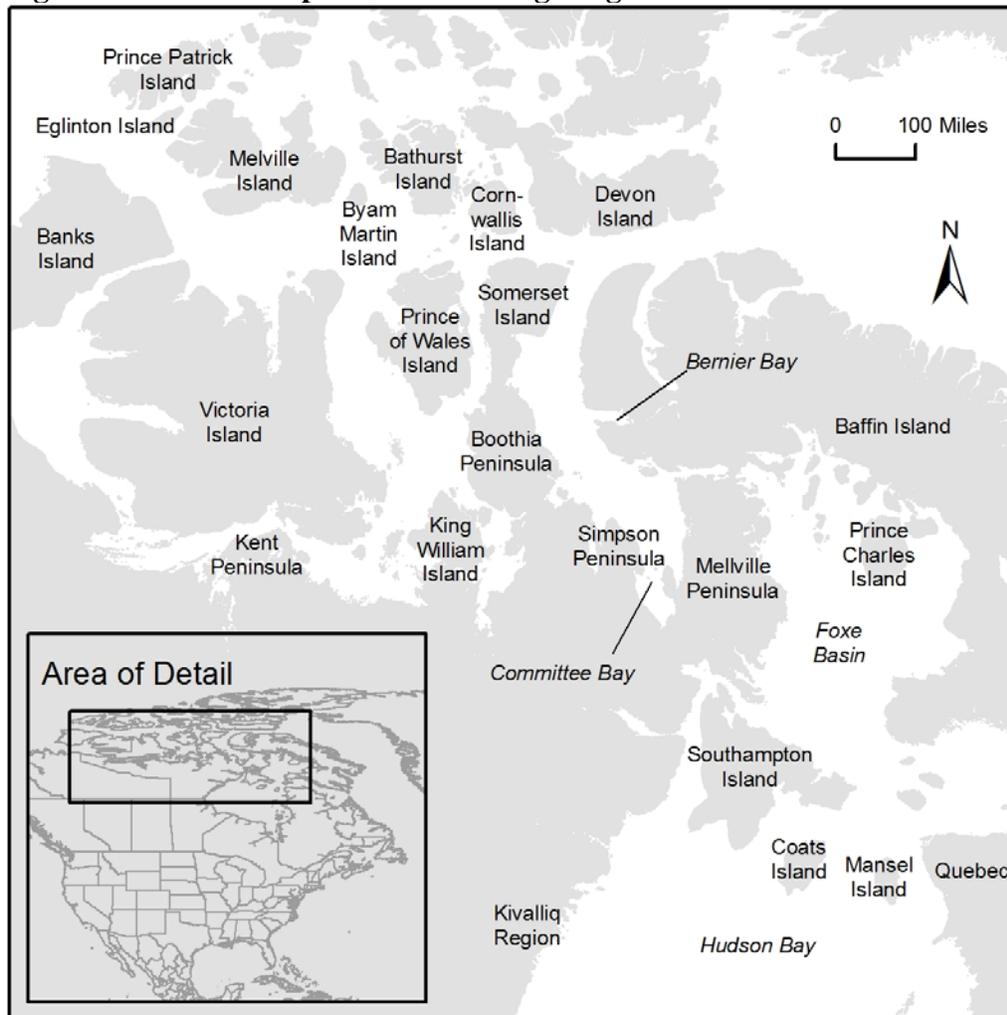
The red knot breeds in the central Canadian Arctic (figure 1), primarily in Nunavut Territory, but with some potential breeding habitat extending into the Northwest Territories.

Breeding red knots have been documented via telemetry on King William Island and Boothia Peninsula, and on the shorelines and islands of Committee Bay (Simpson Peninsula), Foxe Basin, and Hudson Bay, including Melville Peninsula and Baffin, Prince Charles, Southampton, Coats, and Mansel Islands (Niles *et al.* 2008, pp. 15–16). Niles *et al.* (2008, p. 16) and Morrison and Harrington (1992, p. 73) also include southern Victoria Island in the known breeding range. See proposed rule—Factor A—Breeding Habitat Loss for information on the eco-regional classification of the red knot’s breeding range.

Based on habitat modeling, the predicted breeding range of *Calidris canutus rufa* is larger than the documented range discussed above, extending farther east to southern Baffin Island, farther west to northern Victoria and Banks Islands, and farther north through Somerset, Prince of Wales, and western Baffin (around Bernier Bay) Islands up to the southern Queen Elizabeth Islands of Eglinton, Melville, Byam Martin, Bathurst, Cornwallis, and Devon (Niles *et al.* 2008, p. 16). Some of these potential *C.c. rufa* breeding areas are within the breeding range of *C.c. islandica*, as it was mapped by Morrison and Harrington (1992, p. 73). However, CAFF (2010, p. 33) presented a different range for *C.c. islandica* that shows only minimal overlap (e.g., on the northern tip of Melville Island) with the potential *C.c. rufa* breeding range predicted by Niles *et al.* (2008, p. 16). It is not known whether there is any overlap between the actual breeding ranges of these two subspecies (Morrison and Harrington 1992, p. 73), largely due to limitations on research methods (satellite transmitters are too heavy for red knots to carry; geolocators cannot be used to determine location at very high latitudes) and accessibility (field studies of breeding *C. canutus* in North America have been relatively few and localized because the birds are thinly distributed in remote areas across a huge region of the Arctic).

Some shorebird surveys have been conducted within and adjacent to the predicted breeding range of the rufa red knot (as mapped by Niles *et al.* 2008, p. 16), in areas where breeding *Calidris canutus rufa* have not been confirmed to date. One pair of *C. canutus* (subspecies unknown) was observed on Somerset Island in summer 2001 (Bart and Johnston 2012, p. 146). Nine *C. canutus* were observed June 10 to 28, 2008, in the Kivalliq region on the west coast of Hudson Bay (Bart and Johnston 2012, pp. 152, 154). The Kivalliq region is south of the known *C.c. rufa* breeding range and only a few hundred miles north of a known rufa red knot migration stopover at the Nelson River delta; it is unknown if the birds were migrating or breeding in this area. No *C. canutus* were observed during small-scale shorebird surveys of the Kent Peninsula, northwest Quebec, or the southwestern Queen Elizabeth Islands (Prince Patrick, Eglinton, and Melville) in the 2000s (Bart and Johnston 2012, pp. 141–155). No *C. canutus* were observed in northern Victoria Island or Banks Island during extensive surveys in the 1950s (Morrison and Harrington 1992, p. 73).

Figure 1. Known and potential breeding range of the red knot



New geolocator information suggests that red knots are indeed nesting within the known or predicted breeding range (Newstead *et al.* in press; Niles *et al.* in press; Niles 2012a; Niles *et al.* 2010a, pp. 125–126), although information about the breeding range that can be discerned from geolocators is very general in nature. Daylight is continuous during the middle of the arctic summer, so geolocation by monitoring light levels is not possible at very high latitudes (Burger *et al.* 2012a, p. 28). However, some breeding birds arrive or depart close enough to the Arctic Circle where there is a sufficient daily light variation to allow some estimation of breeding location (Burger *et al.* 2012a, p. 28). Despite these limitations, geolocator data are sufficient to suggest a general trajectory (i.e., to or from central Canada, as opposed to Alaska or Russia). Thus, geolocator results are a key piece of evidence indicating that the birds wintering along the north coast of Brazil, along the Gulf coasts of Texas and Florida, and in other parts of the Southeast are *Calidris canutus rufa*. For birds wintering in these areas, all geolocator results to date show migration flight trajectories to and from *C.c. rufa* breeding areas in central Canada, and none show trajectories to or from *C.c. roselaari* breeding areas in Alaska or Russia (Newstead *et al.* in press; Niles *et al.* in press; L. Niles pers. comm. January 4, 2013; Niles 2012a; Niles 2011a; Niles 2011b; Niles *et al.* 2010a, pp. 125–126).

The extent to which rufa red knots from different wintering areas mix on the breeding grounds, and therefore potentially interbreed, is poorly known. Limited evidence from one nesting area, Southampton Island, suggests that mixing does occur in this location. Stable isotope signatures indicate that some of the red knots nesting in this area winter in northern South America or the Southeast. Birds that had been marked in a different wintering region, southern Argentina, have also been seen on the same island (Niles *et al.* 2008, p. 54). Geolocator results also suggest that red knots from the Southeast and Argentina wintering regions both breed on Southampton Island (Niles 2011b) (an inference that may be possible because Southampton Island is just below the Arctic Circle). While limited stable isotope and geolocator data may point to potential interbreeding, further data suggest otherwise. Red knots from different wintering areas exhibit morphological, particularly size, differences; on average, birds from Tierra del Fuego are significantly smaller than those from Brazil or Florida (Niles *et al.* 2008, pp. 9–11). These size differences suggest that red knots from different wintering areas may have discrete breeding areas, but the available information is insufficient to draw any conclusions on this question.

Breeding Habitat and Food

Red knots generally nest in dry, slightly elevated tundra locations, often on windswept slopes with little vegetation. Breeding areas are located inland, but near arctic coasts. Nests may be scraped into patches of mountain avens (*Dryas octopetala*) plants, or in low spreading vegetation on hummocky (characterized by knolls or mounds) ground containing lichens, leaves, and moss. On Southampton Island, nests are located in exposed areas of glacial/shattered rocks and mudboils (bare patches that form on silt or clay soils), and most are located in proximity to suitable wetland foraging areas (Niles *et al.* 2008, p. 27; Harrington 2001, p. 8). After the eggs hatch, red knot chicks and adults quickly move away from high nesting terrain to lower, wetland habitats (Niles *et al.* 2008, p. 27).

In 1999, Niles *et al.* (in Baker 2001, p. 14) found eight previously radio-tagged red knots on Southampton Island. All tagged knots used patches of low-elevation barren tundra within 31 mi (50 km) of the ocean coast. In 2000, these authors found 11 nests. All nests were scraped within small patches of *Dryas* spp. (average patch size of 20 in (51 cm) across) in sparsely vegetated tundra (only 29 percent vegetated within 33 feet (ft) (10 meters (m)) of the nest). Nests were spaced approximately 0.6 mi (1 km) apart on sparsely vegetated, narrow ridges less than 33 ft (10 m) high. All nests occurred within 590 ft (180 m) of an isolated, freshwater wetland. All adults were followed via radio telemetry; birds stayed within 1.2 mi (2 km) of the nest area, appeared to defend an area 0.3-mi (0.5-km) around the nest, and shared wetlands outside that area (Niles *et al.* in Baker 2001, p. 14). Recent findings suggest that knots rarely enter salt water while in the Arctic (Burger *et al.* 2012a, p. 26; Niles *et al.* 2008, p. 61), although two of eight rufa red knots located via aerial radio tracking on Southampton Island in 1999 were found in coastal wetlands (Niles *et al.* 2008, p. 16).

On the breeding grounds, the red knot's diet consists mostly of terrestrial invertebrates, though early in the season, before insects and other macroinvertebrates are active and accessible, *Calidris canutus* will eat grass shoots, seeds, and other vegetable matter (Harrington 2001, p. 11). *Calidris canutus* is able to feed in shallow thawed sod in the Arctic at times when insects are rare and slow-moving due to low-temperature conditions (Gerasimov 2009, p. 227).

Breeding Chronology and Success

The breeding chronology of the rufa red knot is poorly known (Niles *et al.* 2008, p. 25). Other *Calidris canutus* subspecies may be paired or unpaired on arrival in breeding areas in late May or early June, and the start of breeding in *C. canutus* varies with snowmelt conditions. Although males tend to predominate among early arrivals, simultaneous arrival of male and female *C. canutus islandica* has been noted from May to early June, followed by movement into inland nesting habitats within a few days (Niles *et al.* 2008, pp. 25–26). Flocks of *C. canutus* sometimes arrive at breeding latitudes before snow-free habitat is available. Upon arrival, or as soon as favorable conditions exist, male and female *C. canutus* occupy breeding habitat, and territorial displays begin (Harrington 2001, p. 16). In rufa red knots, pair bonds form soon after arrival on breeding grounds and remain intact until shortly after the eggs hatch (Niles *et al.* 2008, p. 25). Female rufa red knots lay only one clutch (group of eggs) per season, and, as far as is known, do not lay a replacement clutch if the first is lost. The usual clutch size is four eggs, though three-egg clutches have been recorded. The incubation period lasts approximately 22 days from the last egg laid to the last egg hatched, and both sexes participate equally in egg incubation. Young are precocial, leaving the nest within 24 hours of hatching and foraging for themselves (Niles *et al.* 2008, p. 27). No information is available regarding chick survival rates (Niles *et al.* 2008, p. 28). Females are thought to leave the breeding grounds and start moving south soon after the chicks hatch in mid-July. Thereafter, parental care is provided solely by the males, but about 25 days later (around August 10) they also abandon the newly fledged juveniles and move south. Not long after, they are followed by the juveniles (Niles *et al.* 2008, p. 14). Niles *et al.* (2008, p. 26) reported that no published information was available for the rufa red knot on mate fidelity between years. In one study site on Southampton Island, Niles *et al.* (2008, p. 26) observed only limited evidence of site fidelity despite the fact that studies of other subspecies suggest breeding site fidelity is high, especially in males.

Data from 19 rufa red knots (adults of undetermined sex) fitted with geolocators from across the subspecies' range show that the median arrival date in the Arctic was June 10, the median departure date was July 22, and the mean time in the Arctic was 44 ± 2.3 days (range 28 to 65 days) (Burger *et al.* 2012a, p. 26). Geocator data have also been used to estimate incubation periods and infer hatching success. Because of 24-hour sunlight during the arctic summer, a prolonged duration of a mainly dark signal indicates that a geocator was not exposed to the ambient light, and a period of nest incubation can be inferred because the bird would be sitting on the leg-mounted device. Of 20 geocator records from the breeding grounds (2 from the same bird in successive years), 17 records (85 percent) indicated initiation of incubation. Of those 17 records, 11 birds (65 percent) incubated for 18 to 24 days, suggesting successful hatching of chicks. Three birds (18 percent) incubated for 9 or 10 days, suggesting nest failure due to abandonment or predators. One bird that incubated for 30 days probably laid infertile eggs, and the nesting success of the two remaining birds could not be inferred from the geocator data (Burger *et al.* 2012a, pp. 34–35). After incubation ended, red knots remained in the Arctic for 1 to 21 days. The sex of the birds was not determined, so it was not possible to verify the presumed gender differences in departure timing (Burger *et al.* 2012a, pp. 31, 33).

Breeding success of High Arctic shorebirds such as *Calidris canutus* varies dramatically among years in a somewhat cyclical manner (see proposed rule—Factor C—Predation). Two main factors seem to be responsible for this annual variation: abundance of arctic lemmings

(*Dicrostonyx torquatus* and *Lemmus sibericus*) and weather. First, lemming abundance is often cyclical, although less so in North America than in Eurasia. Arctic fox (*Alopex lagopus*) and snowy owl (*Nyctea scandiaca*) feed largely on lemmings, which are easily caught when their abundance is high. However, in years when lemming numbers are low, the predators turn to alternative prey, such as shorebird eggs, chicks, and adults. The variation in shorebird production closely follows variations in lemming abundance. Second, production of shorebird young is also very sensitive to adverse weather during the breeding season. Successful shorebird reproduction occurs almost exclusively during peak lemming years when snowmelt is early (see proposed rule—Factor E—Asynchronies) (Piersma and Lindström 2004, pp. 63–64; Blomqvist *et al.* 2002, p. 149; Summers and Underhill 1987, p. 169). Growth rate of *C. canutus* chicks is very high compared to similarly sized shorebirds nesting in more temperate climates and is strongly correlated with weather-induced and seasonal variation in availability of invertebrate prey (Schekkerman *et al.* 2003, p. 332). *Calidris canutus* chicks grow poorly during cold weather due to higher rates of energy expenditure, shorter foraging periods, and reduced prey availability (Piersma and Lindström 2004, p. 64; Schekkerman *et al.* 2003, p. 340).

Nonbreeding Birds

Unknown numbers of nonbreeding red knots remain south of breeding grounds during the breeding season, and many, but not all, of these knots are 1-year-old (i.e., immature) birds (Niles *et al.* 2008, p. 28). Nonbreeding knots, usually individuals or small groups, have been reported during June along the U.S. Atlantic and Gulf coasts, with smaller numbers around the Great Lakes and Northern Plains in both the United States and Canada (eBird.org 2012). All juveniles of the Tierra del Fuego wintering region are thought to remain in the Southern Hemisphere during their first year of life, possibly moving to northern South America, but their distribution is largely unknown (Niles *et al.* 2008, pp. 15, 26). Little information is available about these nonbreeding red knots.

Wintering

In the sections that follow, “winter” is used to refer to the nonbreeding period of the red knot life cycle when the birds are not undertaking migratory movements. Red knots occupy all known wintering areas from December to February, but may be present in some wintering areas as early as September or as late as May. In the Southern Hemisphere, these months correspond to the austral summer (i.e., summer in the Southern Hemisphere), but for consistency in this document the terms “winter” and “wintering area” are used throughout the subspecies’ range.

