

more rufous above than *C. c. rufa* (Harrington 2001). The vent and lower belly, however, are similarly light colored as on *C. c. rufa*, but may be marked with black (Harrington 2001).

MALES—*CALIDRIS CANUTUS ISLANDICA*

Subspecies *C. c. islandica* is similar in appearance to *C. c. rogersi*, but with yellowish fringes on the mantle and has medium-chestnut underparts (Hayman et al. 1986). Coloration of this subspecies is also similar to that of *C. c. canutus*, but with less intense rufous on the underparts, more yellow on the hindneck with more narrow black marks and paired squarish dots of rufous on the tips of the scapulars (Harrington 2001). This subspecies also appears more richly colored than *C. c. rufa* (Harrington 2001).

MALES—*CALIDRIS CANUTUS ROSELAARI*

The coloration of the dorsal plumage of *roselaari* is similar to that of *canutus*, but darker and with more variegated pattern. Ventral coloration is similar to *C. c. rufa*, particularly with respect to the amount of white plumage on the lower belly and vent. Some evidence shows that this subspecies, in the southeastern Atlantic U.S., shows prebasic molt of ventral and dorsal body feathers, as well as actively molting primaries and rectrices during August and September in contrast to other subspecies in the northeastern U.S. Based on analysis of museum specimens, this subspecies is also longer winged than other subspecies (Harrington 2001).

FIRST ALTERNATE PLUMAGE

This is extremely variable among both individuals and subspecies. Individuals that molt few feathers may appear as basic-plumaged birds, but with worn and frayed primaries. Individuals that undergo a more extensive molt may appear as intermediates between definitive basic and definitive alternate plumages.

JUVENILE PLUMAGE

Juvenile plumage is similar to definitive basic plumage, and no difference occurs between the sexes (Harrington 2001). The mantle, scapular and covert feathers have boldly pencilled sub-marginal lines and white fringes which give a characteristic scaly appearance (Hayman et al. 1986). The upper breast is suffused in buff with fine brown streaks and dots (Harrington 2001). The underparts appear suffused in olive to gray ash, slightly darker than in definitive basic plumage (Harrington 2001).

HATCHLINGS

Hatchlings have downy plumage with dull, blackish brown underparts speckled with rows of white or cinnamon hourglass-shaped dots. The plumage lightens on the sides and underparts with a buffy-grayish wash on the breast. The crown is dark with some stripes below the eye, the supercillium, cheek and auriculars are mottled and the chin is white. The bill is blue-gray with a dusky tip; the legs are grayish yellow with dusky spots. (Harrington 2001).

DISTRIBUTION IN TIME AND SPACE

THE ANNUAL CYCLE

The diagrammatic representation of the annual cycle of a Red Knot wintering in Tierra del Fuego (Fig. 5) is based on the approximate dates that Red Knots occur at different sites as more fully set out elsewhere in this review and is merely intended to assist the reader. It is not suggested that any individual Red Knots make exactly the movements shown.

Soon after the chicks hatch in mid-July, the females leave the breeding grounds and start moving south. Thereafter, parental care is provided solely by the males, but about 25 d later (around 10 August) they also abandon the newly fledged juveniles and move south. Not long after, they are followed by the juveniles, which start to appear along the northeast coast of the U.S. in the second half of August. Throughout the flyway, the adults generally precede the juveniles as they move south from stopover to stopover. At each, the adults gradually replace their red breeding plumage with white and gray, but do not molt their flight or tail feathers until they reach their winter quarters.

During southward migration and in some parts of the winter quarters, the number of juveniles gives a good indication of breeding success which tends to show some correlation with predator-prey cycles and weather conditions on the arctic breeding grounds. In some years, when there are many arctic predators and few prey (mainly lemmings *Lemmus* and *Dicrostonyx*), and/or when there is unseasonably cold weather, breeding success may be extremely low and many adults may abandon their breeding territories and move south earlier than usual (van de Kam et al. 2004). In other years, good breeding conditions may mean that substantial proportions of all Red Knots in the flyway are juveniles. However, it seems that although some juveniles of the Tierra del Fuego wintering population migrate all the way to Tierra del Fuego, others