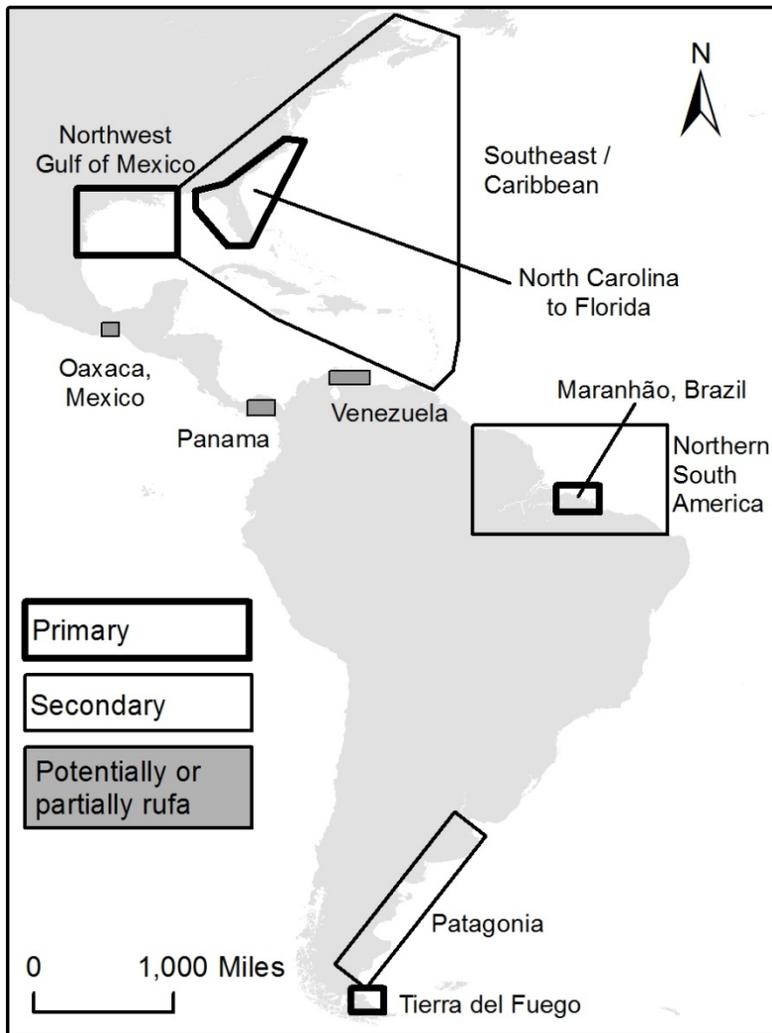
Wintering Distribution and Range

Wintering areas for the red knot (figure 2) include the Atlantic coasts of Argentina and Chile (particularly the island of Tierra del Fuego that spans both countries), the north coast of Brazil (particularly in the State of Maranhão), the Northwest Gulf of Mexico (discussed below) from the Mexican State of Tamaulipas through Texas (particularly at Laguna Madre) to Louisiana, and the Southeast United States (also discussed below) from Florida (particularly the central Gulf coast) to North Carolina (Newstead *et al.* in press; L. Patrick pers. comm. August 31, 2012; Niles *et al.* 2008, p 17). Smaller numbers of knots winter in the Caribbean, and along the central Gulf coast (Alabama, Mississippi), the mid-Atlantic, and the Northeast United States.

Calidris canutus is also known to winter in Central America and northwest South America, but it is not yet clear if all these birds are the *rufa* subspecies (known occurrences of wintering rufa red knots in Central America are discussed further below). The Argentina-Chile and Brazil wintering regions are not discussed below because there are no issues regarding the geographic limits of the areas used by red knots, or regarding the subspecies composition of the *C. canutus* found there.

In some years, more red knots have been counted during a coordinated spring migration survey than can be accounted for at known wintering sites (see Population Surveys and Estimates, below), suggesting there are unknown wintering areas. Indeed, geolocators have started revealing previously little-known wintering areas, particularly in the Caribbean (Niles *et al.* in press; L. Niles pers. comm. January 8, 2013).

Figure 2. Known red knot wintering areas



Southeast United States and the Caribbean

The core of the Southeast wintering area (i.e., that portion of this large region supporting the majority of birds) is thought to shift from year to year among Florida (particularly the central Gulf coast), Georgia, and South Carolina (Niles *et al.* 2008, p. 17). However, the geographic limits of this wintering region are poorly defined. Although only small numbers are known, wintering knots extend along the Atlantic coast as far north as Virginia (L. Patrick pers. comm. August 31, 2012; Niles *et al.* 2006 p. 89), Maryland (Burger *et al.* 2012b, p. 6), and New Jersey (BandedBirds.org 2012; H. Hanlon pers. comm. November 22, 2012; A. Dey pers. comm. November 19, 2012). Still smaller numbers of red knots have been reported between December and February from Long Island, New York, through Massachusetts and as far north as Nova Scotia, Canada (eBird.org 2012).

Further blurring the geographic limits of the Southeast wintering region are small numbers of red knots that winter along the central Gulf coast (Florida Panhandle, Alabama, Mississippi, and eastern Louisiana) (L. Patrick pers. comm. August 31, 2012; Morrison and Harrington 1992, p. 77). It is unclear if red knots that winter in the central Gulf should be considered part of the Southeast wintering group or the Northwest Gulf of Mexico group. Alternatively, the two areas may constitute a single, large wintering region. Further investigation of intra- and inter-annual red knot movements within and between these two wintering regions would be needed to clarify their geographic limits and degree of connectivity.

Although the numbers are poorly known, red knots also winter in the Caribbean islands (Morrison and Harrington 1992, p. 77), which are typically included in the Southeast wintering region. New geolocator results suggest the Caribbean may play a more important role in winter than previously known, with three of eight tracked “Southeast” birds wintering in Cuba or the Bahamas (Niles *et al.* in press). Other geolocator results have also documented red knots wintering in Haiti and Jamaica (L. Niles pers. comm. January 8, 2013; Burger *et al.* 2012c, p. 374). Previously, red knots had been known from the Caribbean islands from every month of the year, but were considered rare or vagrant (Raffaele *et al.* 1998, p. 277). This characterization of only incidental red knot occurrence in the Caribbean is being reconsidered in light of the geolocator results (Niles *et al.* in press). Stable isotope signatures from the Southeast overlap with those from Brazil, suggesting even northern South America may be affiliated with this large wintering region (Atkinson *et al.* 2006a, p. 536).

Northwest Gulf of Mexico

The best available information indicates that *Calidris canutus* in the Northwest Gulf of Mexico wintering area are predominantly the *rufa* subspecies. Resightings of marked birds show considerable movement between Texas and both the Southeast wintering area and the Delaware Bay stopover site (BandedBirds.org 2012; D. Newstead pers. comm. August 20, 2012; Niles *et al.* 2008, p. 74). Further, and significantly, all geolocator results to date (from seven adults) show Texas-wintering birds migrating to and from *C. canutus rufa* (central Canada) rather than *C.c. roselaari* (Alaska and eastern Russia) breeding grounds (Newstead *et al.* in press; Niles 2012a). However, it appears that some movement does occur of birds from the Pacific coast (presumed or possibly *C.c. roselaari*) to the Northwest Gulf of Mexico. As of January 2013, three such movements (involving five birds) had been documented, with birds moving between

Texas and Grays Harbor (Washington), Guerrero Negro (State of Baja California Sur, Mexico), and Laguna Superior (State of Oaxaca, Mexico) (Carmona *et al.* in press). All three of these documented movements involved birds observed in Texas during spring, and, to date, there are no documented instances of the *roselaari* subspecies wintering in the Northwest Gulf region. Nevertheless, because the *rufa* and *roselaari* subspecies cannot be distinguished in the field due to physical variability among individuals (D. Newstead pers. comm. September 14, 2012), it is possible that some of the birds wintering in the Northwest Gulf of Mexico are *C.c. roselaari* (D. Newstead pers. comm. September 14, 2012). However, based on geolocator and resighting data available to date, we consider all or nearly all of the *C. canutus* wintering the Northwest Gulf of Mexico to be *rufa* red knots.

Central America, Colombia, and Venezuela

Calidris canutus have been reported from Central America in winter (December to February), extending from southern Mexico through Panama (eBird.org 2012; Buehler 2002, p. 43; Morrison and Harrington 1992, p. 77) (see figure 2 from Oaxaca, Mexico to Panama). Wintering *Calidris canutus* have also been documented on the Caribbean coasts of Colombia and western Venezuela (Niles *et al.* in press; Ruiz-Guerra 2011, entire; Morrison and Ross 1989, Vol. 2, p. 149) (see figure 2), and small, isolated groups of wintering birds extend along most of the northern coast of South America (L. Niles pers. comm. January 8, 2013). To date, no known *C. canutus roselaari* have been confirmed wintering south of Guerrero Negro on Mexico's Baja Peninsula (Carmona *et al.* in press) (roughly 1,500 mi (2,600 km) northwest of Oaxaca, Mexico). On the Gulf coast of Mexico, *C.c. rufa* are confirmed only as far south as the State of Tamaulipas (Newstead *et al.* in press; D. Newstead pers. comm. September 14, 2012), which borders Texas (roughly 1,900 mi (3,000 km) northwest of the Venezuela-Colombia border). Therefore, the subspecies compositions of *C. canutus* wintering on both coasts of Central America, from central Mexico to Venezuela, is not fully known. No evidence has pointed to *C.c. roselaari* wintering in this region, but it is possible since available information is fragmentary.

Available information suggests at least some of the birds wintering in this region are *Calidris canutus rufa*. Three birds marked in Texas in April 2010 were resighted together in February 2012 at the Laguna Superior on the southeast Pacific coast of Mexico (State of Oaxaca); however, it is unknown if these birds were *C.c. rufa* or *C.c. roselaari* (Carmona *et al.* in press). Evidence is stronger for *rufa* red knots in Panama. To date, all (three) resightings of marked birds on the Pacific coast of Panama indicate movement from known *C.c. rufa* areas. Two birds observed in Panama in February and March 2002 had been marked in Argentina in previous years (Niles *et al.* 2008, p. 73; Buehler 2002, p. 42), and a bird seen in November 2008 had been marked in Delaware Bay (B. Watts pers. comm. August 28, 2012; B. Paxton pers. comm. November 9, 2008). The bird that had been marked in Delaware Bay had a stable isotope signature just outside the main cluster of northern-wintering birds from the eastern Caribbean (N. Clark pers. comm. November 10, 2008). In addition, a red knot fitted with a geolocator in Massachusetts in September 2009 wintered that year near the border between Colombia and Venezuela (Niles *et al.* in press). Based on this information, at least some of the *C. canutus* wintering from southern Mexico to Venezuela are considered *C.c. rufa*.

Wintering Period

Red knots occupy the southernmost wintering areas, in Tierra del Fuego, from late October to February, with some birds arriving as early as late September (Niles *et al.* 2008, p. 15; Morrison and Harrington 1992, p. 76). Birds wintering in the Caribbean or the United States typically stay later, through March or even May (Newstead *et al.* in press; Niles *et al.* in press; Niles 2012a; Niles 2009, p. 10). Birds wintering in the Southeast seem to arrive in November (Niles *et al.* in press), while birds wintering in Texas seem to arrive much earlier, in late July or August (Newstead *et al.* in press; Niles 2012a). Geolocator results to date (from seven adults) showed that knots wintering in the Northwest Gulf of Mexico spent nearly the entire nonbreeding phase of their annual cycle (286 days, or 78 percent of the calendar year) on the Texas coast (Newstead *et al.* in press).

Wintering Area Fidelity

Red knots are generally thought to return to the same wintering region each year. Resightings of marked birds show few or no inter-annual movements of red knots between the Brazil and Tierra del Fuego wintering areas, or between the Southeast and Tierra del Fuego wintering areas (Baker *et al.* 2005, pp. 13–14; Harrington 2005a, p. 1). Extensive searches of Brazil in the winters of 2004 and 2005 failed to find any red knots marked from Tierra del Fuego or from the Southeast, but observation rates are too low to draw a firm conclusion because few knots have been marked in Brazil (Niles *et al.* 2008, pp. 9, 55; Baker *et al.* 2005, pp. 13–14). Using modeling and resighting rates, Schwarzer *et al.* (2012, p. 729) found that the estimated probability of surviving birds that had been banded as juveniles in Florida returning to Florida as adults during the following winter was 0.70 ± 0.08 , and the estimated probability of winter-to-winter fidelity for surviving adults banded in Florida was 0.81 ± 0.05 . It is unknown if the surviving birds that failed to return subsequently wintered elsewhere in the Southeast or in another region.

Examples of red knots changing wintering region do exist, but are few. Records of band resightings include about six birds that were observed in Florida during the core winter months (December to February) of one year, and in Chile between December and February of another year (BandedBirds.org 2012). One marked knot seen on February 20, 2002, in Panama had been banded in Tierra del Fuego in February 1995, and another seen in Panama on March 15 and 28, 1995, had been banded in San Antonio Oeste, Argentina, in March 1998 (Niles *et al.* 2008, p. 73; Buehler 2002, p. 42). These observations from Panama suggest other possible instances of red knots switching wintering regions.

Juveniles

There is little information on where juvenile red knots spend the winter months (USFWS and Conserve Wildlife Foundation 2012, p. 1), and there may be at least partial segregation of juvenile and adult red knots on the wintering grounds. Juvenile birds are typically under-represented in catches of red knots made in major wintering areas such as Chile and Florida (A. Dey pers. comm. April 7, 2008). In winter 2008–2009, Niles (2009, pp. 9–10) found the percentage of juvenile red knots peaked in January (13 to 15 percent) compared to catches made in November (3 to 6 percent) and February (0 percent). The overall low frequency suggests that

juveniles may winter separately from adults or may occupy unknown habitats not used by adults (Niles 2009, pp. 9–10). Many of the *Calidris canutus* seen in Panama in January and February 2002 were identified as juveniles based on leg color (Niles *et al.* 2008, p. 73). Because we lack specific information on juvenile red knots, we use the best available data from adult red knots to draw conclusions about juvenile foraging and habitat use.

Migration

Each year red knots make one of the longest distance migrations known in the animal kingdom, traveling up to 19,000 mi (30,000 km) annually. Red knots undertake long flights that may span thousands of miles without stopping. As *Calidris canutus* prepare to depart on long migratory flights, they undergo several physiological changes. Before takeoff, the birds accumulate and store large amounts of fat to fuel migration and undergo substantial changes in metabolic rates. In addition, leg muscles, gizzard (a muscular organ used for grinding food), stomach, intestines, and liver all decrease in size, while pectoral (chest) muscles and heart increase in size. Due to these physiological changes, *C. canutus* arriving from lengthy migrations are not able to feed maximally until their digestive systems regenerate, a process that may take several days. Because stopovers are time-constrained, *C. canutus* requires stopovers rich in easily digested food to achieve adequate weight gain (Niles *et al.* 2008, pp. 28–29; van Gils *et al.* 2005a, p. 2609; van Gils *et al.* 2005b, pp. 126–127; Piersma *et al.* 1999, pp. 405; 412) that fuels the next migratory flight and, upon arrival in the Arctic, fuels a body transformation to breeding condition (Morrison 2006, pp. 610–612). At stopover sites, body mass varies greatly from very light birds that have just arrived to very heavy birds that are just about to depart. In Delaware Bay, for example, some red knots arrive as light as 3.1 oz (89 g) (32 percent below fat-free weight), whereas near departure some birds may exceed 8.5 oz (240 g) (85 percent above fat-free weight).

Red knots tend to migrate in single-species flocks with departures typically occurring in the few hours before twilight on sunny days. Size of the departing flocks tends to be large (greater than 50 birds) (Niles *et al.* 2008, p. 28). Likewise, based on observations of other *Calidris canutus* subspecies departing from Iceland towards Nearctic breeding grounds in spring 1986 to 1988, Alerstam *et al.* (1990, p. 201) found mean flock sizes of 100 to 200 individuals. These *C. canutus* leaving Iceland in spring departed in flight formations during the afternoon or evening, and during rising or high tide; their departures had significant differences in daily timing between seasons that was associated with between-year differences in the tidal cycle. Within the season, departures took place earlier in relation to high tide as the season progressed (Alerstam *et al.* 1990, p. 201). Consistent with the afternoon and evening departures of *C. canutus* from Iceland, rufa red knots are inferred to migrate during both night and day based on the duration and distance of migratory flight segments estimated from geolocator results (Normandeau Associates, Inc. 2011, p. 203).

Red knots from different wintering areas appear to employ different migration strategies, including differences in timing, routes, and stopover areas. However, there is not full segregation of migration strategies, routes, or stopover areas among red knots from different wintering areas. Figure 3 shows well-known red knot stopover areas for reference; however, large and small groups of red knots, sometimes numbering in the thousands, occur in suitable habitats all along the Atlantic, Caribbean, and Gulf coasts.

Figure 3. Known red knot migration stopover areas.



Spring Distribution and Timing

Atlantic Coast

Major spring stopover areas along the Atlantic coast include Río Gallegos, Península Valdés, and San Antonio Oeste (Patagonia, Argentina); Lagoa do Peixe (eastern Brazil, State of Rio Grande do Sul); Maranhão (northern Brazil); the Virginia barrier islands (United States); and Delaware Bay (Delaware and New Jersey, United States) (see figure 3) (Cohen *et al.* 2009, p. 939; Niles *et al.* 2008, p. 19; González 2005, p. 14). However, large and small groups of red knots, sometimes numbering in the thousands, may occur in suitable habitats all along the Atlantic and Gulf coasts from Argentina to Massachusetts (Niles *et al.* 2008, p. 29).

From geolocators, examples of spring migratory tracks are available for three red knots that wintered in South America. One flew about 4,000 mi (6,400 km) over water from northeast Brazil in 6 days. Another flew about 5,000 mi (8,000 km) from the southern Atlantic coast of Brazil (near Uruguay) over land (the Amazon) and water (the eastern Caribbean) in 6 days. Both touched down in North Carolina, and then used Delaware Bay as the final stopover before departing for the arctic breeding grounds (Niles *et al.* 2010a, p. 126). A third red knot, which had wintered in Tierra del Fuego, followed an overland route through the interior of South America, departing near the Venezuela-Colombia border. This bird then flew over the Caribbean to Florida, and finally to Delaware Bay (Niles 2011a).

Notwithstanding the one geocator result showing an overland route, knots that winter in Tierra del Fuego tend to work their way up the southern Atlantic coast, using stopover sites in Argentina and Uruguay before departing from Brazil (Niles *et al.* 2008, p. 15). For example, based on banding studies from 1984 to 1991, Antas and Nascimento (1996, p. 63) found that red knots using Lagoa do Peixe in the spring had originated from southern Argentina and Chile; these birds migrated north to Punta Rasa (at Bahía Samborombón in northern Argentina) and the coast of Rio Grande do Sul (which includes Lagoa do Peixe in southeastern Brazil), then to Maranhão (northern Brazil), and then to Delaware Bay. Although a few birds may depart before the end of January, the main red knot movement north from Tierra del Fuego occurs in February. The northward migration through South America is rapid, with only brief stopovers (Niles *et al.* 2008, p. 15). Birds moving north from Argentina typically arrive in Brazil in April (Niles *et al.* 2008, p. 29). Departure from Brazil tends to occur in the first half of May (Niles *et al.* 2010a, p. 126; Niles *et al.* 2008, pp. 15, 29).

Available data indicate that red knots wintering in the Southeast (including the Caribbean) use at least two different spring migration routes. Geocator results for six knots from this wintering region showed most birds moving up the U.S. coast, using stopovers between the Carolinas and Massachusetts before departing for the Arctic (Niles *et al.* in press). These findings are supported by stable isotope analysis and resightings of marked birds, showing that at least a portion of the Southeast-Caribbean wintering group uses mid-Atlantic coastal stopovers including Virginia and Delaware Bay (BandedBirds.org 2012; Smith *et al.* 2008, p. 16; Atkinson *et al.* 2006a, p. 536; Atkinson *et al.* 2005, p. 738). However, the geocator on one southeastern bird showed an inland route, flying northwest to central Canada directly from the wintering area in South Carolina, passing over Kentucky and the Great Lakes (Niles *et al.* in press). Use of an interior route through the United States and Canada has also been documented by resightings in Manitoba and Alberta, Canada of birds that had been marked in Florida (Morrison and Harrington 1992 p. 77). Existence of an inland route is further supported by a lack of resightings in Delaware Bay (despite extensive searches) of birds marked in South Carolina or Georgia (Harrington 2005a, p. 1). Geocator results to date show birds departing the Caribbean in March and leaving the Southeast from late April through May (Niles *et al.* in press). From these same geocator data (for six birds using Southeast-Caribbean wintering areas), the total time spent along the U.S. Atlantic coast (including spring, fall, and for some birds winter) averaged 218 days (range 121 to 269 days) (Burger *et al.* 2012b, p. 1), or about 60 percent of the calendar year.

Some red knots from the Southeast-Caribbean wintering area, and from South American wintering areas, utilize spring stopovers along the Southeast United States, from Florida to North Carolina. The length of stopover at these locations is generally believed to be brief (Niles *et al.* 2008, p. 29), but geolocator data show two birds stopped in South Carolina for longer periods (4 to 7 weeks) from late March through early May (Niles *et al.* in press). Red knot numbers tend to peak in the Southeast earlier than in the mid-Atlantic (Virginia to Massachusetts) (M. Bimbi pers. comm. June 27, 2013). Some (but not all) birds migrate north in hops along coast from the Southeast to a final stopover location in the mid-Atlantic (while other birds use an inland route from the Southeast directly to central Canada, as discussed above).

Red knots typically use mid-Atlantic stopovers from late April through late May or early June (Cohen *et al.* 2009, p. 941; Niles *et al.* 2008, p. 15). The stopover time in Delaware Bay is about 10 to 14 days (Niles *et al.* 2008, p. 15). From Delaware Bay and other mid-Atlantic stopovers, birds tend to fly overland directly northwest to the central Canadian breeding grounds, with many stopping briefly along the shores of James and Hudson Bays (Niles *et al.* in press; Niles *et al.* 2010a, pp. 125–126; Cohen *et al.* 2009, p. 943; Niles *et al.* 2008, pp. 20, 24; Morrison and Harrington 1992, p. 79). Large numbers of knots have been observed in James Bay, Canada, on the day following a mass departure from Delaware Bay. Red knots pass rapidly through southern James Bay, sometimes stopping less than one day. In some years, concentrations of red knots (400 to 1,500 birds, but more typically fewer than 100) have been observed at locations around the Great Lakes, and may represent weather-induced stops (eBird.com 2012; Morrison and Harrington 1992, p. 79).

One study of Delaware Bay and the Virginia barrier islands found high stopover site fidelity within a particular spring stopover season (Cohen *et al.* 2009, p. 942). Fidelity among years is apparently much lower. Duerr *et al.* (2011, p. 16) found 60 percent of knots using the Virginia stopover did not use that site in the following year, although as many as 48 percent returned to Virginia in subsequent years. Watts (2009a) reported that 49 percent of marked red knots observed in Virginia had also been observed in Delaware Bay between 2005 and 2009. This included 326 movements between these spring stopover sites from year to year, and 88 movements that occurred within a given year. Preliminary analysis of these observations suggested that, in some years, movements of red knots from Delaware Bay to Virginia (southward) within a given spring migration season may equal the number of birds that move from north from Virginia to Delaware Bay (Watts 2009a). Thus, there is some flexibility in red knots' use of the final Atlantic spring stopover site.

Both northbound and southbound intra-year movements have also been reported between two spring stopovers about 119 mi (192 km) apart on Argentina's coast—San Antonio Oeste (to the north) and Península Valdés (to the south) (see figure 3). Monitoring of marked birds was carried out between February and May from 2006 to 2010 at both sites. In this 5-year period, 75 knots were detected moving south from San Antonio Oeste to Península Valdés. Approximately 13 percent of the detected individuals made this southward movement in more than 1 year of the study, and some southward movements occurred in each year of the study. One red knot was observed in San Antonio Oeste and Península Valdés on the same day in 2009 (D'Amico *et al.* 2011, entire).

These observations from both Argentina and the mid-Atlantic suggest that red knots may use clusters of suitable habitats as a regional stopover complex. As the near and far ends of the Delaware Bay and Virginia stopovers are separated by about 35 and 155 mi (56 and 250 km), respectively, observed movements of marked birds from the mid-Atlantic and from Argentina show that separation distances of about 100 mi (160 km) between suitable habitats are not a barrier to intra-regional movements during a single spring migration season, even in a southward direction.

Northwest Gulf of Mexico

Geolocator results from eight red knots (one with 2 years of data) wintering in Texas showed that all these birds used a central, overland flyway across the Midwest United States. Birds flew 1,600 to 2,000 mi (2,600 to 3,300 km) to the first stopover. A Northern Great Plains stopover (Saskatchewan, Canada, and North Dakota, United States) was used by five of six birds in 2010, while southern Hudson Bay in Manitoba, Canada (the Nelson River delta and James Bay), was used by 1 bird in 2010 and all three birds in 2011 (Newstead *et al.* in press). These findings support earlier reports of large numbers (1,000 to 2,500) of red knots in Saskatchewan and Alberta, Canada, between January and June (Skagen *et al.* 1999).

All birds departed Texas in the second half of May, and spent an average of 18.3 ± 3.2 days (range of 13 to 22 days) at the northbound stopover (Newstead *et al.* in press). Although these geolocator results show consistent use of the central flyway, resightings of marked birds suggest a more complex pattern of movements between Texas and the Atlantic coast, including both the Southeast wintering areas and Delaware Bay (BandedBirds.org 2012; D. Newstead pers. comm. August 20, 2012; Niles *et al.* 2008, p. 74). In addition, at least one bird marked in Argentina passed through Texas during spring migration (Niles *et al.* 2008, p. 74).

As previously mentioned, some movements of Pacific coast birds (presumed or possibly *Calidris canutus roselaari*) to the Northwest Gulf of Mexico have been documented during spring migration. Two *C.c. roselaari* marked on the west coast (one in Guerrero Negro, Mexico, the other in Grays Harbor, Washington) were resighted in Texas in spring 2012. The bird from Washington was subsequently resighted back at its original banding site 10 days after it was observed in Texas. Three birds marked in Texas in April 2010 were resighted together in winter 2012 at the Laguna Superior on the southeast Pacific coast of Mexico (State of Oaxaca); it is unknown if these three birds were *C.c. rufa* or *C.c. roselaari* (Carmona *et al.* in press).

Fall Timing and Distribution

Departure from the breeding grounds begins in mid-July and continues through August. Females are thought to leave first, followed by males and then juveniles (Niles *et al.* 2008, pp. 14–15; Harrington 2001, p. 6). Adult *Calidris canutus* pass through stopover sites along the migratory route earlier in years with low reproductive success than in years with high reproductive success (Blomqvist *et al.* 2002, p. 149). At each stopover, the adults gradually replace their red breeding plumage with white and gray, but generally they do not molt their flight or tail feathers until they reach their wintering areas (Niles *et al.* 2008, p.15; Morrison and Harrington 1992, pp. 79–80).

Important fall stopover sites include southwest Hudson Bay (including the Nelson River delta), James Bay, the north shore of the St. Lawrence River, the Mingan Archipelago, and the Bay of Fundy in Canada; the coasts of Massachusetts and New Jersey and the mouth of the Altamaha River in Georgia, United States; the Caribbean (especially Puerto Rico and the Lesser Antilles); and the northern coast of South America from Brazil to Guyana (see figure 3) (Newstead *et al.* in press; Niles 2012a; D. Mizrahi pers. comm. October 16, 2011; Niles *et al.* 2010a, pp. 125–136; Schneider and Winn 2010, p. 3; Niles *et al.* 2008, pp. 30, 75, 94; B. Harrington pers. comm. March 31, 2006; Antas and Nascimento 1996, p. 66; Morrison and Harrington 1992, p. 74; Spaans 1978, p. 72). However, birds can occur all along the coasts in suitable habitat. In the mid-Atlantic, southbound red knots start arriving in July. Numbers of adults peak in mid-August and most depart by late September, although geolocators are showing some birds stay through November. Migrant juveniles begin to appear along the U.S. Atlantic coast in mid-August, occurring in much lower numbers and scattered over a much wider area than adults (Niles *et al.* in press; Harrington 2001, p. 2; Morrison and Harrington 1992, p. 75).

Based on surveys from 1975 to 1978, Morrison and Harrington (1992, p. 75) reported that 60 to 90 percent of south-bound migrating red knots on the U.S. Atlantic coast occurred in 2 states, Massachusetts and New Jersey, and the relative importance of sites within these States varied from year to year. Studying migration stopover areas in Massachusetts, Harrington *et al.* (2010a, p. 357) found that red knots from different wintering areas (Argentina-Chile versus the Southeast) had different migration chronologies, plumage characteristics, flight feather molt, foods, foraging habitats, stopover durations, and uses of foraging and roosting habitats. Based on banding studies from 1984 to 1991, Antas and Nascimento (1996, p. 63) found that southbound migrants arriving in Brazil originated from South Carolina and Massachusetts in July and August, and from Guyana in September.

Several studies suggest that adult red knots fly directly to South America from the eastern seaboard of the United States, arriving in northern South America in August (Niles *et al.* 2008, p. 29). Geolocator data from one bird that wintered in Tierra del Fuego showed a fall migration from the Arctic through Massachusetts, then over open ocean to the boundary area between Venezuela and Guyana; this bird then flew overland through the interior of South America to the coast of Argentina, finally working its way down the Patagonian coast to Tierra del Fuego (Niles 2011a). This geolocator result of an inland route over Amazonia is consistent with observations of two birds at Bahía de Asunción in Paraguay, one in October 1987 and one in November 1988 (Niles *et al.* 2008, p. 29; Hayes *et al.* 1990, p. 953).

As with the red knot bound for Tierra del Fuego, geolocators on three birds wintering in Brazil all showed an over-water route from the eastern seaboard of the United States to northern South America. Two of these birds stopped in the Lesser Antilles for a few days in September, and two of these birds added hundreds of flight miles to avoid storms (Niles *et al.* 2010a, pp. 125–126). Geolocators on eight birds heading south from Massachusetts to Southeast-Caribbean wintering areas all followed a direct route over water, though much closer to the coast than the birds heading to Brazil. These birds tended to stay on the U.S. coast later into the fall, typically departing in early November. Only two of the eight knots departing from Massachusetts stopped en route—one in Virginia and one in South Carolina (Niles *et al.* in press). Geolocators on seven birds wintering in Texas showed they all used a similar and direct interior flyway during the

south-bound migration, except for one bird that deviated by stopping briefly in eastern Louisiana before returning to Texas. Red knots bound for Texas tended to leave Hudson Bay in early July, and all flew overland directly to the Gulf coast (Newstead *et al.* in press; Niles 2012a).

Migration and Wintering Habitat

Long-distance migrant shorebirds are highly dependent on the continued existence of quality habitat at a few key staging areas. These areas serve as stepping stones between wintering and breeding areas. Conditions or factors influencing shorebird populations on staging areas control much of the remainder of the annual cycle and survival of the birds (Skagen 2006, p. 316; International Wader Study Group (IWSG) 2003, p. 10). At some stages of migration, very high proportions of entire populations may use a single migration staging site to prepare for long flights. Red knots show some fidelity to particular migration staging areas between years (Duerr *et al.* 2011, p. 16; Harrington 2001, pp. 8–9, 21).

This section focuses on the red knot's coastal nonbreeding habitats. Red knots are restricted to ocean coasts during winter, and occur primarily along the coasts during migration. However, small numbers of rufa red knots are reported annually across the interior United States (i.e., greater than 25 miles from the Gulf or Atlantic Coasts) during spring and fall migration—these reported sightings are concentrated along the Great Lakes, but multiple reports have been made from nearly every interior State (eBird.org 2012). We lack information on the specific noncoastal stopover habitats used by red knots.

Habitats used by red knots in migration and wintering areas are similar in character, generally coastal marine and estuarine (partially enclosed tidal area where fresh and salt water mixes) habitats with large areas of exposed intertidal sediments. In North America, red knots are commonly found along sandy, gravel, or cobble beaches, tidal mudflats, salt marshes, shallow coastal impoundments and lagoons, and peat banks (Cohen *et al.* 2010a, pp. 355, 358–359; Cohen *et al.* 2009, p. 940; Niles *et al.* 2008, pp. 30, 47; Harrington 2001, pp. 8–9; Truitt *et al.* 2001, p. 12). In many wintering and stopover areas, quality high-tide roosting habitat (i.e., close to feeding areas, protected from predators, with sufficient space during the highest tides, free from excessive human disturbance) is limited (K. Kalasz pers. comm. November 26, 2012; L. Niles pers. comm. November 19, 2012).

In Delaware Bay, red knots are found primarily on beaches of sand or peat at the mouths of tidal creeks, along the edge of tidal marshes dominated by salt marsh cordgrass (*Spartina alterniflora*) and saltmeadow cordgrass (*S. patens*), and in salt pannes (shallow, high salinity, mud-bottomed depressions on the marsh surface) and shallow coastal ponds or embayments (K. Clark, pers. comm. April 11, 2012; Cohen *et al.* 2009, p. 940; Niles *et al.* 2008, pp. 33–34; Karpanty *et al.* 2006, p. 1706; Meyer 1999, p. ii; Burger *et al.* 1997, p. 288). Radio tracking showed that most of the time red knots roosted along the shoreline or in sandy washovers above the high tide line, but knots also roosted in bare, shallow-water openings 0.5 to 1.3 mi (850 to 2,050 m) inland in the adjacent salt marsh (Zimmerman 2010, pp. 9, 13, 26). The preference for inland roost sites was greater at night and during spring tides, and Delaware Bay is the only area in which rufa red knots have been observed roosting inland (Zimmerman 2010, pp. 1, 13). Some red knots that feed primarily in Delaware Bay regularly move to the Atlantic coast of New Jersey to roost in inlet habitats (Clark *et al.* 2009, pp. 87, 89; Sitters 2005, p. 6; Sitters 2001, p. 2;

Harrington 1996, p. 76). In Delaware, salt pannes are an important roosting habitat (K. Kalasz, pers. comm. November 17, 2011).