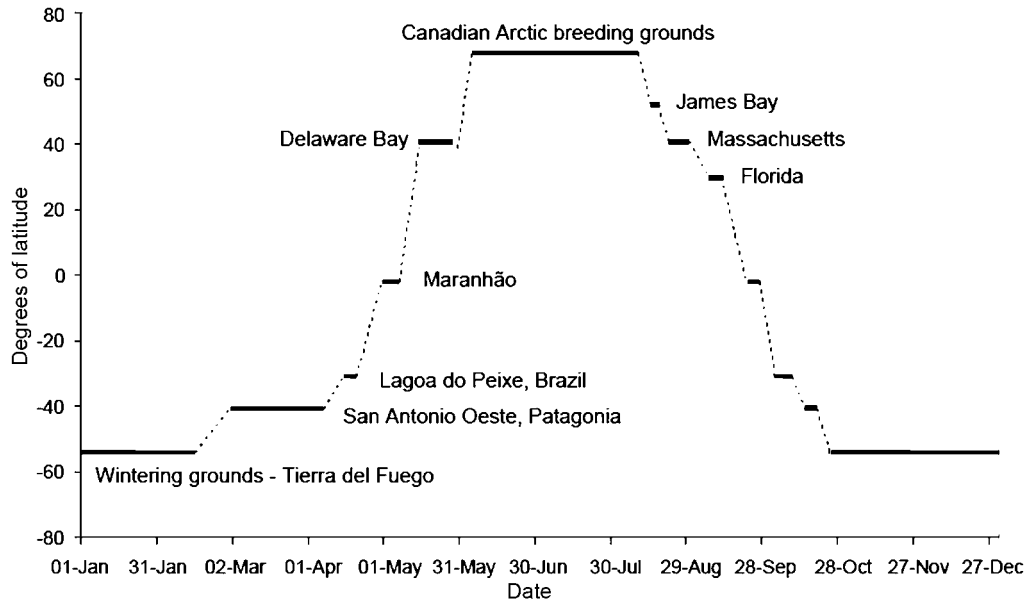


FIGURE 5. Diagrammatic representation of the annual cycle of a typical Tierra del Fuego wintering Red Knot (*Calidris canutus rufa*) in terms of latitudinal location and date. Horizontal lines represent periods when birds stay on the breeding or wintering grounds or stopover while on migration; dotted lines represent largely non-stop migratory flights.

winter farther north in South America (P. M. González, unpubl. data).

Arrival in Tierra del Fuego is from late September through October. As soon as they arrive, the adults start their annual molt of flight and tail feathers which they finish in January. Although a few may depart before the end of January, the main movement north is not until February. At each stopover as they move north along the coast of South America they molt into breeding plumage with most of the change from white/gray to red taking place during March and early April. From Maranhão in northern Brazil, most probably fly directly to Delaware Bay or to the southeastern coast of the U.S. In Delaware Bay, they feed heavily on horseshoe crab eggs, and in an average of 10–14 d, almost double their weight and depart at the end of May on the 3,000 km flight to their arctic breeding grounds (S. Gillings et al., unpubl. data). This stopover duration is much shorter than final stopovers by other populations of Red Knots (21–28 d) and reflects the rapid mass gains possible when feeding on *Limulus* eggs (4.9 g/d) compared with other prey (2.7–3.0 g/d; S. Gillings et al., unpubl. data; Piersma et al. 2005).

It is thought that most or all of the juveniles of the Tierra del Fuego population remain in South America during their first year of life.

Those that have spent the austral summer in Tierra del Fuego move farther north, while others that have wintered in the mid- or northern latitudes of the continent may move relatively little. Eventually, in about September, these birds move to Tierra del Fuego in advance of most of the returning adults and commence their first molt of flight and tail feathers. After spending the austral summer in Tierra del Fuego, these immatures migrate with the rest of the adults to the Arctic where they breed for the first time at 2 yr of age.

BREEDING RANGE

Morrison and Harrington (1992) considered that the breeding range of *C. c. rufa* extended across the central Canadian Arctic from Southampton Island to Victoria Island, but pointed out that uncertainty existed as to whether it occurred in all parts of this range owing to lack of coverage. In May 1999, biologists from the New Jersey Department of Environmental Protection Division of Fish and Wildlife (NJDFW) and the Royal Ontario Museum (ROM) attached radio transmitters to 65 Red Knots passing through Delaware Bay on their way to the breeding grounds. In July 1999, aerial radio tracking was carried out on Southampton Island where eight birds were

relocated. Six were found in the barren tundra uplands characteristic of most of the island, but two were found in the coastal wetlands. In a subsequent ground search, the nest of one radio-tagged *C. c. rufa* was located.

Using land cover characteristics at the sites where the eight Red Knots were relocated in 1999, biologists with the NJDFW, ROM and Rutgers University Center for Remote Sensing and Spatial Analysis (CRSSA) developed a simple model based on three main characteristics: elevation, amount of vegetation cover, and distance to ocean coast. Using land cover images of the entire eastern Arctic the team created a map

predicting the location of Red Knot habitat (Fig. 6). Additional refinements to the habitat predictive model were added based on results from the radio-tracking work.

Over the next 3 yr, 200 more transmitters were attached to birds which were tracked throughout the Canadian Arctic as far west as Victoria Island, east to Baffin Island, north to Prince of Wales Island and south to Coats and Mansel Islands. In all, 20 birds were relocated, all within areas predicted to be Red Knot habitat. Additional refinements to the habitat predictive model were added based on the new relocated birds.