In Massachusetts, red knots use sandy beaches and tidal mudflats during fall migration. In New York and the Atlantic coast of New Jersey, knots use sandy beaches during spring and fall migration (Niles *et al.* 2008, p. 30). In the southeastern U.S., red knots forage along sandy beaches during spring and fall migration from Maryland through Florida. During migration, knots also use the tidal mudflats in Maryland and along North Carolina's barrier islands in North Carolina. In addition to the sandy beaches, red knots forage along peat banks for mussel spat in Virginia and along small pockets of peat banks where the beach is eroding in Georgia (Niles *et al.* 2008, p. 47). In Florida, red knots use salt marshes, brackish lagoons, tidal mudflats, and mangrove areas (Niles *et al.* 2008, p. 47). In Lee County on Florida's Gulf coast, Lott *et al.* (2009, pp. 18–19) found that red knots during fall migration used intertidal substrates on ocean beaches, almost exclusively at inlets. Along the Texas coast, red knots forage on beaches, oyster reefs, and exposed bay bottoms and roost on high sand flats, reefs, and other sites protected from high tides (USFWS 2011b, p. 5). In addition to using the Gulf beaches, red knots in Texas use extensive tidal flats on the bay sides of barrier islands (Newstead *et al.* in press).

In South American wintering areas, red knots are found principally in intertidal marine habitats, especially near coastal inlets, estuaries, and bays. Habitats used include sandy beaches, mudflats, mangroves, saltwater and brackish lagoons, and “restinga” formations (an intertidal shelf of densely-packed dirt blown by strong, offshore winds) (Niles *et al.* 2008, pp. 30, 50; Harrington 2001, pp. 8–9). Red knots were recently observed using rice fields in French Guiana (Niles 2012b) and in Trinidad (eBird.org 2012). In the Mingan Islands Archipelago in Canada (Province of Quebec), migrant red knots forage on limestone flats that are similar in habitat structure to red knot foraging areas in Argentina (USFWS 2011b, p. 8). In Suriname in the early 1970s, small numbers of red knots were observed on firm and tough clay banks emerging from eroding coastline and in shallow lagoons, but knots were never found on soft tidal flats (Spaans 1978, p. 72); these observations suggest a deviation from the red knot's typical nonbreeding habitats.

In Delaware Bay, red knots preferentially feed in microhabitats where horseshoe crab (*Limulus polyphemus*) eggs are concentrated, such as at horseshoe crab nests (Fraser *et al.* 2010, p. 99), at shoreline discontinuities (e.g., creek mouths) (Botton *et al.* 1994, p. 614), and in the wrack line (Nordstrom *et al.* 2006a, p. 438; Karpanty *et al.* 2011, pp. 990, 992). (The wrack line is the beach zone just above the high tide line where seaweed and other organic debris are deposited by the tides.) Wrack may also be a significant foraging microhabitat outside of Delaware Bay, for example where mussel spat (i.e., juvenile stages) are attached to deposits of tide-cast material. Wrack material also concentrates certain invertebrates such as amphipods, insects, and marine worms (Kluft and Ginsberg 2009, p. vi), which are secondary prey species for red knots (see Migration and Wintering Food, below).

For many shorebirds, the supra-tidal (above the high tide) sandy habitats of inlets provide important areas for roosting, especially at higher tides when intertidal habitats are inundated (Harrington 2008, pp. 4–5). Along the Atlantic coast, dynamic and ephemeral (lasting only

briefly) features are important red knot habitats, including sand spits, islets, shoals, and sandbars, often associated with inlets (Harrington 2008, p. 2; Winn and Harrington in Guilfoyle *et al.* 2006, pp. 8–10; Harrington in Guilfoyle *et al.* 2007, pp. 18–19). From South Carolina to Florida, red knots are found in significantly higher numbers at inlets than at other coastal sites (Harrington 2008, pp. 4–5).

In some localized areas, red knots will use artificial habitats that mimic natural conditions, such as nourished beaches, dredged spoil sites, elevated road causeways, or impoundments. For example, in Long Island and Delaware Bay, some nourished beaches and managed impoundments support important concentrations of red knots (Niles *et al.* 2008, pp. 30, 42). In Delaware Bay, Botton *et al.* (1994, p. 614) found that artificial obstructions such as jetties can, in the same manner as natural shoreline discontinuities, act to concentrate drifting horseshoe crab eggs and thereby attract shorebirds. In Florida, A. Schwarzer (pers. comm. March 25, 2013) has observed multiple instances of red knots using artificial structures such as docks, piers, jetties, causeways, and construction barriers, but we have limited information regarding the frequency, regularity, timing, or significance of red knots' use of use of these artificial habitats.

Migration and Wintering Food

Across all subspecies, *Calidris canutus* is a specialized molluscivore, eating hard-shelled mollusks, sometimes supplemented with easily accessed softer invertebrate prey, such as shrimp and crab-like organisms, marine worms, and horseshoe crab eggs (Piersma and van Gils 2011, p. 9; Harrington 2001, pp. 9–11). *Calidris canutus* do not necessarily prefer hard-shelled mollusks (in fact they do not, when given the choice), but they are specialized in finding and processing such prey. Due to this specialization, *C. canutus* have less ability to find the actively crawling soft-bodied worms and small crustaceans on which other sandpiper species specialize. One of this species' sensory capacities, the ability to use pressure gradients around hard objects in soft, wet sediments, has not been described in any other animal. This remote detection of buried hard-shelled prey is probably enabled by a bill-tip organ, a dense group of pressure sensors clustered in sensory pits of the mandibles. The mollusk prey is swallowed whole and crushed in the gizzard, which in *C. canutus* is the largest (relative to body size) among any shorebird species evaluated (Piersma and van Gils 2011, pp. 9–11). Large gizzards are another specialization to a mollusk diet, allowing *C. canutus* to grind the hard shells of its prey. *Calidris canutus* prefer thin-shelled to thick-shelled prey species because they are easier to digest (Zwarts and Blomert 1992, p. 113). From studies of other subspecies, Zwarts and Blomert (1992, p. 113) concluded that *C. canutus* cannot ingest prey with a circumference greater than 1.2 in (30 millimeters (mm)). Foraging activity is largely dictated by tidal conditions, as *C. canutus* rarely wade in water more than 0.8 to 1.2 in (2 to 3 cm) deep (Harrington 2001, p. 10). Due to bill morphology, *C. canutus* is limited to foraging on only shallow-buried prey, within the top 0.8 to 1.2 in (2 to 3 cm) of sediment (Gerasimov 2009, p. 227; Zwarts and Blomert 1992, p. 113). Table 1 gives prey items that have been reported for rufa red knots in wintering and migration areas.

Red knots and other shorebirds that are long-distance migrants must take advantage of seasonally abundant food resources at migration stopovers to build up fat reserves for the next non-stop, long-distance flight (Clark *et al.* 1993, p. 694). During the migration period, although foraging red knots can be found widely distributed in small numbers within suitable habitats,

birds tend to concentrate in those areas where abundant food resources are consistently available from year to year. The spatial distribution of red knots in Georgia, Virginia, and Delaware Bay stopover areas has been correlated with the distribution of the primary prey species (Fraser *et al.* 2010, p. 97; Cohen *et al.* 2010a, p. 355; Niles *et al.* 2008, pp. 17, 19; Smith *et al.* 2008, p. 15; Karpanty *et al.* 2006, p. 1706; Botton *et al.* 1994, p. 605).

Table 1. Reported red knot prey items in wintering and stopover areas

Prey	Location	Source
small periwinkles (<i>Littorina</i> spp.), tiny blue mussels (<i>Mytilus edulis</i>)	Mingan Islands, Canada	USFWS 2011b, p. 8
blue mussel (<i>Mytilus edulis</i>) spat (preferred), gem clams (<i>Gemma gemma</i>) (not preferred), amphipods, naticid snails	Massachusetts	Harrington 2001, p. 11
mussel spat, clams	Stone Harbor, Atlantic coast of New Jersey	Sitters 2001, p. 4
polychaete worms, insect larvae, crustaceans, mussel spat, clams	Atlantic coast beaches and marshes, New Jersey	Cohen <i>et al.</i> 2010b, p. 659
horseshoe crab eggs (preferred)	Delaware Bay, New Jersey and Delaware	Harrington 2001, p. 11; see section that follows
coquina clams (<i>Donax variabilis</i>), crustaceans	Virginia barrier islands	Cohen <i>et al.</i> 2010a, p. 355
blue mussel (<i>Mytilus edulis</i>) spat	Virginia barrier islands (especially on peat banks)	Karpanty <i>et al.</i> 2012, p. 1; Truitt <i>et al.</i> 2001, p. 12
coquina clams (<i>Donax variabilis</i>)	South Carolina (spring)	Harrington and Winn in Baker 2001, p. 12
small clams including coquina (<i>Donax</i> spp.) and dwarf surf (<i>Mulinia lateralis</i>) in winter; also horseshoe crab eggs in spring	Georgia	Schneider and Winn 2010, p. 2
amphipod crustaceans (<i>Emerita</i> spp.), bivalves (<i>Donax</i> spp.)	Gulf coast of Florida, Southern Brazil, Gulf of Venezuela	Harrington 2001, p. 10
clams (<i>Donax</i> spp. (preferred) and <i>Crassatellidae</i> spp.), snails (<i>Cypraeidae</i> spp.)	Tampa Bay Region, Gulf coast of Florida	Schwarzer 2011, pp. 74–75
horseshoe crab eggs (preferred but present in low densities)	Cedar Key, Gulf coast of Florida	Schwarzer 2011, p. 83
coquina (dwarf surf) clams (<i>Donax variabilis</i> , <i>D. texasianae</i>)	Gulf coast of Texas	Newstead <i>et al.</i> in press; Niles <i>et al.</i> 2009, p. 1
mainly bivalves (<i>Tellina</i> , <i>Macoma</i> , <i>Donax</i> , <i>Gemma</i> , <i>Iphigenia</i> , <i>Tivella</i> , and <i>Arca</i> spp.), also gastropods	State of Ceará, northeast Brazil	Carlos <i>et al.</i> 2010, pp. 16, 17
<i>Donax</i> spp. (especially <i>D. hanleyanus</i>), <i>Emerita</i> spp.	State of Rio Grande do Sul, southeast Brazil	Vooren and Chiaradia 1990, p. 20
mud snail (<i>Littoridina australis</i>)	Lagoa do Peixe, Brazil (State of Rio Grande do Sul)	Niles <i>et al.</i> 2008, p. 49

Table 1. Reported red knot prey items in wintering and stopover areas

Prey	Location	Source
mud snail (<i>Littoridina australis</i>) (preferred); Scarabaeidae beetle (<i>Dyscinetus</i> spp.)	Punta Rasa, Argentina (Bahía Samborombón)	Ieno <i>et al.</i> 2004, p. 493; Alemany <i>et al.</i> 2001, p. 17
a clam (<i>Darina solenoides</i>) in sandflats, a small mussel (<i>Brachidontes rodriguezii</i>) on restingas	San Antonio Oeste, Argentina	Barzola <i>et al.</i> 2006, p. 60; González <i>et al.</i> 1996, p. 575
bivalves (<i>Darina solenoides</i> and <i>Tellina petitiiana</i>)	Península Valdés, Argentina	Hernández 2009, p. 208
clam (<i>Darina solenoides</i>)	Fracasso Beach (north embayment of Península Valdés), Argentina	Musmeci 2011, entire
clam (<i>Darina solenoides</i>), polychaete (<i>Travisia olens</i>)	Colombo Beach (south embayment of Península Valdés), Argentina	Musmeci 2011, entire
clam (<i>Darina solenoides</i>)	Bahía Lomas, Tierra del Fuego, Chile	Niles <i>et al.</i> 2008, p. 50; Espoz <i>et al.</i> <i>in</i> Lanctot 2007, p. 10
clam (<i>Darina solenoides</i>) in soft sediments, mussels (mainly <i>Mytilus edulis</i> , <i>Aulacomya ater</i> , and <i>Perumytilus purpuratus</i>) on restingas	Río Grande, Tierra del Fuego, Argentina	Escudero <i>et al.</i> 2012, p. 356; Baker <i>et al.</i> 1996, p. 103

Horseshoe Crab Eggs

A prominent departure from typical prey items occurs each spring when red knots feed on the eggs of horseshoe crabs, particularly during the key migration stopover within the Delaware Bay of New Jersey and Delaware. Delaware Bay serves as the principal spring migration staging area for the red knot because of the abundance and availability of horseshoe crab eggs (Clark *et al.* 2009, p. 85; Harrington 2001, pp. 2, 7; Harrington 1996, pp. 76–77; Morrison and Harrington 1992, pp. 76–77). Horseshoe crab eggs are a superabundant source of easily digestible food.

Horseshoe crabs occur along the Atlantic coast from Maine to Florida, along Florida’s Gulf coast, and along Mexico’s Yucatan Peninsula (Brockman *in* Shuster *et al.* 2003, p. 33; Botton and Ropes 1987, p. 807). Within this geographic range, horseshoe crabs are most abundant between Virginia and New Jersey (Botton and Ropes 1987, p. 807), with the largest population occurring in Delaware Bay (Gerhart 2007, p. 2; Walls *et al.* 2002, pp. 43–44). Each spring, adult horseshoe crabs migrate from deep bay waters and the Atlantic continental shelf to spawn on intertidal sandy beaches. Beaches within estuaries are preferred spawning areas because they are low energy environments and are protected from the surf (Atlantic States Marine Fisheries Commission (ASMFC) 2004, pp. 7–8). Horseshoe crab spawning generally occurs from March through July, with the peak spawning activity occurring around the evening

new and full moon high tides in May and June (Smith and Michels 2006, p. 487; Shuster and Botton 1985, p. 368).

Over repeated spawning events, a female horseshoe crab deposits most of her 80,000 eggs in clumps of around 4,000 eggs, at depths of about 4 to 8 in (10 to 20 cm) beneath the surface of the sand, a distance beyond the reach of most shorebirds including red knots. However, wave action and burrowing by subsequent spawning horseshoe crabs move eggs toward the surface. Thus, a high density of spawning horseshoe crabs, such as occurs in Delaware Bay, is needed for the eggs to become available to shorebirds (Smith 2007, p. 287; Pooler *et al.* 2003, p. 698; USFWS 2003, p. 5; Berkson and Shuster 1999, p. 7; Clark *in* Farrell and Martin 1997, p. 24; Botton *et al.* 1994, p. 614; Shuster and Botton 1985, pp. 367–368).

Horseshoe crabs and surface egg availability are not found in similar densities in other areas on the Atlantic coast, which may explain why shorebirds concentrate in the Delaware Bay (Berkson and Shuster 1999, p. 7). Besides supporting red knots, Delaware Bay supports high numbers of other shorebird species, including semipalmated sandpiper (*Calidris pusilla*), ruddy turnstone (*Arenaria interpres*), and sanderling (*C. alba*), and ranks among the 10 largest shorebird migration staging sites in the Western Hemisphere (Clark *et al.* 2009, pp. 85, 90). Despite significant shorebird predation on horseshoe crab eggs, such activity probably has little impact on the horseshoe crab population, since the surface eggs consumed by birds typically do not survive anyway due to desiccation (ASMFC 2004, pp. 8–9; Botton *et al.* 1994, pp. 613–614).

Outside of Delaware Bay, horseshoe crab eggs are eaten opportunistically when available in nonbreeding habitats but are not considered a primary food resource for red knots in these areas (Schwarzer and Brush 2011, p. 3; Cohen *et al.* 2010a, pp. 355, 358; Cohen *et al.* 2010b, pp. 659–660; Schneider and Winn 2010, p. 2; González *et al.* 2006, p. 111; Harrington 2001, p. 11; Truitt *et al.* 2001, p. 12).

Delaware Bay provides the final Atlantic coast stopover for a significant majority (50 to 80 percent) of the red knot population making its way to the arctic breeding grounds each spring (Clark *et al.* 2009, p. 90; Brown *et al.* 2001, p. 10). Red knots stopping in Delaware Bay depend on horseshoe crab eggs to achieve remarkable rates of weight gain. Weight gains recorded on the Delaware Bay are the most rapid of any recorded for all known stopover populations of *Calidris canutus* in the world (Cohen *et al.* 2010a, p. 356; Piersma *et al.* 2005, p. 268) and are among the highest rates observed in the animal kingdom (Atkinson *et al.* 2007, p. 890). Although a single horseshoe crab egg contains a very small amount of energy, eggs are present in such superabundance that birds can eat enough in 2 weeks to nearly double their weights. No single stopover area is more important for the red knot than the Delaware Bay because the nutritive yield of the bay is so high (Harrington 1996, p. 73).