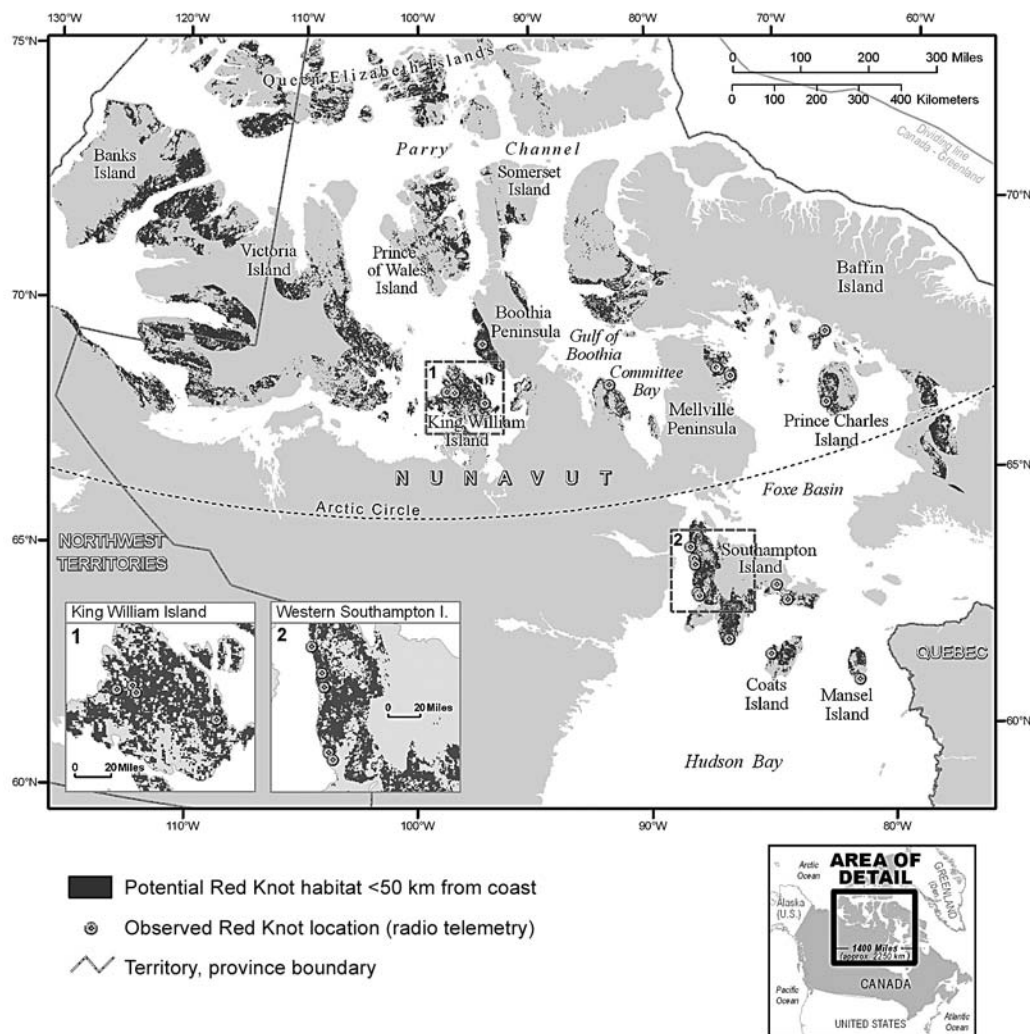


FIGURE 6. Predicted Red Knot nesting habitats based on land cover types in the Canadian Arctic and point locations of Red Knots obtained by radio telemetry (Red Knot data from New Jersey Department of Environmental Protection Endangered and Nongame Species Program; potential Red Knot habitat data from Grant F. Walton Center for Remote Sensing and Spatial Analysis (CRSSA) Rutgers University; boundary data from GeoCratis Canada).

In summary, our knowledge of the breeding range of *C. c. rufa* is sparse and we can only be sure that it extends to those places where birds have been found as shown in Fig. 6. There are no data to indicate whether the range or distribution has changed over time.

WINTER (NON-BREEDING) RANGE

After breeding, all Red Knot populations migrate south to spend the northern winter in large flocks at a relatively small number of key intertidal wetlands. These invariably provide hard-shelled bivalves as the Red Knots' main food resource. These are swallowed whole, the shells being crushed in the gut and excreted by defecation.

Red Knots that are or might be of the *C. c. rufa* subspecies winter in four distinct coastal areas of the Western Hemisphere (Fig. 7): (1) the southeastern U.S. (mainly Florida and Georgia, with smaller numbers in South Carolina), (2) Texas, (3) Maranhão in northern Brazil, and (4) Tierra del Fuego (mainly Bahía Lomas in Chile and Bahía San Sebastián and Río Grande in Argentina with smaller numbers northwards along the coast of Patagonia). Other Red Knots, presumed to be *C. c. roselaari* winter on the Pacific coast of California and Baja California, parts of the Pacific northwest coast of Mexico in

the Gulf of California, and probably also farther south (Morrison and Ross 1989; Morrison et al. 1992, 2004; Page et al. 1997, 1999; Baker et al. 2005a, 2005b).

In the 1982–1985 survey of South America (Morrison and Ross 1989), Red Knots were found wintering along the coast of Patagonia from Tierra del Fuego north to Buenos Aires Province in Argentina. However, because the southern wintering population has declined, only extremely low numbers of Red Knots have been observed in Patagonia north of Tierra del Fuego, with no birds found in some years (Morrison et al. 2004).

In the southern U.S., the wintering Red Knot population is believed to be distributed variably from year-to-year between Florida, Georgia, and South Carolina (Fig. 8), depending on invertebrate prey abundance (B. A. Harrington and Winn, unpubl. data).

The number of wintering Red Knots in Georgia varies between and within years. Results of an annual winter ground survey of the entire Georgia coast since 1996 during the last 2 wk of January into early February show the minimum number of Red Knots to be in the hundreds and the highest to be nearly 5,000. The distribution of wintering Red Knots is generally unpredictable and dispersed over much of the barrier coast and appears to be linked