Research indicates this weight gain is important to sustain the birds on their final flights from Delaware Bay to the arctic breeding grounds. Stored fat and protein are used also for initial survival on the breeding grounds (McGowan *et al.* 2011a, p. 9; Piersma *et al.* 2005, p. 270; Baker *et al.* 2004, p. 876), particularly when conditions are adverse upon arrival (e.g., snow cover, lack of insect prey). Such body stores may also be used by *Calidris canutus* for physical transformations necessary for breeding (Morrison *et al.* 2005, p. 449; Morrison 2006, p. 610–

612). For example, a female red knot radio-tagged in May 1999 in Delaware Bay and recaptured incubating 4 eggs 6 weeks later in Canada had used up 2.1 oz (60 g) of reserves (about one-third of the optimal migration weight), demonstrating the importance of weight gain during migration stopovers (Baker *et al.* 2001, pp. 5–6). Morrison and Hobson *et al.* (2004, p. 341) found that *C.c. islandica* rely on stored fat to sustain them for a week or more upon arriving at the breeding grounds if there is still snowpack (as cited in Karpanty *et al.* 2011 p. 984). Using data on energetic flight costs by Kvist *et al.* (2001, p. 731), Baker *et al.* (2004, p. 876) calculated that red knots in the Delaware Bay need to achieve a departure mass of at least 6.3 to 7.1 oz (180 to 200 g) to cover the energetic demands of the flight to the breeding grounds and to survive an initial few days of snow cover.

Evidence for Reliance on Horseshoe Crab Eggs

The fact that red knots in Delaware Bay feed almost exclusively on horseshoe crab eggs is strongly supported by several lines of evidence, including physiological analyses, experiments, temporal and spatial correlations, direct field observation of foraging birds, and stable isotope analysis. For example, in 1996 and 1997, Tsipoura and Burger (1999, p. 640) found that horseshoe crab eggs accounted for greater than 60 percent to greater than 80 percent of food items found in the guts of Delaware Bay red knots. Using experimental feeding trays in the field, Gillings *et al.* (2007, p. 507) found that mixed flocks of red knots and other shorebirds consumed 80 percent of surface eggs in 5 minutes.

The timing of the arrival of red knots and other shorebirds in Delaware Bay typically coincides with the annual peak of the horseshoe crab spawning period (Clark *et al.* 2009, p. 91; Clark *in* Farrell and Martin 1997, p. 23; Morrison and Harrington 1992, p. 77). All indicators show that feeding conditions for red knots were poor in those years when the timing of the horseshoe crab spawn was out of sync with the birds' spring stopover period, such as occurred in 2003, 2005, and 2008 (Atkinson *et al.* 2007, p. 892; Dey *et al.* 2011a, p. 7).

As early as 1982, Wander and Dunne (1982, pp. 61–62) observed that red knots in Delaware Bay eat horseshoe crab eggs almost exclusively and found temporal correlations between shorebird abundance and horseshoe crab spawning activity, as well as spatial correlations of shorebird distribution relative to horseshoe crab spawning activity. Shuster and Botton (1985, p. 366) also found a spatial correlation between horseshoe crab spawning intensity and density of foraging shorebirds. In 1990 and 1991, Botton *et al.* (1994, pp. 605, 614) confirmed a spatial correlation between densities of horseshoe crab eggs and shorebirds in Delaware Bay, and found that shorebirds aggregated near shoreline discontinuities (e.g., salt-marsh creeks, jetties) that concentrated passively drifting eggs. Horseshoe crab eggs were the most abundant food item on these beaches, and there were few other available macroinvertebrates (Botton *et al.* 1994, pp. 605, 614).

In 2003 and 2004, Hernandez (2005, p. 29) found that red knot foraging responses were best explained by models that use horseshoe crab egg parameters only, mainly surface egg density and patchiness. In 2004, Karpanty *et al.* (2006, p. 1706) found that the crab egg biomass was more than 3.5 times larger at points used by red knots than at random points. The number of horseshoe crab eggs was the most important variable in their models predicting habitat usage, although incorporating secondary prey types (*Donax* clams and mussel spat) improved the

models' predictions. Karpanty *et al.* (2006, p. 1706) also found red knots shifting from other habitat toward horseshoe crab spawning beaches as spawning activity increased. In 2005, Fraser *et al.* (2010, p. 97) found that red knot feeding activity was concentrated at horseshoe crab nests relative to random beach points. Several studies have found the wrack line is a preferred microhabitat for foraging because horseshoe crab eggs become concentrated there (Nordstrom *et al.* 2006a, p. 438; Karpanty *et al.* 2011, pp. 990, 992).

Using stable isotope diet tracking and captive feeding trials, Haramis *et al.* (2007, entire) demonstrated that red knots in Delaware Bay rely almost entirely on horseshoe crab eggs to support their very high rates of weight gain (as cited in Cohen *et al.* 2010a, p. 356) and established horseshoe crab eggs as a unique and likely critical resource to migratory shorebirds along the east coast of the United States (Haramis *et al.* 2007, p. 373). Haramis *et al.* (2007, p. 373) attributed the value of horseshoe crab eggs to red knots and other shorebirds to the eggs' predictable abundance in Delaware Bay, rapid digestion and assimilation, demonstrated importance to rapid fattening during the migration stopover, and selected preference in the diet by the birds themselves. Further, Haramis *et al.* (2007, p. 373) were unable to identify alternative food sources in Delaware Bay with comparable quality (i.e., the combined abundance and digestibility of horseshoe crab eggs).

Possible Differential Reliance on Horseshoe Crab Eggs

Research supports the hypothesis that *Calidris canutus* of several subspecies select migration stopover sites on the basis of prey quality (i.e., flesh-to-shell ratios) to maximize daily net energy income (i.e., gain weight quickly to fuel migration) (van Gils *et al.* 2005a, p. 2611). For shellfish-eating *C. canutus* (including *rufa*), prey qualities at stopover sites average twice those at wintering sites. Consistent with ecological theory, field research shows that poor-quality stopovers are skipped (van Gils *et al.* 2005a, pp. 2610, 2614). Work has begun to extrapolate the "prey quality" concept to horseshoe crab eggs, which differ fundamentally from mollusks because they lack a hard shell.

As indicated above, research has provided strong evidence that a majority of red knots stop at the Delaware Bay during the spring migration, and that these birds are highly reliant on a superabundance of horseshoe crab eggs to gain weight during their stopover period. Newer research is examining possible differences in the use of, and reliance on, the Delaware Bay horseshoe crab resources among knots from different wintering regions. Some researchers have postulated that red knots from southern wintering areas (Argentina and Chile) are more reliant on horseshoe crab eggs than are birds from northern wintering areas (the Southeast) because southern birds cannot digest hard-shelled prey with the reduced digestive organs knots typically exhibit during long migration flights (Niles *et al.* 2008, p. 36; Atkinson *et al.* 2006b, p. 41). It is hypothesized that the northern birds are either able to arrive in the mid-Atlantic earlier than southern birds and re-grow their digestive apparatus to deal with hard-shelled prey, or do not undergo the major physiological changes of gut size reduction that the southern migrants undergo. This postulated difference in the stopover diet is attributed to differences in migration strategy (shorter flights or "hops" for northern birds, versus longer flights or "jumps" for southern birds), as well as absolute distance travelled. According to this hypothesis, knots wintering in Tierra del Fuego are particularly dependent on horseshoe crab eggs for successful

fattening and are more vulnerable to a decline in the availability of those eggs than are northern-wintering birds (Niles *et al.* 2008, p. 36; Atkinson *et al.* 2006b, p. 41).

Support for this hypothesis comes from stable isotope work showing that catches of red knots in 2005 from New Jersey's Atlantic coast (where horseshoe crab eggs are not an important part of the diet) contained a much higher proportion of migrants from the Southeast than did catches from Delaware Bay (Atkinson *et al.* 2006a, p. 536). Birds with a Southeast isotope signature constituted over half of the red knots from the Atlantic coast, but less than a quarter of knots from locations on either side of Delaware Bay (P. Atkinson pers. comm. November 8, 2012). In addition, radio tracking suggests at least partial segregation between birds that use Delaware Bay and birds that use the Atlantic coast during the spring stopover (Cohen *et al.* 2010b, p. 660). Further support comes from geolocator results and resightings of marked birds indicating that birds wintering in the Caribbean and the Southeast tend to bypass Delaware Bay (Niles *et al.* in press; Harrington 2005a, p. 1). In addition, red knots feeding on hard shelled prey in Virginia and Massachusetts may have to feed both day and night, while birds stopping in Delaware Bay can apparently meet their energy needs foraging (on superabundant, high-quality horseshoe crab eggs) only by day (Cohen *et al.* 2011, p. 352; Harrington 1996, p. 76).

In spring 2005, Atkinson *et al.* (in Wader Study Group 2005, p. 15) used observations of individually marked red knots to estimate return rates and residence time of birds in Delaware Bay. Based on observations of about 500 birds for which wintering areas were known from stable isotope analyses, both return rates and residence times within the Bay varied by wintering region. There were also slight differences in arrival and departure patterns. The longest distance migrants from Argentina and Chile showed lower return rates and greater heterogeneity in arrival, such that the total passage period of the group was longer, though the stopover length of individuals did not significantly exceed that of other groups (Atkinson *et al.* in Wader Study Group 2005, p. 15). These results further suggest that differences exist among the migration strategies of red knots from different wintering regions (also see Harrington *et al.* 2010a for similar findings from Massachusetts).

However, there is not a strict correlation between wintering area and stopover diet because there is considerable mixing of birds from various wintering regions at the mid-Atlantic stopover sites. Stable isotope analysis of Delaware Bay birds (eating horseshoe crab eggs almost exclusively) in 2003 found only 64 percent had chemical signatures from Argentina or Chile, while 30 percent had Florida-type signatures (the rest were unclassified) (Atkinson *et al.* 2005, p. 738). Results were similar in 2004, with about 56 percent from Chile or Argentina, 13 percent from the Southeast, 22 percent from Brazil, and 9 percent unknown (Atkinson *et al.* 2006a, p. 536). In 2006 and 2007 in Virginia (where horseshoe crab eggs are not an important part of the diet), about 43 percent of banded birds were from Argentina or Chile, 2 percent were from Brazil, and 52 percent had been banded in the United States (which may include other stopover sites as well as the Southeast wintering area) (Smith *et al.* 2008, p. 16). Thus, it is clear that at least some southern (Argentina-Chile) red knots do eat prey other than crab eggs, while some northern (Southeast) birds do feed on crab eggs during their final spring stopovers along the mid-Atlantic.

Physiologically, the gizzards of red knots feeding on horseshoe crab eggs are about seven times larger than would be predicted from extrapolations of mollusk prey quality (i.e., with no shells to grind, gizzards during the Delaware Bay stopover should be very small, but they are not) (van Gils *et al.* 2005a, p. 2616; van Gils *et al.* 2003, p. 3369). Further, only Delaware Bay red knots have small stones in their gizzards, presumably to grind the leathery surface of the eggs. These findings suggest that the grinding of horseshoe crab eggs is a fundamentally different process than crushing the outer shells of mollusks (van Gils *et al.* 2005a, p. 2616). So although horseshoe crab eggs are clearly a “super high quality” food (van Gils *et al.* 2005a, p. 2616), there are still energetic costs associated with the digestive processing of the eggs.

The time and energy required to process horseshoe crab eggs, compared to high-quality mollusk prey, have not been investigated. (See Piersma *et al.* 2003a, p. 3365 and van Gils *et al.* 2003, p. 3374 for time and energy costs, respectively, of digesting mollusk prey of various qualities.) Without this information and comparative digestive anatomy of northern versus southern birds upon arrival in the mid-Atlantic, it is not yet possible to conclude if there are significant differences in stopover diet based on wintering region. Although the relative importance of horseshoe crab eggs to birds from various wintering areas is still being refined, it is clear that this resource is crucial to the rufa red knot.

Historical accounts of red knot distribution, along with re-creations of pre-historic conditions in Delaware Bay, suggest that the exploitation of horseshoe crab eggs by migrating shorebirds may be a relatively recent phenomenon (Cohen *et al.* 2008, pp. 8–27; Fraser 2008, entire; Botton *et al.* *in* Shuster *et al.* 2003, pp. 24–26). If true, this would reflect some flexibility in the red knot’s migration strategies. It cannot be presumed, however, that alternative coastal habitats could necessarily fulfill the birds’ energy needs as well as Delaware Bay does today. The fact that stopover sites must function in precise sequence both in time and in space means that functional alternatives to current staging areas are unlikely (Botton *et al.* *in* Shuster *et al.* 2003, pp. 24–26; Myers *et al.* 1987, p. 22).

Historical Distribution and Abundance

The current geographic distribution of the red knot has not changed relative to that recorded in historical writings, with the notable exception of Delaware Bay (discussed further below). Several early writers reported that red knots breed in the Arctic and winter along the U.S. Gulf coast and in South America including Brazil and Tierra del Fuego (Lowery 1974, p. 309; Hellmayr and Conover 1948, p. 167; Bent 1927, p. 143; Ridgway 1919, p. 233; Forbush 1912, p. 262; Eaton 1910, p. 307; Shriner 1897, p. 94; Mackay 1893, p. 25; Audubon 1844, plate 328). Bent (1927, p. 143) included Jamaica and Barbados as part of the possible wintering range of red knots, and described knots as “rarely” wintering in parts of Louisiana and Florida. Hellmayr and Conover (1948, p. 167) noted the use of the West Indies (Jamaica, Barbados, and Trinidad) during migration. Several writers described the red knot as occurring primarily along the coasts with relatively few sightings inland, but interior migration routes through the central United States were also known (Lowery 1974, p. 309; Hellmayr and Conover 1948, p. 167; Bent 1927, pp. 133, 145; Ridgway 1919, p. 233; Forbush 1912, pp. 262–263; Eaton 1910, pp. 307–308; Audubon 1844, plate 328). As with the geographic distribution, a number of historical accounts suggest that the timing of the red knot’s spring and fall migrations along the Atlantic coast was generally the same in the past as it is today (Myers and Myers 1979, p. 192; Urner and

Storer 1949, p. 189; Stone 1937, p. 459; Bent 1927, entire; Forbush 1912, pp. 262–263; Shriner 1897, p. 94; Dixon 1895 in Barnes and Truitt 1997, p. 114; Mackay 1893, p. 26; Stearns and Coues 1883, p. 229; Roosevelt 1866, p. 151; Giraud 1944, p. 225; Wilson 1829, pp. 140–141).

Although the large-scale geographic distribution of migration stopover habitats does not seem to have changed, some authors have noted regional changes in the patterns of red knot stopover habitat usage along the U.S. Atlantic coast. For example, based on a review of early literature, Cohen *et al.* (2008) suggested that red knots had a more extensive spring stopover range a century ago than now, with thousands of birds noted in spring in Massachusetts, New York, New Jersey, and Virginia. Harrington *et al.* (2010b, pp. 188, 190) found changing regional patterns of stopover habitat use in Massachusetts, as well as a shift in the wintering destination of birds stopping in Massachusetts in fall (see Population Surveys and Estimates—Fall Stopover Areas, below).

In Delaware Bay and Tierra del Fuego, the era of modern surveys for the red knot and other shorebird species began in the early 1980s. Systematic red knot surveys of other areas began later, and for many portions of the knot's range, available survey data are patchy (see Population Surveys and Estimates, below). Prior to the 1980s, numerous natural history accounts are available, but provide mainly qualitative or localized population estimates. Nonetheless, a consistent narrative emerges across many historical accounts that red knots were extremely abundant in the early 1800s, decreased sharply starting in the mid-1800s, and may have begun to recover by the mid-1900s. Most writers agree the cause of this historical decline was intensive sport and market hunting (see proposed rule—Factor B).

Audubon (1844, plate 328) observed red knots in spring and fall along the U.S. and Canadian coasts from Texas to the entrance of the Bay of Fundy in southeastern Canada. He found knots in winter in East Florida, concluding that “some of the species do not proceed beyond our southern limits at that season.” Red knots were reported as “quite abundant in South Carolina,” during both spring and fall migrations (Audubon 1844, plate 328). While in Galveston Bay, Texas, in April 1837, Audubon (1844, plate 328) observed groups of knots arriving daily and proceeding east along the shores of the Gulf of Mexico. Audubon (1844, plate 328) did not observe any interior migration through the United States, but did conclude that red knots migrate overland in Canada for the last part of their northbound migration “when they have reached the entrance to the Bay of Fundy.” Regarding the breeding range, “it is certain that they reach a very high latitude, and that some stop to breed about Hudson's Bay” (Audubon 1844, plate 328). Providing more recent documentation of the migration route through Canada, Hope and Short (1944, p. 574) reported “huge flocks” of red knots at a site called Big Piskwanish on James Bay, Canada in July 1942; some of the flocks contained from 200 to 500 birds.

Herbert (1853, p. 160) reported the red knot was “very abundant” among the small islets of Long Island, New York. Roosevelt (1866, p. 150) described red knots as “far from plentiful,” but locally “exceedingly numerous” at Egg Harbor, New Jersey (Roosevelt 1866, p. 97). Coues (1868, p. 293) described the red knot as “abundant” along the New England coast in spring and autumn migration. Hallock (1877, p. 168) described the red knot as “an abundant species found along the shores of Long Island and New Jersey in numbers.” Stearns and Coues (1883, p. 229)

reported the red knot “is a common spring and autumn migrant through New England, where it is found chiefly in small flocks along the seashore.”

Mackay (1893, p. 26) described an earlier era when thousands of knots occurred on Cape Cod for about a week during spring migration. Prior to 1850, red knots were more numerous in parts of Cape Cod “than in all the rest of New England combined, and being very gregarious they would collect in those places in exceedingly large numbers, estimates of which were useless...immense numbers of these birds could be seen, as they rose up in clouds...” (Mackay 1893, p. 29). Mackay (1893, pp. 25, 30) described a considerable population decline caused by intensive hunting, “It is not my intention to convey the impression that the Knots are nearly exterminated, but they are much reduced in numbers, and are in great danger of extinction, and comparatively few can now be seen in Massachusetts, where formerly there were twenty to twenty-five thousand a year, which I consider a reasonable estimate of its former abundance.” Mackay (1893, p. 31) noted that red knots were still found “in greater or less numbers along the Atlantic coast south of Chesapeake Bay.” From Virginia as late as 1895, Dixon (1895 in Barnes and Truitt 1997, p. 114) reported flocks mid-May of 10,000 “red-breasted snipe,” which likely refers to red knots based on the feeding habits and timing of occurrence described in that account.

Echoing Mackay (1893), Shriner (1897, p. 94) reported, “This bird was formerly very plentiful in migrations in New Jersey, but it has been killed off to a great extent...” Eaton (1910, p. 307) reported that the red knot breeds in Arctic regions and migrates along the coast and inland waters, wintering from the Gulf coast to South America. “It is one of the best known beach birds on the south coast of Long Island, but like all the shorebirds is much less common than formerly” (Eaton 1910, pp. 307–308).

Forbush (1912, p. 263) provided an early account of red knots migrating through the interior United States, reporting that the red knot “...migrates principally along the Atlantic coast, both spring and fall, but in the spring, numbers of the species arrive in Texas, Louisiana and other southern States, going north through the Mississippi valley region.” Forbush (1912, pp. 263–266) described red knots formerly reaching the shores of New England “in immense numbers,” but went on to cite Mackay (1893) and numerous other sources in documenting a substantial population decline. This author concluded that the decrease occurred earlier in the northern part of the U.S. range than in the Southeast. “The Knot had decreased considerably near Boston before the middle of the last century,” but “[up] to about 1900 they were still very plentiful in the Carolinas” (Forbush 1912, pp. 263–264). Despite some recent localized increases, Forbush (1912, p. 264) determined that the “numbers of this bird have decreased tremendously all along the Atlantic coast within the last seventy-five years.” Although numerous sources cited by Forbush (1912, pp. 263–266) agreed that over-hunting was the chief cause of the decline (see proposed rule—Factor C), one source attributed a local decrease to a “lack of feed” (Forbush 1912, p. 265), perhaps an early indication of the red knot’s sensitivity to reduced prey availability (see proposed rule—Factor E). Forbush (1912, p. 266) concluded, “The decrease is probably due, however, to shooting both spring and fall all along our coasts, and possibly to some extent in South America. Evidently we are doing more than driving the Red-breast off our coast, and while the utter extinction of such a cosmopolitan bird is not

imminent, its extirpation from the Atlantic coast of North America is one of the possibilities of the near future.”

By 1929, Bent (1927, p. 132) noted signs of red knot population recovery, “Excessive shooting, both in spring and fall reduced this species to a pitiful remnant of its former numbers; but spring shooting was stopped before it was too late and afterwards this bird was wisely taken off the list of game birds; it has increased slowly since then, but is far from abundant now.” Bent (1927, p. 132) noted flocks of 1,500 to 3,000 in Long Island in 1910, and described the red knot as “very common” in South Carolina in May.

In spring and fall surveys of New Jersey’s Atlantic coast from 1935 to 1938, Urner and Storer (1949, pp. 178–183) noted peak annual spring counts of 500 to 3,000 knots, and peak annual fall counts of 725 to 1,600 knots. These authors found the red knot to be common or locally abundant in both spring and fall, with a large increase in numbers over previous years (Urner and Storer 1949, pp. 185–188). Urner and Storer (1949, pp. 192–193) noted increases in several medium- and large-bodied shorebird species, continuing a trend that began in 1931, and concluded, “...it is obvious that the species which have increased the most are, for the most part, those which in the past bore the brunt of the hunting pressure.” Based on his bird studies of Cape May, New Jersey, Stone (1937, p. 465) was “inclined to think that, while its numbers were sadly depleted, the Knot never reached such a low ebb on our coast as some have supposed, and since the abolishing of the shooting of shore birds it has steadily increased in abundance.” It is unclear whether the red knot population fully recovered its historical numbers (Harrington 2001, p. 22) following the period of unregulated hunting.

Perhaps an early indication of the red knot’s sensitivity to human disturbance, Stone (1937, p. 465) noted that knots avoided those beaches “most frequented by summer visitors.” Fraser (2008, p. 3) noted an even earlier report of the effects of disturbance (see proposed rule—Factor E) and development (see proposed rule—Factor A) on shorebirds in the mid-Atlantic, from the August 9, 1890, New York Times: “Once in a while a nice fat snipe or bay bird is knocked over at Sandy Hook and farther down the Jersey coast. They do not come in there in large flights as they did years ago, because of so much building of Summer homes along the beach. Snipe like to keep at a good distance from human beings and are fond of roaming over wild stretches of sand. There is yet quite a barren stretch of sand dunes that keeps the ocean from pouring into the Great South Bay, and this section is the only good snipe ground near the city.” According to Roosevelt (1866, p. 93), red knots were among the shorebird species commonly referred to as “bay-snipie,” so may have been among the species referred to in the 1890 observations.

Delaware Bay

Delaware Bay was not recognized as a major shorebird stopover area until the early 1980s, despite detailed shorebird studies (e.g., Urner and Storer 1949; Stone 1937) in the South Jersey region (Clark *et al.* 2009, p. 85; Botton *et al.* *in* Shuster *et al.* 2003, p. 6; Clark *in* Farrell and Martin 1997, p. 23; Clark *et al.* 1993, p. 695). There were some early anecdotal reports involving horseshoe crabs, as summarized by Botton *et al.* (*in* Shuster *et al.* 2003, p. 6). Wilson (1829, pp. 145–146) noted that ruddy turnstones in the bay fed “almost wholly on the eggs, or spawn, of the great King Crab,” but no similar accounts were made of red knots (Wilson 1829,

pp. 140–144). Forbush (1912, p. 267) noted that red knots “are fond of the spawn of the horsefoot crab, which, often in company with the Turnstone, they dig out of the sand...” Stone (1937, p. 400) observed ruddy turnstones and black-bellied plovers (*Pluvialis squatarola*) regularly feeding on dead horseshoe crabs in Delaware Bay. Stone (1937, p. 400) also mentions flights of ruddy turnstones across the Cape May Peninsula in the spring, as happens today when they go to roost at night along the Atlantic coastal marshes (Botton *et al.* *in* Shuster *et al.* 2003, p. 6). Interestingly, no mention of horseshoe crab eggs as food is found in Stone’s (1937) accounts of any shorebird in the Cape May area, or in the decade-long study by Urner and Storer (1949) (Botton *et al.* *in* Shuster *et al.* 2003, p. 6). During his early studies of horseshoe crabs in 1951, C. Shuster observed many shorebirds feeding along Delaware Bay beaches, including red knots. However, another 30 years elapsed before scientists began to study the shorebird-horseshoe crab relationship in detail, and documented the very large numbers of shorebirds using the bay as a stopover (Botton *et al.* *in* Shuster *et al.* 2003, pp. 6–7). Lack of earlier scientific documentation cannot be attributed to remoteness. Delaware Bay is located within a few hours’ drive of millions of people, and university marine laboratories were established many years ago on both shores of the bay (Botton *et al.* *in* Shuster *et al.* 2003, p. 6).

It is unclear if the large magnitude of the shorebird-horseshoe crab phenomenon was simply missed by science until 1981, or if the distribution of the red knot and other shorebird species changed over the period of the historical record. For much of the 20th century, this phenomenon in Delaware Bay may have been much reduced (relative to 1980s levels), and therefore easier to miss, due to the occurrence of low points in the abundance of both shorebirds (caused by hunting, see proposed rule—Factor B) and horseshoe crabs (caused by intensive harvest, see proposed rule—Factor E) (Botton *et al.* *in* Shuster *et al.* 2003, p. 25; Clark *in* Farrell and Martin 1997, p. 23). Alternatively, it may be that the red knot did not make extensive use of Delaware Bay prior to its population decline a century ago. Under this scenario, red knots came to rely on Delaware Bay because their populations were recovering at the same time that Atlantic-side stopover habitats in the region were becoming developed and the shorelines stabilized (Cohen *et al.* 2008, pp. 23–27) (see proposed rule—Factor A). We have no means to determine how long shorebirds have been reliant on horseshoe crab eggs in Delaware Bay (Botton *et al.* *in* Shuster *et al.* 2003, pp. 24–26) prior to the early 1980s.

Summary—Historical Distribution and Abundance

The current geographic distribution of the red knot has not changed relative to that recorded in historical writings, with the notable exception of Delaware Bay. Likewise, a number of historical accounts suggest that the timing of the red knot’s spring and fall migrations along the U.S. Atlantic coast was generally the same in the past as it is today. Although we lack quantitative data, a sharp red knot population decline from the late 1800s to the early 1900s is noted across numerous historical accounts from the U.S. Atlantic coast, driven by unregulated hunting, and followed by signs of recovery once hunting ceased. Outside of the U.S. Atlantic coast, we have no information regarding the red knot’s historical abundance or population trends.

Delaware Bay was not recognized as a major shorebird stopover area until the early 1980s, despite detailed shorebird studies in the South Jersey region. It is unclear if the large magnitude of the shorebird-horseshoe crab phenomenon was missed by science until 1981, or if the distribution of the red knot and other shorebird species changed over the period of the

historical record. The middle part of 20th century coincided with recovery of shorebird populations following the regulation of hunting (Urner and Storer 1949, pp. 192–193; Bent 1927, p. 132), a low point in horseshoe crab abundance following a period of intensive harvest (Atlantic States Marine Fisheries Commission (ASMFC) 2009, p. 1), and the large-scale development and stabilization of Atlantic coast beaches in the mid-Atlantic region (Nordstrom and Mauriello 2001, pp. 20–21; Nordstrom 2000, pp. 7–11). Any or all of these factors may have influenced the red knot's use of, and reliance on, Delaware Bay as its primary Atlantic stopover site in spring.

Population Surveys and Estimates

Localized and regional red knot surveys have been conducted across the subspecies' range with widely differing levels of geographic, temporal, and methodological consistency. Available survey data are presented in detail below, along with the sources and methodologies for each. Some general characterizations of the available data are noted here.

- No population information exists for the breeding range because, in breeding habitats, red knots are thinly distributed across a huge and remote area of the Arctic. Despite some localized survey efforts, (e.g., Bart and Johnston 2012, pp. 141-155; Niles *et al.* 2008, p. 62), there are no regional or comprehensive estimates of breeding abundance, density, or productivity (Niles *et al.* 2008, pp. 52–53).
- Few regular surveys are conducted in fall because southbound red knots tend to be less concentrated than during winter or spring.
- Some survey data are available for most wintering and spring stopover areas. For some areas, long-term data sets have been compiled using consistent survey methodology.
- Because there can be considerable annual fluctuations in red knot counts, longer-term trends are more meaningful. At several key sites, the best available data show that numbers of red knots declined and remain low relative to counts from the 1980s, although the rate of decline appears to have leveled off since the late 2000s; specific data are presented and analyzed below.
- Inferring long-term population trends from various national or regional datasets derived from volunteer shorebird surveys and other sources, Andres (2009, p. 6) and Morrison *et al.* (2006, pp. 71, 76, 77) also concluded that red knot numbers declined, probably sharply, in recent decades.

Wintering Areas

Counts in wintering areas are particularly useful in estimating red knot populations and trends because the birds generally remain within a given wintering area for a longer period of time compared to the areas used during migration. This eliminates errors associated with turnover or double-counting that can occur during migration counts.

Argentina and Chile

Aerial surveys of Tierra del Fuego (Chile and Argentina) and the adjacent Patagonian coast to the north (Argentina) (see figures 2 and 3) have been conducted since 2000, and previously in the early 1980s, by the same observers using consistent methodology (Morrison *et al.* 2004, p. 62). This is the best available long-term data set for a wintering area. However, as these are not the only red knot wintering areas, the survey results are best interpreted as one indicator of population trends rather than estimates of the total population.

As shown in table 2, counts have been markedly lower in recent years. Comparing the average counts for Tierra del Fuego from 1985 and 2000 (52,244) with 2010 to 2012 (13,437), the recent counts are about 75 percent lower than the earlier counts. An independent population estimate, using resighting data from Río Grande fitted to binomial models, supports the observation that declines did not begin until after 2000. González *et al.* (2004, p. 361, as cited in Niles *et al.* 2008, pp. 65–67) estimated the 1995 wintering population in Argentina and Chile at 74,193 (95 percent confidence interval 50,000 to 110,000). This same model produced population estimates that were within 5 to 15 percent of the aerial counts from 2001 to 2003, giving confidence in the model results.

Table 2. Aerial counts of red knots in Chile and Argentina, winters 1982 to 2012

(Morrison and Ross 1989, Vol. 2, pp. 226, 252; Morrison *et al.* 2004, p. 65; Dey *et al.* 2011a, p. 2; G. Morrison pers. comm. August 31, 2012).

Year	Tierra del Fuego	Patagonia	Total
1982		14,314	
1985	53,232		
2000	51,255		
2001	29,745*		
2002	27,242	2,029	29,271
2003	29,915	560	30,475
2004	30,778	880	31,658
2005	17,653		
2006	17,211		
2007	17,360		
2008	14,800		
2009	17,780		
2010	16,260		
2011	9,850		
2012	14,200	574	14,774

*Only the single largest wintering area (Bahía Lomas) and one small adjacent site were surveyed on Tierra del Fuego in 2001.

As shown in table 2, declines were even sharper (about 96 percent) along the roughly 1,000 mi (1,600 km) of Patagonian coast than in the core area on Tierra del Fuego. The population thus appears to have contracted to the core sites, leaving few birds at the “peripheral”

Patagonian sites (COSEWIC 2007, p. 11). Reflecting the larger downward trend in Patagonia, local winter counts at Península Valdés went from 8,000 red knots in 1994 to a low of 650 red knots in 2008, with the most recent (2010) at 825 knots (Western Hemisphere Shorebird Reserve Network (WHSRN) 2012).

Northern South America and Central America

Counts of wintering red knots along the north coast of South America have been sporadic and have varied in geographic coverage. Morrison and Ross (1989, Vol. 2, p. 183) conducted aerial surveys of the entire South American coast in the 1980s. In northern Brazil, red knots were found in three out of four survey segments (table 3): North, North-Central, and Northeast. No red knots were observed in the Amazon survey segment of Brazil, which is between North and North-Central (Morrison and Ross 1989, Vol. 2, p. 183). Using the same surveyor team and methods as the 1986 survey, the North-Central segment of Brazil was again surveyed by air in 2011 (D. Mizrahi pers. com. November 17, 2012; Morrison *et al.* 2012, p. 126). As shown in table 3, the 2011 total was 3,660 red knots (D. Mizrahi pers. comm. November 17, 2012), which may suggest a decline. These 2011 results require further confirmation; however, redistribution of birds to the west is an unlikely explanation for the lower numbers in 2011, based on recent surveys of Guyana, Suriname, and French Guiana (discussed below) (Morrison *et al.* 2012, p. 126).

Covering about 30 percent (by linear miles of coastline) of the North-Central Brazil survey segment, Baker *et al.* (2005, p. 12) counted 7,575 knots in western Maranhão during an aerial survey in February 2005. In a repeat of this survey in December 2006 (winter of 2007), only 3,000 knots were counted (Niles *et al.* 2008, p. 134) (table 3). The shores of Maranhão are complex and highly fragmented making accurate counting more difficult. To allow for this, aerial coverage was more extensive and included not only the ocean shore but also a variety of back bays and channels (Niles *et al.* 2008, p. 134).

In December 2007 (winter of 2008), ground surveys were conducted at 2 sites in the Brazilian State of Ceará, within the Northeast Brazil survey segment (where only 15 red knots had been counted in 1983). Only small numbers of knots (average peak of 8 ± 8.5) were observed at Ilha Grande, but an average peak count of 481 ± 31 red knots was recorded at Cajuais Bank (Carlos *et al.* 2010, pp. 10–11, 13). Lower numbers (up to 80) of red knots have been observed in winter at 4 other sites in Ceará (Serrano 2007, p. 16).