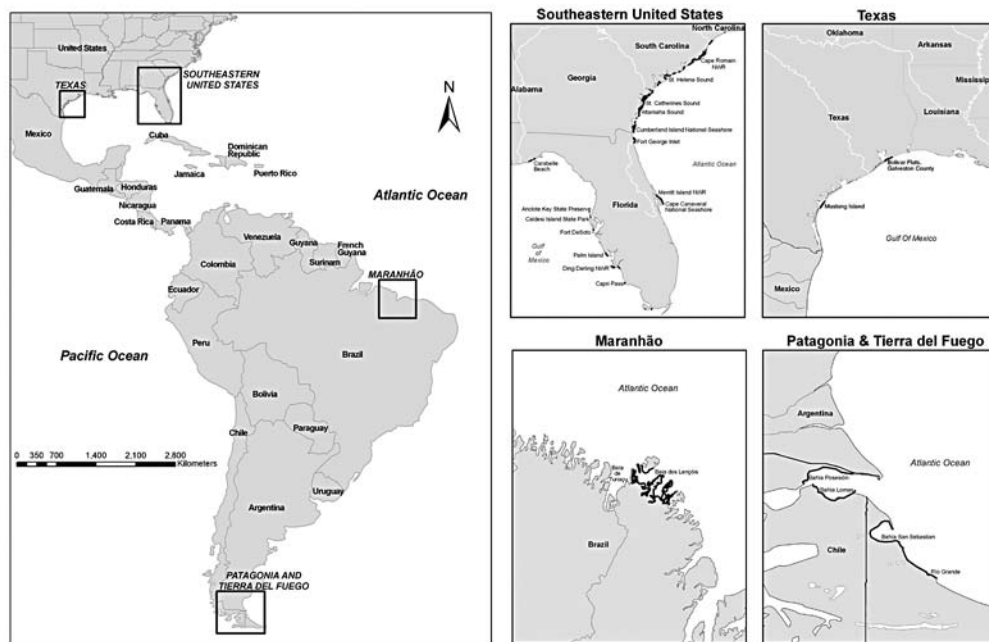


FIGURE 7. Red Knot wintering areas in the Western Hemisphere. Each area boxed in the left map is shown in greater detail and delineated in black.



FIGURE 8. International Shorebird Survey Data (ISS) showing distribution of Red Knots in winter in the U.S. before year 2000 (upper) and during 2000–2004 (lower). The level of ISS survey effort declined after 2000; therefore, the differences in numbers before and since 2000 may partly represent reduced survey effort (Brian Harrington, pers. comm.).

closely with the abundance and availability of dwarf surf clams (*Mulinia lateralis*). The Red Knots feed primarily on dwarf surf clams and secondarily on coquina clams (*Donax variabilis*).

In Florida, frequent beach replenishment in areas such as Fort Myers and Estero Island (N. Douglass, pers. comm.) may cause the loss of invertebrate prey populations and displace wintering Red Knots to more productive foraging areas elsewhere in Florida and Georgia.

In Texas, the wintering population was of the order of 3,000 during 1985–1996 with the largest numbers occurring on the Bolivar flats (Skagen et al. 1999). However, this population seems to have declined. The only recent count of any size is of 300 in January 2003 (B. A. Harrington, unpubl. data).

MIGRATORY RANGE AND MAJOR STOPOVER AREAS

While migrating, all Red Knot populations are dependent on a limited number of stopover sites that provide adequate food resources. These act like stepping stones in that if one is lost because the food supply fails, a whole population of Red Knots may be jeopardized. For the subspecies *C. c. rufa*, Delaware Bay is a particularly vital link in its migration between Tierra del Fuego and the Canadian Arctic, since it is at this final stopover that the birds need to be able to accumulate both fuel for the journey and additional body stores to enable them to survive and attain good breeding condition after arrival in the Arctic.

The southbound 15,000 km migratory journey of *C. c. rufa* begins in August and takes it from its breeding grounds in the central Canadian Arctic through Hudson Bay and James Bay, through some parts of eastern Canada, such as the Mingan Islands in the Gulf of St Lawrence, and through most of the east coast states of the U.S. (Fig. 9). At this time, they tend to use northern sites in Massachusetts, Connecticut, and Rhode Island more than they do in spring. After a final U.S. stopover, they fly to northern Brazil and then on through Argentina to Tierra del Fuego. The majority of the population winters on the main island of Tierra del Fuego, where in one bay in the Chilean sector, Bahía Lomas, most of the population can be found from November to February (Morrison and Ross 1989, Morrison et al. 2004). Other Red Knot populations begin their migration from the Arctic about the same time as the Tierra del Fuego birds, but stop to over-winter in the southeastern U.S. (mainly Florida) and Maranhão, Brazil (Morrison and Ross 1989, Baker et al. 2005b). As discussed in the taxonomy section of this volume, the subspecific status of these populations is uncertain.

In comparison with the southward migration, the northbound flight to the Arctic is more time-constrained and demanding, especially in the northern parts of the route, because it is important for successful breeding and survival that the adults arrive on their arctic breeding grounds at the right time and in good condition for breeding, and with sufficient resources to sustain themselves while arctic food is in short supply.

After departing Tierra del Fuego, major stopover sites are found at Río Gallegos, Península Valdés, San Antonio Oeste, and Punta Rasa in Argentina and Lagoa do Peixe in southern Brazil. From there, the birds fly across Amazonia to a possible last feeding stop in South America in the Maranhão region of northern Brazil (Fig. 10). From Maranhão, the majority fly directly to Delaware Bay, with a smaller proportion making landfall farther south along the U.S. East Coast, anywhere from Florida to Virginia (Fig. 11). The Red Knots that have wintered in Maranhão are also thought to fly directly to the East Coast of the U.S., but it is not known whether they migrate with or at the same time as the birds from Tierra del Fuego. The evidence is sparse, but it is possible that at least some Tierra del Fuego birds migrate directly from Lagoa do Peixe to Delaware Bay, a distance of 8,000 km, which is around the limit of a Red Knot's potential flight range (Harrington and Flowers 1996). Most important stopover sites are depicted in Fig. 12.