Table 3 Aerial and ground counts of red knots on the northern coast of Brazil (from west to east), winters 1986 to 2011 (D. Mizrahi pers. comm. November 17, 2012; Niles *et al.* 2008, p. 134; Baker *et al.* 2005, p. 12; Morrison and Ross 1989, Vol. 2, p. 183)

Winter	North Survey Segment (State of Amapá)	North-Central Survey Segment (from Belém, State of Pará to Baía de Sarnambi, State of Maranhão)	From Baía da Mutuoca to São Luís (State of Maranhão, within North-Central Survey Segment)	Northeast Survey Segment (from Baía de Sarnambi, State of Maranhão through State of Ceará)	Cajuais Bank** (in the State of Ceará, within Northeast Survey Segment)
1982	120				
1983				15	
1986		8,191			
2005			7,575		
2007*			3,000		
2008*					481 ± 31
2011		3,660			

*December of the previous year.

**Ground survey; all others were aerial. Peak monthly average of repeated counts from December to February; all others were one-time counts.

Morrison and Ross (1989, Vol. 2, p. 149) also documented 520 *Calidris canutus* in western Venezuela in 1982. Ruiz-Guerra (2011, p. 194) documented 20 *C. canutus* at Musichi (Department of La Guajira) on the Caribbean coast of Colombia near Venezuela in January 2008. It is not known if the birds observed around the Colombia-Venezuela border were all of the *rufa* subspecies, but recent geolocator results suggest at least some of the winter birds in this area are *C. canutus rufa* (Niles *et al.* in press). During the 1980s surveys, no red knots were observed between western Venezuela and the west end of Brazil (the North segment), with no knots recorded in eastern Venezuela, Trinidad, Guyana, Suriname, or French Guiana (Morrison and Ross 1989, Vol. 1, p. 41). With the same survey team and methods from the 1980s, aerial shorebird surveys were recently repeated in Guyana (January 2010), Suriname (December 2008, January 2010, and January 2011), and French Guiana (December 2008 and January 2010) (Morrison *et al.* 2012, p. 121). No red knots were detected in 2011, and a negligible number in December 2008 (i.e., winter 2009) and in 2010 (D. Mizrahi pers. comm. November 17, 2012 and October 16, 2011). However, small, isolated groups of wintering red knots may extend along most of the northern coast of South America (L. Niles pers. comm. January 8, 2013).

On the southern (Pacific) coast of Panama, Buehler (2002, p. 43) counted 100 *Calidris canutus* near Panama City and another 100 near Chitré in February 2002. Another researcher, B. Watts (pers. comm. August 28, 2012), has also surveyed this area, and agrees with an estimate of about 200 wintering *C. canutus*. It is not known if all the birds observed in Panama were of the *rufa* subspecies, but three marked birds resighted in Panama were all banded in known *C.*

canutus rufa areas (B. Watts pers. comm. August 28, 2012; Niles *et al.* 2008, p. 73; Buehler 2002, p. 42). Thus, as least some of these birds are considered rufa red knots. Also on the Pacific, Laguna Superior (State of Oaxaca, Mexico) is a recently documented wintering area for *C. canutus* (D. Newstead pers. comm. August 20, 2012), with over 300 birds reported in the winters of 2011 and 2012 (eBird.org 2012). Three birds marked in Texas in April 2010 were resighted at Laguna Superior in February 2012; it is unknown if these three birds or others in this wintering area are *C.c. rufa*, *C.c. roselaari*, or both (Carmona *et al.* in press).

Northwest Gulf of Mexico

Except for localized areas, there have been no long-term systematic surveys of red knots in Texas or Louisiana, and no information is available about the number of knots that winter in northeastern Mexico. From survey work in the 1970s, Morrison and Harrington (1992, p. 77) reported peak winter counts of 120 red knots in Louisiana and 1,440 in Texas, although numbers in Texas between December and February were typically in the range of 100 to 300 birds. Records compiled by Skagen *et al.* (1999) give peak counts of 2,838 and 2,500 red knots along the coasts of Texas and Louisiana, respectively, between January and June over the period 1980 to 1996, but these figures could include spring migrants. Morrison *et al.* (2006, p. 76) estimated only about 300 red knots wintering along the Texas coast, based on surveys in January 2003 (Niles *et al.* 2008, p. 19). Higher counts of roughly 700 to 2,500 knots have recently been made on Padre Island, Texas, during October, which could include wintering birds (Newstead *et al.* in press; Niles *et al.* 2009, p. 1).

Foster *et al.* (2009, pp. 1081, 1084) found a mean daily abundance of 61.8 red knots on Mustang Island, Texas, based on surveys every other day from 1979 to 2007. Similar winter counts (26 to 120 red knots) were reported by Dey *et al.* (2011a, p. 2) for Mustang Island from 2005 to 2011. From 1979 to 2007, mean abundance of red knots on Mustang Island decreased 54 percent, but this may have been a localized response to increasing human disturbance, coastal development, and changing beach management practices (Newstead *et al.* in press; Foster *et al.* 2009, p. 1079) (i.e., it is possible these birds shifted elsewhere in the region).

There are no current estimates for the size of the Northwest Gulf of Mexico wintering group as a whole (Mexico to Louisiana). The best available current estimates for portions of this wintering region are about 2,000 in Texas (Niles 2012a), or about 3,000 in Texas and Louisiana, with about half in each State and movement between them (C. Hunter pers. comm. September 20, 2012).

Southeast United States and Caribbean

Harrington *et al.* (1988, p. 440) reported that the mean count of birds wintering in Florida was 6,300 birds ($\pm 3,400$, one standard deviation) based on 4 aerial surveys conducted from October to January in 1980 to 1982. These surveys covered the Florida Gulf coast from Dunedin to Sanibel-Captiva, sometimes going as far south as Cape Sable (B. Harrington pers. comm. November 12, 2012). Based on these surveys and other work, the Southeast wintering group was estimated at roughly 10,000 birds in the 1970s and 1980s (Harrington 2005a, p. 1).

Based on resightings of birds banded in South Carolina and Georgia from 1999 to 2002, the Southeast wintering population was estimated at 11,700 ± 1,000 (standard error) red knots. Although there appears to have been a gradual shift by some of the southeastern knots from the Florida Gulf coast to the Atlantic coasts of Georgia and South Carolina, population estimates for the Southeast region in the 2000s were at about the same level as during the 1980s (Harrington 2005a, pp. 1, 15). Based on recent modeling using resightings of marked birds staging in Georgia in fall, as well as other evidence, the Southeast wintering group may number as high as 20,000 (B. Harrington pers. comm. November 12, 2012), but field survey data are not available to corroborate this estimate.

Red knots in the Southeast were counted incidentally to the International Piping Plover (*Charadrius melodus*) Census in 2006 and 2011, a ground survey from Louisiana to Virginia (table 4). Because knots were not the focus of the piping plover survey, the level of effort varied and red knot numbers may be potentially underestimated. Table 4 also shows results from Georgia of regular Statewide ground counts conducted during a narrow window in late January or early February (Schneider and Winn 2010, p. 3).

Table 4. Red knot counts in the in the Southeast United States, winters 1997 to 2011
(L. Patrick pers. comm. August 31, 2012; M. Bimbi pers. comm. November 1, 2012;
Niles *et al.* 2006 p. 89)

	Virginia	North Carolina	South Carolina	Georgia	Florida	Louisiana-Alabama-Mississippi (estimates)	Total
1997				411			
1999				175			
2001				4,689			
2002				1,080			
2003				1,247			
2004				586			
2005				3,363			
2006	26	455	583	485	3,020	500	5,069
2007				1,083			
2008				208			
2009				1,748			
2010				577			
2011		157	1,201	1,160	1,046	250 to 375	3,814 to 3,939

Florida

Extensive data for Florida are available from the International Shorebird Survey and other sources. However, geographic coverage has been inconsistent, ranging from 1 to 29 sites per year from 1974 to 2004. Statewide annual totals ranged from 5 knots (1 site in 1976) to

7,764 knots (7 sites in 1979). The greatest geographic coverage occurred in 1993 (4,265 knots at 25 sites) and 1994 (5,018 knots at 29 sites) (Niles *et al.* 2008, pp. 177–180).

Sprandel *et al.* (1997) identified the top 60 sites for wintering shorebirds in Florida and surveyed these areas in 1994. Red knots were found at 27 sites, mainly on the central Gulf coast. Adding the average number of birds counted at each site, these authors estimated a Statewide total of 1,452 red knots, with the following regional estimates: 124 in the Panhandle (3 sites); 0 in the Big Bend (0 sites); 1,092 in the Southwest (18 sites); 183 in the Everglades (4 sites); and 53 in the Northeast (2 sites) (Sprandel *et al.* 1997, p. 33). During frequent surveys of 9 sites along about 55 mi (89 km) of the central Florida Panhandle, Smith (2010, p. 48) found a mean of about 84 wintering red knots in the winter of 2007. Smith (2010, p. 45) covered roughly 25 percent of the Panhandle region as delineated by Sprandel *et al.* (1997, p. 6), with the survey sites clustered on the eastern end of that region.

Niles (2009) conducted winter aerial and ground counts along Florida’s Gulf coast from 2006 to 2010 (table 5), covering essentially the same area in which Harrington *et al.* (1988, p. 440) had reported an average of 6,300 red knots ($\pm 3,400$) in the winters of 1980 to 1982. As the more recent aerial counts were lower, red knot numbers may have decreased in west Florida, perhaps due to birds shifting elsewhere within the larger Southeast wintering region (Harrington 2005a, p. 2). However, a comparison of the geographic coverage of Sprandel *et al.* (1997, p. 6) with Niles (2009, p. 2) suggests that red knot numbers did not change much from 1994 to 2010. The Panhandle and Big Bend regions (124 red knots total in 1994) generally correspond to the Honeymoon Key to St. George Island segment (2 flocks in 2009). The Southwest region (1,092 red knots in 1994) roughly corresponds to the Anclote Key to Cape Romano segment (5-year average of 1,451 from 2006 to 2010).

Table 5. Red knot counts along the Gulf coast of Florida, winters 2006 to 2010
(Niles 2009, p. 4; Dey *et al.* 2011a, p. 2)

Survey Segment	2006	2007	2008	2009	2010
Florida Gulf coast, Honeymoon Key to St. George Island (aerial)				2 flocks (Cedar Key and St. Mark’s National Wildlife Refuge)	
Florida Gulf coast, Anclote Key to Cape Romano (aerial)	2,301	1,530	515	1,532	1,378
Florida Gulf coast, Anclote Key to Cape Romano (ground)	2,142		458	1,463	
Florida Gulf coast, Cape Romano to Cape Sable (aerial)		0	0	0	Included in the total for Anclote Key to Cape Romano

Other Areas

Small numbers of wintering red knots have been reported from Maryland, United States, to Nova Scotia, Canada (Burger *et al.* 2012b, p. 6; BandedBirds.org 2012; eBird.org 2012; H. Hanlon pers. comm. November 22, 2012; A. Dey pers. comm. November 19, 2012), but no systematic winter surveys have been conducted in these northern areas. In surveys of 5 sites within North Carolina's Outer Banks in 1992 and 1993, Dinsmore *et al.* (1998, p. 178) found over 500 red knots per year.

Two recent winter estimates are available for the central Gulf of Mexico. As shown in table 4, 250 to 500 knots were counted from Alabama to Louisiana during the International Piping Plover Censuses in 2006 and 2011 (L. Patrick pers. comm. August 31, 2012). From work related to the Deepwater Horizon oil spill, an estimated 900 red knots were reported from the Florida Panhandle to Mississippi (C. Hunter pers. comm. September 20, 2012). Older surveys recorded similar numbers from the central Gulf coast, with peak counts of 752 red knots in Alabama (1971) and 40 knots in Mississippi (1979) (Morrison and Harrington 1992, p. 77).

Numbers of red knots wintering in the Caribbean are essentially unknown, but in the course of piping plover surveys in February 2011 in the Bahamas, 70 red knots were observed on the Joulter's Cays just north of Andros Island, and 7 knots were observed on the Berry Islands. In December 2012 (i.e., winter 2013), 52 red knots were observed in the Green Turtle Cay flats in Abaco, Bahamas (M. Jeffery pers. comm. February 13, 2013). Roughly 50 red knots occur annually on Green Turtle Cay (eBird.org 2012; T. Pover pers. comm. December 9, 2012).

Spring Stopover Areas

Records of migrating red knots have been collected at many sites along the Atlantic coast. Not all migration areas are well surveyed, and considerable turnover of individuals occurs as birds migrate through an area. Consequently, using counts of migrating red knots as a basis for population estimates may lead to inaccuracies due to errors associated with turnover or double-counting. However, long-term counts made at a specific location are good indicators of usage trends for that area and, considered together, may reflect trends in the overall population of the red knot.

South America

Peak counts of red knots declined at three South American stopover sites from the 1990s through the mid-2000s (table 6). Although trends at stopover areas can reflect changing usage of the site, the timing of these declines over roughly the same period as those in Tierra del Fuego and Delaware Bay (late 1990s to early 2000s) is more suggestive of a decrease in the overall subspecies. At Fracasso Beach on Península Valdés in Argentina, ground surveys were conducted weekly from February through April (González 2005, p. 4). At Bahía San Antonio in Argentina, the surveys were ground-based counts conducted January to April, weekly through 1999, but varying from daily to every 10 days from 2000 to 2005 (González 2005, p. 4). Counts at Lagoa do Peixe in Brazil were obtained during expeditions that covered the peak spring passage in April (Niles *et al.* 2008, p. 58). Other observers noted 5,000 red knots at Lagoa do

Peixe in April 2005 (Fedrizzi and Carlos *in* Lanctot 2009, p. 132) suggesting that usage of this site had partially rebounded.

Table 6. Peak counts of red knots at two Atlantic coast stopover sites in South America, spring 1990 to 2005 (Fedrizzi and Carlos *in* Lanctot 2009, p. 132; Niles *et al.* 2008, p. 58; González 2005, p. 14)

	Fracasso Beach, Argentina	Bahía San Antonio, Argentina	Lagoa do Peixe, Brazil
1990		19,700	
1992		15,000	
1994	8,000		
1995	2,625		10,000
1996	3,200	20,000	6,200
1997	2,000	15,000	7,500
1998		9,000	5,500
1999	3,020	10,500	7,000
2000	3,000	10,000	
2001		7,000	1,500
2002	80	12,000	1,200
2003	1,000	5,000	900
2004	2,000	5,500	
2005	500	6,500	5,000*

*Different observer(s) than the rest of the data for Lagoa do Peixe.

Virginia

Aerial surveys of the entire chain of barrier island beaches in Virginia have been conducted since 1995 using consistent methods and observers (table 7). Although the number of surveys has varied from one to six per year, the aerial survey effort has consistently covered the peak period during the last week of May (B. Watts pers. comm. November 15, 2012). Since 2007, Karpenty *et al.* (2012, p. 2) have estimated total red knots based on ground counts at 100 to 150 randomly selected points throughout Virginia’s barrier island beaches including peat banks, with each location visited from one to three times per stopover season (table 8). Although the recent ground surveys show an upward trend, the aerial counts have been relatively steady since the mid-1990s. Because of differences in methodology and timing, the two data sets are not comparable.

Because birds pass in and out of a stopover area, the peak count (the highest number of birds seen on a single day) for a particular year is lower than the total passage population (i.e., the total number of birds that stopped at that site over the course of that migration season). Using resightings of marked birds, several attempts have been made to estimate the total passage population of Virginia through mathematical modeling (table 9).

Table 7. Peak counts of red knots in Virginia from aerial surveys, spring 1995 to 2012 (B. Watts pers. comm. November 15, 2012)

Year	Count
1995	7,958
1996	8,922
2005	9,150
2006	5,783
2007	5,939
2008	7,802
2009	6,079
2010	8,167
2011	6,086
2012	8,482

Table 8. Estimated peak abundance of red knots in Virginia from ground sampling, spring 2007 to 2012 (Karpanty *et al.* 2012; Cohen *et al.* in prep)

Year	Estimate	95 Percent Confidence Interval
2007	3,888	1,279 to 6,497
2008	5,176	1,926 to 8,426
2009	6,046	2,535 to 9,558
2010	6,271	2,496 to 10,045
2011	9,257	3,208 to 15,307
2012	11,781	5,236 to 18,327

Table 9. Estimates of total passage population in Virginia, spring 2006 to 2012

Year	Peak Count	Estimated Passage Population	95 Percent Confidence Interval	Source
2006	5,783	7,224	6,460 to 7,986	Cohen <i>et al.</i> 2009, p. 942
2006	5,783	9,785		Duerr <i>et al.</i> 2011, p. 12
2007	5,939	8,332	6,924 to 9,740	Cohen <i>et al.</i> 2009, p. 942
2007	5,939	12,611		Duerr <i>et al.</i> 2011, p. 12
2008*	8,465	14,688		Duerr <i>et al.</i> 2011, p. 12
2009	6,079	13,398		Duerr <i>et al.</i> 2011, p. 12
2010*	8,172	12,959		Duerr <i>et al.</i> 2011, p. 12

* Peak count differs slightly from peak counts reported by B. Watts (pers. comm. November 15, 2012).