Some birds arrive in Delaware Bay in a greatly depleted condition, weighing as much as 30% below their normal fat-free mass. There they spend about 2 wk feeding on horseshoe crab eggs and virtually double their mass. Some of the birds that have spent the winter in Florida pass through Delaware Bay, but it seems that many migrate northward along the Atlantic coast of the U.S. feeding on bivalves (mainly *Donax* and blue mussel spat) and bypass Delaware Bay altogether (P. Atkinson et al., unpubl. data; S. Karpanty, pers. comm.). At the end of May, *C. c. rufa* depart on the last leg of their flight to the Arctic. In the final days before departure, the birds almost cease feeding and undergo physiological changes to prepare for migration including reducing their digestive organs and increasing flight muscle size (Piersma and Gill 1998, Piersma et al. 1999). They leave Delaware Bay heading inland north-northwest toward their breeding grounds. This route takes them across the vast boreal forest and low tundra of Canada, which in late May to early June can be a hostile environment to shorebirds. Many pass through and along the coasts of James Bay and Hudson Bay, although

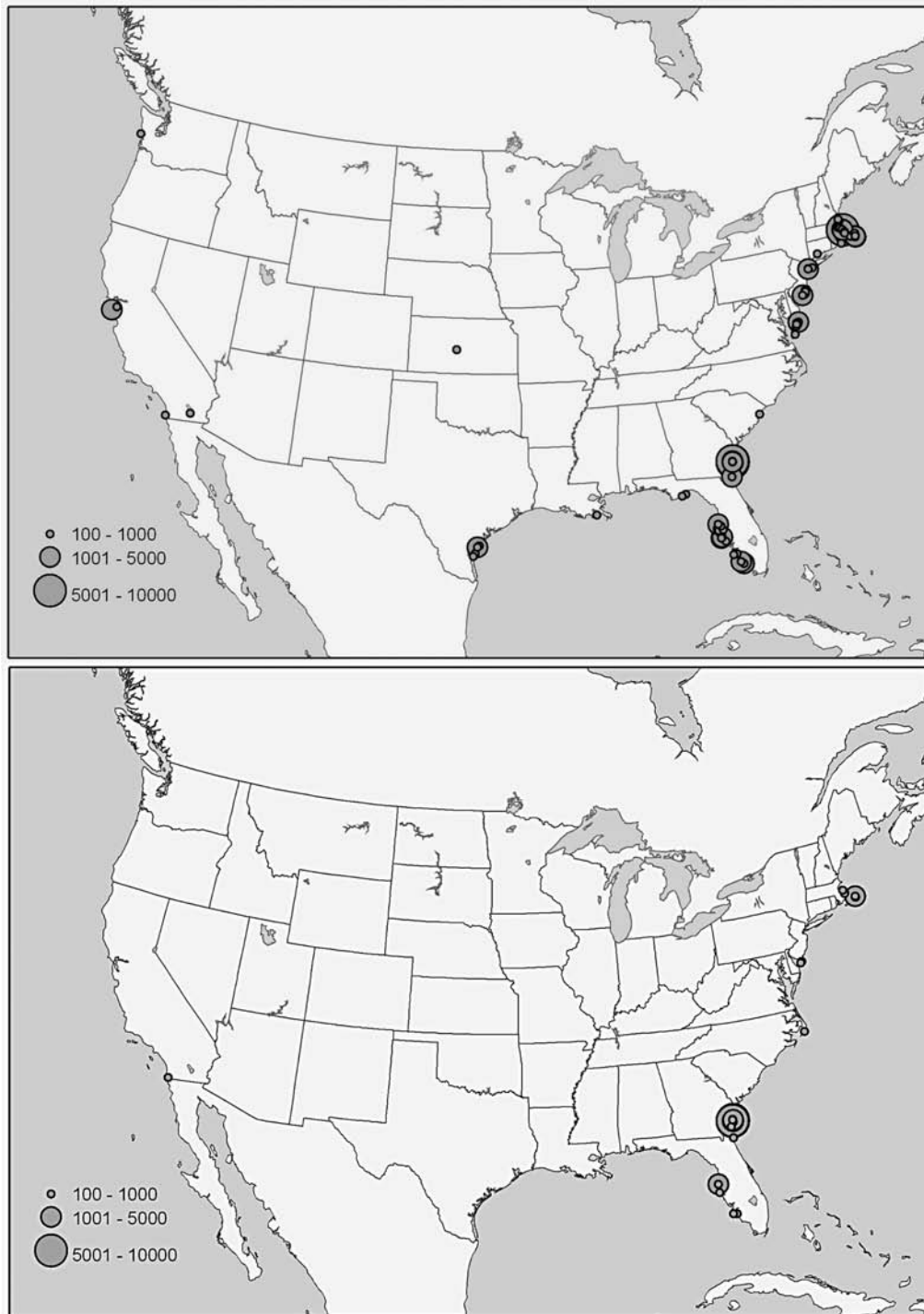


FIGURE 9. International Shorebird Survey (ISS) Data showing distribution of Red Knots during fall migration in the U.S. before year 2000 (upper) and during 2000-2004 (lower). The level of ISS survey effort declined after 2000; therefore, the differences in numbers before and since 2000 may partly represent reduced survey effort (Brian Harrington, pers. comm.).



FIGURE 10. Critical stopover sites used by Red Knots during northward and southward migration in South America.

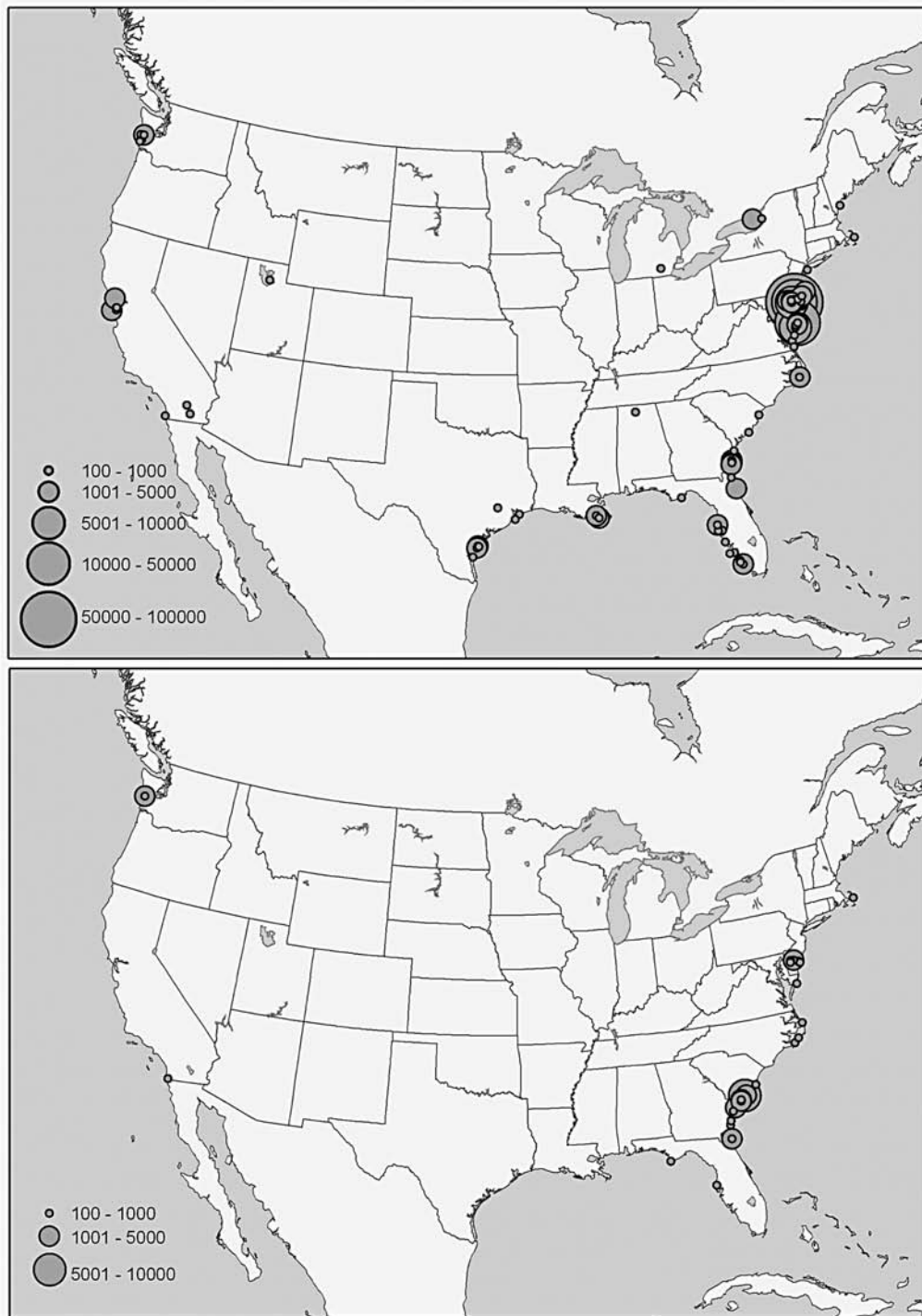


FIGURE 11. International Shorebird Survey (ISS) Data showing distribution of Red Knots during spring migration in the U.S. before 2000 (upper) and during 2000-2004 (lower). The level of ISS survey effort declined after 2000; therefore, the differences in numbers before and since 2000 may partly represent reduced survey effort (Brian Harrington, pers. comm.).