Delaware Bay

Aerial surveys have been conducted in Delaware Bay since 1981 (table 10). Methods and observers were consistent from 1986 to 2008. The methodology during this period involved weekly counts; thus, it was possible the absolute peak number of birds was missed in some years. However, since most shorebirds remain in Delaware Bay at least a week, it is likely that the true peak was captured in most years (Clark *et al.* 1993, p. 700). The surveys covered consistent areas of New Jersey and Delaware from the first week of May to the second week of June. All flights were conducted 3 to 4 hours after high tide, a period when birds are usually feeding on the beaches (Clark *et al.* 2009, p. 87).

Methodologies and observers changed several times from 2009 to 2012. Flights are now flown only during the end of May. In addition, aerial counts for 2010 and 2011 were adjusted with ground counts from Mispillion Harbor, Delaware to more accurately reflect large concentrations of birds at this key site (Dey *et al.* 2011a, p. 4). Further, problems in 2009 and 2012 prevented accurate aerial counts, and ground counts have been substituted. Caution should be used in comparing ground and aerial counts (see Research Methods, above, and Laursen *et al.* 2008, p. 165). Differences between the two methods may account for markedly higher counts in 2009 and 2012. Although aerial counts had typically been higher than ground counts prior to 2009, this was likely because many areas that could be surveyed by air were inaccessible on the ground. Since 2009, ground survey crews have attempted to minimize the access problem by using boats in remote areas (A. Dey pers. comm. April 26, 2013; K. Clark pers. comm. March 4, 2013).

As with other stopover areas, it is impossible to separate population-wide trends from trends in usage of a particular spring site. Thus, differences in the number of birds in Delaware Bay may reflect stopover patterns rather than (or in addition to) trends in the overall red knot population (Clark *et al.* 1993, p. 702). However, the pattern and timing of these declines in Delaware Bay relative to Tierra del Fuego and other stopovers is suggestive of a decrease in the overall population. Comparing 4 different time periods, average red knot counts in Delaware Bay declined from 59,946 (1981 to 1983), to 46,560 (1986 to 1992), to 40,709 (1993 to 2002), to 16,287 (2003 to 2012). Average counts for the last time period (2003 to 2012) are about 70 percent lower than during the earliest period (1981 to 1983).

Because birds pass in and out of a stopover area, the peak count for a particular year is lower than the total passage population. Using resightings of marked birds, several attempts have been made to estimate the total passage population of Delaware Bay through mathematical modeling (table 11).

Table 10. Peak counts of red knots in Delaware Bay from aerial and ground surveys, spring 1991 to 2012 (A. Dey pers. comm. October 12, 2012; Dey *et al.* 2011a, p. 3; Clark *et al.* 2009, p. 88; Kochenberger 1983, p. 1; Dunne *et al.* 1982, p. 67; Wander and Dunne, 1982, p. 60)

Year	Peak Count	Year	Peak Count
1981*	67,450	1998	50,360
1982	95,530	1999	49,805
1983	16,859	2000	43,145
1986	58,156	2001	36,125
1987	38,790	2002	31,695
1988	34,750	2003	16,255
1989	95,490	2004	13,315
1990	45,860	2005	15,345
1991	27,280	2006	13,445
1992	25,595	2007	12,375
1993	44,000	2008	15,395
1994	52,055	2009**	24,000
1995	38,600	2010	14,475
1996	19,445	2011	12,804
1997	41,855	2012**	25,488

*Only New Jersey was surveyed in 1981. For reference, the total numbers of red knots in Delaware Bay was relatively evenly distributed between New Jersey and Delaware from 1986 to 1992 (Clark *et al.* 1993, p. 700), suggesting that the true peak count for the bay could have been roughly double the number recorded in 1981.

** Ground counts. For 2009, the actual peak ground count was 27,187, but Niles *et al.* (2010b, p. 10) chose to report 24,000 as the low end of an estimated 10 percent error range. The peak ground count in 2012 was also adjusted down (from roughly 29,400 to 25,458) based on concerns that some flocks in New Jersey were double counted.

Table 11. Estimates of total passage population in Delaware Bay, spring 1998 to 2012

Year	Peak Count	Estimated Passage Population	Range	Source
1989	95,490	152,900	±50,300 Standard Deviation	Harrington 2001, p. 22
1998-2001	36,125-50,360	77,000 (per year)	28,000 to 126,000 (per year) 95% Confidence Interval	Atkinson <i>et al.</i> 2001, p. 11
2004	13,315	17,108	14,515 to 19,701 95% Confidence Interval	Cohen <i>et al.</i> 2009, p. 942

Table 11. Estimates of total passage population in Delaware Bay, spring 1998 to 2012

Year	Peak Count	Estimated Passage Population	Range	Source
2004	13,315	17,707	12,800 to 22,614 95% Confidence Interval	Gillings <i>et al.</i> 2009, p. 58
2006	13,445	19,555	17,927 to 21,184 95% Confidence Interval	Cohen <i>et al.</i> 2009, p. 942
2012	25,458	44,680	42,610 to 46,960 95% Confidence Interval	J. Lyons pers. comm. August 10, 2012

Atlantic Coastwide United States

Beginning in 2006, coordinated red knot surveys have been conducted from Florida to Delaware Bay during 2 consecutive days from May 20 to 24 (table 12). This period is thought to represent the peak of the red knot migration. There has been variability in methods, observers, and areas covered. From 2006 to 2010, there was no change in counts that could not be attributed to varying geographic survey coverage (Dey *et al.* 2011a, p. 12); thus, we do not consider any apparent trends in these data before 2010.

Table 12. Red knot counts along the Atlantic coast of the United States, May 20 to 24, 2006 to 2012 (A. Dey pers. comm. October 12, 2012; Dey *et al.* 2011a, p. 12)

State	2006	2007	2008	2009	2010	2011	2012
New Jersey	7,860	4,445	10,045	16,229	8,945	7,737	23,525
Delaware	820	2,950	5,350		5,530	5,067	3,433
Maryland			663	78	5	83	139
Virginia	5,783	5,939	7,802	3,261	8,214	6,236	8,482
North Carolina	235	304	1,137	1,466	1,113	1,868	2,832
South Carolina		125	180	10	1,220	315	542
Georgia	796	2,155	1,487		260	3,071	1,466
Florida			868	800	41		10
Total	15,494	15,918	27,532	21,844	25,328	24,377	40,429

Because red knot numbers peak earlier in the Southeast than in the mid-Atlantic (M. Bimbi pers. comm. June 27, 2013), the late-May coast-wide survey data likely reflect the movement of some birds north along the coast, and may miss other birds that depart for Canada from the Southeast along an interior (overland) route prior to the survey window. Thus, greater numbers of red knots may utilize Southeastern stopovers than suggested by the data in Table 12. For example, a peak count of over 8,000 red knots was documented in South Carolina during spring 2012 (South Carolina Department of Natural Resources 2012, p. 24). Peak counts of over 1,000 birds were observed at just a single Florida site (Cape Romano) between April 1 and June 10 of 1983, 1987, and 1989, and several other Florida sites routinely supported hundreds of red

knots (peak counts) during spring from the 1980s through the 2000s (Niles *et al.* 2008, pp. 173–176). Dinsmore *et al.* (1998, pp. 174, 178) found a mean of 1,363 (± 725) red knots in North Carolina during spring 1992 and 1993, with a peak count of 2,764 birds.

Fall Stopover Areas

Few regular surveys are conducted in fall because southbound red knots tend to be less concentrated than during winter or spring. No regular surveys are conducted in Hudson Bay or James Bay, Canada. However, aerial surveys of the Ontario coastlines of James Bay and Hudson Bay in the late 1970s produced totals of 7,000 to 10,000 red knots, with more recent surveys reporting 5,000 to 10,000 (Morrison and Harrington 1992, p. 74). There were numerous reports of 100 to 1,300 red knots at James Bay (Ontario) in August 2011, and one report of nearly 4,000 birds in this area (eBird.org 2012). Based on intensive field work and analysis of resightings of marked birds, at least 7,200 red knots are estimated to have used the Mingan Islands Archipelago (Canada) in fall 2008 (USFWS 2011b, p. 8; Wilson *et al.* 2010, p. 192).

Using daily checklist data submitted by birdwatchers during fall migration 1976 to 1998 in southern Quebec, Canada, Aubry and Cotter (2001, pp. 21–22) found a statistically significant decline in sightings of red knots. In surveys of Eastern Canada (New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland), fall counts of red knots dropped 5.3 to 15.3 percent per year (depending on the statistical method used) from 1974 to 1991, with considerably greater decreases later in the study period; however, the findings were not statistically significant (Morrison *et al.* 1994, pp. 436, 439). Analyzing more years from this same data set from 1974 to 1998, Morrison *et al.* (2001, pp. 35–36) found a statistically significant (p less than 0.05) annual decrease of 17.6 percent.

Fall peak counts from International Shorebird Survey sites along the U.S. Atlantic coast ranged from 6,000 to 9,000 red knots during the mid- to late-1970s (Morrison and Harrington 1992, p. 75). In a review of numbers and distribution of red knots on the Massachusetts coast during southward migration, Harrington *et al.* (2010b, pp. 188, 190) found that overall red knot numbers increased from the late 1940s to the early 1970s, especially on the mainland (western Cape Cod Bay), with a smaller increase on outer Cape Cod (see Historic Distribution and Abundance, above). After 1975, counts declined significantly on the mainland, but increased significantly on outer Cape Cod (Harrington *et al.* 2010a, p. 190). Evidence suggests that both the mainland and the Cape Cod areas were historically used by knots having Argentina-Chile destinations, but that recently the Cape Cod locations have increasingly been used by knots with wintering destinations in the Southeast United States, thus balancing out the declining numbers of knots with Argentina-Chile wintering destinations (Harrington *et al.* 2010a, p. 188). By 2008, peak counts of Argentina-Chile knots in Massachusetts had fallen to about 1,000 birds, while birds from the Southeast group increased to about 800 (Harrington *et al.* 2010b, p. 361).

No regular counts are currently conducted in Massachusetts (S. Koch pers. comm. November 19, 2012), but flocks of over 100 knots are routinely reported from Monomoy National Wildlife Refuge (eBird.org 2012). About 1,500 red knots were present in Avalon on the Atlantic coast of New Jersey in the fall of 2011 (USFWS 2011c, p. 27). Also on the Atlantic coast of New Jersey, hundreds of red knots are regularly reported from North Brigantine and Stone Harbor, sometimes in flocks of over 500 (eBird.org 2012). Islands at the mouth of the

Altamaha River, Georgia, support the only known late summer and fall staging site on the east coast of the United States, attracting as many as 12,000 knots at one time (Schneider and Winn 2010, p. 2).

The Caribbean islands may be an important refuge for shorebirds migrating during storms (Nebel 2011, p. 217). In the Bahamas, up to 50 knots have been reported from Abaco in October and November (eBird.com 2012). In the Bahamas in October 2012, 124 red knots were documented on the Joulter Cays, one with a band, and 43 were observed on the Berry Islands, some roosting in mangroves (M. Jeffery pers. comm. February 13, 2013). Puerto Rico and the some of the Lesser Antilles (e.g., St. Croix in the U.S. Virgin Islands, Guadeloupe, Barbados, and Trinidad) are also used as fall stopover areas (Niles *et al.* 2010a, pp. 125–126; eBird.org 2012), with birds occurring regularly but in small numbers. In Guadeloupe, the red knot is an uncommon but regular visitor during fall migration, typically in small groups of up to 3 birds, but as many as 16 have been observed in a flock (A. Levesque pers. comm. October 11, 2011). In Barbados, the red knot is a fairly regular fall transient in small numbers, usually occurring as single individuals and in small groups, but very exceptionally knots may occur in flocks of up to a dozen birds, and a group of 63 birds was recorded in 1951. Detailed records from 1950 to 1965 show an average of about 20 red knots per year in Barbados (Hutt and Hutt 1992, p. 70). Flocks of up to a dozen red knots were reported from Trinidad each year from 2008 to 2011, with multiple sightings each fall (eBird.org 2012).

In late August 2012, 1,700 knots were observed in rice fields near Mana, French Guiana, and a large number of these birds had been marked in the Chile portion of Tierra del Fuego (Niles 2012b). Based on this survey and recent geolocator results, French Guiana is emerging as an important fall stopover area (Niles 2012b). Adjacent Suriname and Brazil are also used in fall (Niles *et al.* 2010a, pp. 125–127; Spaans 1978, p. 72), but little information is available regarding the numbers of birds in these areas. In Suriname, a total of nearly 160 red knots were counted during 2 surveys conducted in late August of 1970 to 1973. Larger red knot numbers apparently do not occur in Suriname as the habitat is not ideal (B. Harrington pers. comm. March 31, 2006); see Migration and Wintering Habitat, above. In September 2007, the average peak count of red knots at Cajuais Bank in the Brazilian State of Ceará was 434 ± 95 (Carlos *et al.* 2010, pp. 10–11). During aerial surveys of Panama Bay in the fall of 1997, Watts (1998, p. 11) documented a peak count of 2,460 *Calidris canutus* in September; the subspecies composition is unknown. Watts (1998, p. 38) reported that *C. canutus* counts in Panama were likely underestimated.

Summary—Population Surveys and Estimates

We have carefully reviewed available survey data from areas regularly used by substantial numbers of red knots in spring, fall, and winter. For some areas, available data are insufficient to substantiate any conclusions regarding trends over time. For other areas, there are apparent trends, but associated with relatively low confidence. For a few key areas, the consistency of geographic coverage, methodologies, and surveyors lead us to greater confidence in apparent trends.

- Patagonia and Tierra del Fuego wintering region – declines through the 2000s, possibly stabilizing at a relatively low level since 2008, associated with higher confidence.
- North-Central Brazil wintering region – apparent decline comparing surveys with similar methods, coverage, and observers in 1982 and 2011, associated with lower confidence due to the availability of only two data points, and the complexity of the shoreline that makes surveying difficult. Partial surveys in the winters of 2005 and 2007 suggest that any declines occurred after 2005.
- Northwest Gulf of Mexico wintering region – insufficient data for trend analysis.
- Southeast wintering region – apparent decline on Florida’s Gulf coast comparing aerial surveys from 1980 to 1982 with similar surveys (using different surveyors) of approximately the same area from 2006 to 2010, associated with lower confidence because birds may have simply shifted elsewhere within this large wintering region. The two regionwide survey efforts to date (from the 2006 and 2011 piping plover surveys) are associated with lower confidence inherent in the methodology (red knots are not the focus of this survey), but do tend to support the perception that knots shift from state to state within this region among years. A long-term data set from Georgia, showing wide inter-annual fluctuations, also supports this perception. Data from the Caribbean are insufficient to infer any trends. Comparing ground surveys of Florida’s Gulf coast in 1994 to aerial surveys of about this same area from 2006 to 2010, red knot counts were roughly the same over this time period.
- South American spring stopover sites – apparent declines at three key stopover sites from the late 1990s through the mid-2000s, associated with moderate confidence because we have little information regarding the consistency of methodologies or surveyors and because no data are available after 2005.
- Virginia barrier islands spring stopover area – no apparent trend based on aerial surveys since 1995, associated with high confidence. A newer data set based on ground surveys suggests an increase since 2007.

- Delaware Bay spring stopover area – highly variable data set showing possible declines in the 1990s, and more consistent and substantial declines through the mid-2000s, associated with high confidence during the core years of 1986 to 2008. Numbers may have stabilized from 2009 to 2012, but we have lower confidence in trends over this later period due to multiple shifts in methodology and surveyors.
- Atlantic coast spring window survey – apparent increase from 2010 to 2012, but associated with lower confidence because, despite improvements, methodology and geographic coverage are still stabilizing and because only 3 years of (relatively consistent) data are available.
- Fall stopover areas – insufficient data for trend analysis in most areas. Since the 1970s, there were probable declines in some parts of eastern Canada and changes in red knot usage of Massachusetts (mainland versus Cape Cod, proportion of birds bound for Southeast versus Argentina-Chile wintering destinations).

In conclusion, we have high confidence in two data sets from key red knot areas, Tierra del Fuego and Delaware Bay, showing declines over roughly the same period. Data sets associated with lower confidence from the Brazil wintering region and three South American spring stopovers also suggest declines roughly over this same timeframe. We conclude that the Virginia spring stopover was stable during this period (the 2000s). We do not conclude that the Southeast wintering region declined, due to the likelihood that knot usage shifted geographically within this region from year to year. In summary, our analysis of the best available data concludes that an overall, sustained decline of red knot numbers occurred in the 2000s, and that red knot populations may have stabilized at a relatively low level in the last few years. Inferring long-term population trends from various national or regional datasets derived from volunteer shorebird surveys and other sources, Andres (2009, p. 6) and Morrison *et al.* (2006, pp. 71, 76, 77) also concluded that red knot numbers declined, probably sharply, in recent decades.