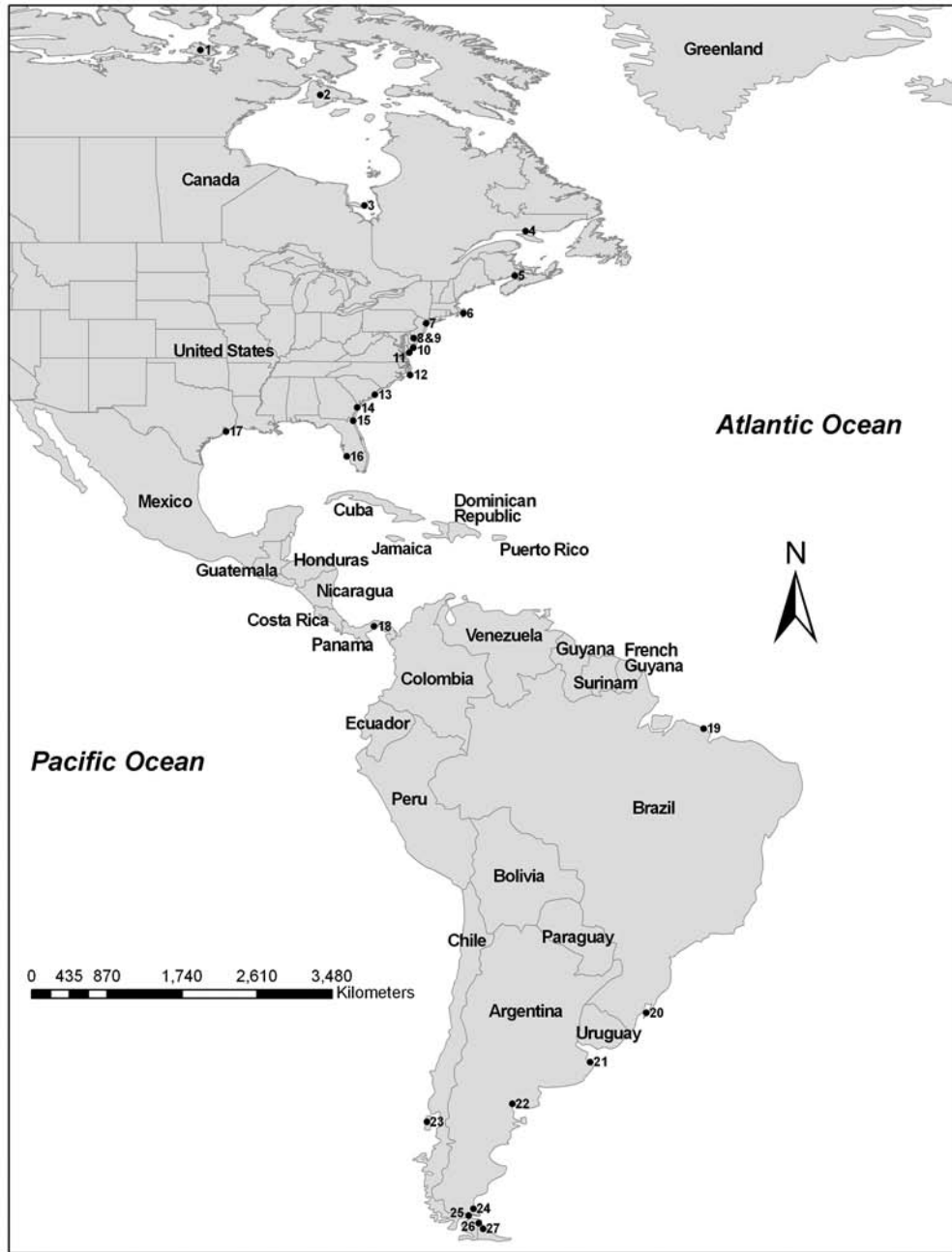


FIGURE 12. Critical breeding, migration stopover, and wintering habitat for the Red Knot *Calidris canutus rufa*. Numbers on the map correspond with the numbers in Table 6.

they are not believed to stop in these areas for any significant period (R. I. G. Morrison, unpubl. data; M. Peck, unpubl. data).

Once they arrive on their breeding grounds, their digestive systems are restored, but often little food is available. Therefore their survival and their ability to attain good breeding condition may depend on surplus fat resources brought to the breeding grounds (Morrison et al. 2005) from Delaware Bay. This in turn may be affected by weather and feeding conditions further south because if Red Knots arrive in Delaware Bay late and/or in poor condition they may have insufficient time to store the resources they require. In this way any problems further south may result in a cascade effect that jeopardizes their ability to survive and reproduce.

Of all the sites visited by the *C. c. rufa*, Delaware Bay is one of the most critical (Harrington and Flowers 1996, Harrington 2001). Without the ability to obtain sufficient resources in Delaware Bay, both the survival of the adult birds and their productivity may decline (Baker et al. 2004). As early as 1986, the importance of Delaware Bay to Red Knots and at least five other shorebird species was recognized when it became the first Western Hemisphere Shorebird Reserve. This recognition was also part of the impetus for the development of shorebird reserves throughout the western hemisphere (Myers et al. 1987).

The number of shorebirds stopping over in Delaware Bay has declined dramatically in the last 10 yr. In the 1980s and early 1990s, horseshoe crabs covered the beaches and, along much of the bayshore, the eggs within reach of a Red Knot's bill in the top 5 cm of sand exceeded 50,000 m⁻² at a number of sites around Delaware Bay. In the 1980s, the combined peak counts of the three shorebird species that feed almost entirely on horseshoe crabs' eggs (Red Knot, Sanderling [*Calidris alba*], and Ruddy Turnstone [*Arenaria interpres*]) averaged 163,000. Now, egg densities at many sites are <4,000 eggs m⁻² and peak shorebird aerial census numbers for 2003–2005 were down to 66,500 with Red Knots showing the greatest drop from 1980s maxima of 95,000–15,000 in 2005 (Clark et al. 1993; K. Clark, unpubl. data). Although the Red Knots from northern wintering populations exploit other food resources in the vicinity of Delaware Bay (such as blue mussels and surf clams on the Atlantic coast of New Jersey), horseshoe crab eggs are crucially important for the long-distance migrants from Tierra del Fuego. As explained in the habitats section of this review, a combination of physiological and time constraints means that they cannot utilize

the alternative foods and rely on the more easily digested eggs.

The harvest of horseshoe crabs along the northeast coast of the U.S., and the associated reduced availability of their eggs as a food resource for migrating shorebirds, was first identified as a serious threat in the mid-1990s. Until 1993, the crab harvest, mainly for eel and minnow bait, was minimal and accounted for no more than about 400,000 per year, which were mostly taken by hand or as by-catch. However, in 1993, collapsing fisheries in New England and elsewhere led commercial fishermen to the profitable conch fishery, for which horseshoe crabs are the preferred bait. This brought commercial fishermen to Delaware Bay, where the harvest increased dramatically as the conch fishery expanded in the mid-Atlantic coast. By 1996, the annual harvest from Virginia to New York, both mechanical and manual, exceeded 2,000,000 crabs (Fig. 13). According to a Delaware Department of Natural Resources and Environmental Control, Division of Fish and Wildlife (DDFW) survey, the population of crabs fell by about 85% between 1990 and 1998 (S. Michels, pers. comm.). While minor restrictions were imposed, the intensive harvest of horseshoe crabs continued (Fig. 13). By 2000, egg densities had fallen from an average of well over 10,000 to <4,000 eggs m⁻². Only a few places favored by crabs, such as Mispillion Harbor, held significantly greater densities.

The greatest risk of the declining availability of horseshoe crab eggs in Delaware Bay to Red Knots is that it jeopardizes their ability to achieve the mass required to reach the Arctic and attain good breeding condition. Between 1998 and 2002, the proportion of Red Knots that had attained an estimated threshold departure mass of 180 g around the normal departure date (28 May) declined by >60% (Baker et al. 2004). This decline may be the result of arriving late in Delaware Bay and/or in poor condition as well as an inadequate supply of crabs' eggs (Robinson et al. 2003, Clark et al. 2004). Moreover these factors could interact and exacerbate the birds' predicament. Birds might arrive late or in poor condition and find an inadequate supply of eggs. Bala et al. (2005, pers. comm.) and M. Hernández (unpubl. data) report that northward passage of Red Knots through Peninsula Valdés, Patagonia, Argentina has become 1–2 wk later since year 2000. There is some evidence that this has been reflected by later arrival into Delaware Bay, in 2000, 2001, and especially in 2003 (Baker et al. 2004; K. Clark, unpubl. data).

Baker et al. (2004) found a decline in the Red Knot's annual survival rate from an

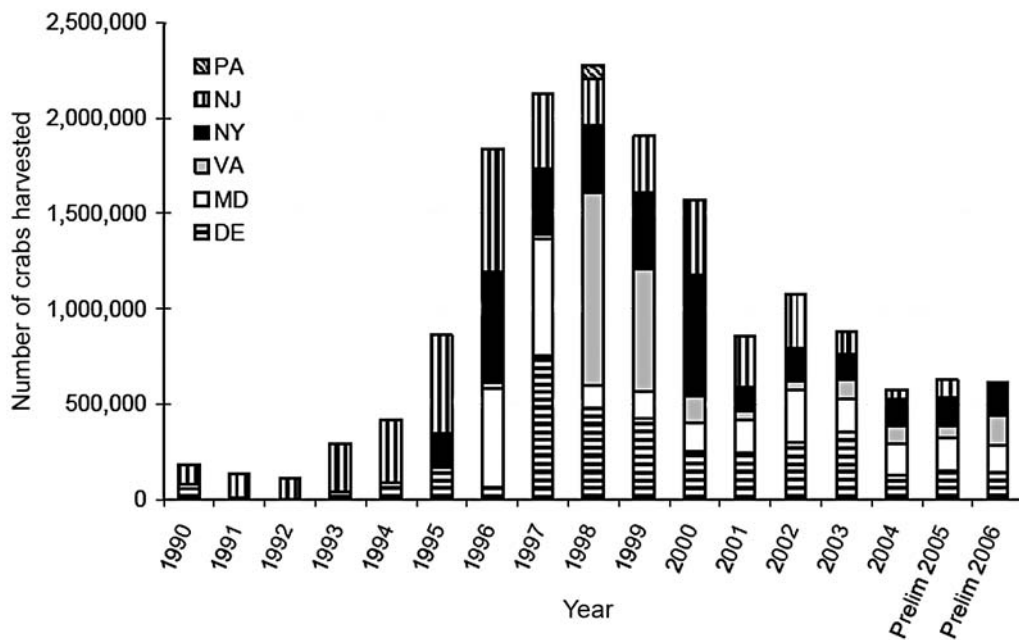


FIGURE 13. Annual landings of horseshoe crabs in Virginia, Maryland, Pennsylvania, Delaware, New Jersey, and New York, 1990–2006 (Morrison et al. 2004). Most states had mandatory reporting by 1996 and all did by 1998, so landings data prior to 1998 may be underrepresented.

average of 85% during 1994–1998 to 56% during 1998–2001. They further showed that over the years 1997–2002, birds caught in Delaware Bay at a lower mass were less likely to survive than heavier birds and that there had been a significant increase in the proportion of poorly conditioned, low-weight birds at the end of May. This was postulated to be the result of a trend for birds to arrive later and/or in poor condition and/or an inadequate food supply. This change in survival coupled with almost zero recruitment of juveniles to the adult population (P. Atkinson, unpubl. data) lies behind the decrease in the Tierra del Fuego wintering population from over 50,000 in 2000 to 30,000 in 2002–2004. Baker et al. (2004) predicted that if annual survival of the Tierra del Fuego population remained stable at 56%, the population could approach extinction by 2010. It is not possible to predict future survival, but the most recent count of 17,221 in January 2006 shows that the trend is following this worst-case scenario trajectory and the risk of extinction is high.

BIOLOGY AND NATURAL HISTORY

Except as otherwise indicated, this account of the biology and natural history of *C. c. rufa*

and the following account of its habitat is based on the Red Knot species text in Harrington (2001). This source is founded on an extensive review of the literature and the works cited in it are not repeated here. Some of the information from Harrington (2001) is quoted verbatim.

REPRODUCTION

Red Knots are thought to have a monogamous mating system in which single pairs mate and nest in territories. Pair bonds form soon after arrival on breeding grounds and remain intact until shortly after the eggs hatch (L. J. Niles et al., unpubl. data) when the females leave their broods. Thereafter, the males look after the chicks until they fledge at about 25 d when they too abandon them. Little information is available for *C. c. rufa* on mate fidelity, though many Red Knots return to the same area to breed from year to year (Morrison et al. 2005; R. I. G. Morrison, unpubl. data).

The breeding chronology of *C. c. rufa* is poorly known. Other races may be paired or unpaired on arrival in breeding areas in late May–early June; start of breeding varies with snowmelt conditions. Simultaneous arrival of male and female *C. c. islandica* has been noted in late May–early June, though males tend to