

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

predominate amongst early arrivals (Morrison et al. 2005), followed by movement into inland nesting habitats within a few days.

No published information is available for *C. c. rufa* on mate fidelity between years or duration of courtship between reunited mates versus new mates. On a 9.15 km² study site on Southampton Island, Nunavut, Canada, we observed only limited evidence of site fidelity despite the fact that studies of other subspecies suggest that breeding site fidelity is high, especially in males. In 5 yr of monitoring breeding densities, we observed one male return to his territory of the previous year and only one female return to the study site but to a different territory (L. J. Niles et al., unpubl. data). In some instances, Red Knots have been thought to arrive on breeding grounds in pairs. Flocks sometimes arrive at breeding latitudes before snow-free ground is available in breeding habitats. Upon arrival or as soon as favorable conditions exist, males and females occupy breeding habitat and territorial displays begin.

Age of first breeding is uncertain but for most birds is probably 2 yr (Harrington 2001). All juveniles of the Tierra del Fuego wintering population are thought to remain in the Southern Hemisphere during their first northern summer though their distribution is largely unknown (P. M. González, unpubl. data). Some basic-plumaged Red Knots arrive in Delaware Bay in May and can constitute a considerable proportion of the individuals remaining at the end of the stopover. It would seem likely that these are 1-yr-old birds from northern wintering populations that will remain in the vicinity of Delaware Bay throughout the breeding season, but this has yet to be proved.

Mating displays

During early breeding stages, Red Knots show a variety of behaviors associated with area defense and advertisement which may begin on the day of arrival. Most agonistic behaviors involve territorial males. Fighting, though uncommon, is mostly seen between males. Song flights, performed only by males, occur as soon as males return to breeding grounds and evidently continue into the incubation period. Song flights usually begin and end in the territory, though they may extend well beyond its boundaries. Other aerial displays include the v-wing flight, which resembles a simple, low song flight originating and ending in territories, and aerial chases which are initiated by territorial males and are the most frequently seen agonistic behaviors.

Ground displays include the two-wing lift, ground singing, and horizontal point. The two-wing lift involves a standing bird, usually a male, and is often given after a song flight or a v-wing flight, but often immediately before flying or when one member of a pair lands near its mate, or by males landing near their chicks. Another display, ground singing, is most commonly performed by a standing male on territory when other males are singing overhead, performing v-wing flights, or singing from the ground nearby. Horizontal point displays are performed by males in response to another male singing, at territorial borders, at a neighbor ground-singing male and is also given as a precursor to attacking intruders, when it is typically accompanied by singing.

The tail-up display is a common behavior seen in varied contexts, typically presented by a male to the receiver laterally or posteriorly. This display is most often seen during courtship or as prelude to copulation. It is also occasionally observed in pairs reuniting after a separation, in activity after roosting, during a nest-scape ceremony, or after fights with intruding females. This display is not seen after the egg clutch has been completed.

The tail-drop fan display is given by a male as a prelude to nest-scape advertisement, by a stationary male when his mate comes close, during a fight with an intruding female when the male walks away from his mate, and by a male after copulation. Males in the nest give the nest-scape advertisement display, after arrival of females. Once the female settles in the scrape, the male assumes a ground point display.

Sexual behavior

The behaviors leading up to copulation are variable though more predictable prior to mounting. A male typically follows behind a female in a tail-up display. Meanwhile, he begins the rapid, high-pitched copulation call while pecking rapidly at the female's back. If the female is receptive, the male flies up on to her back to begin copulation while continuing to flutter his wings.

The rate of male calling increases prior to cloacal contact. Meanwhile, the female drops her wings slightly to expose the back and rump. The female's tail is then raised, the male bends his tail under it, and cloacal contact is made. Coition lasts roughly 1 min. Following contact, the male falls off the female's back and holds her head, neck, or nape feathers in his bill for 1–30 sec.

Copulation attempts are evidently initiated by the male, and take place throughout the day.

In one pair, copulation was seen within 1–2 hr after arrival of the female; in another pair it was not seen for the first 36 hr. In three pairs, copulation was first noted 3, 5, and 8 d before the first egg is laid.

No data are available on the occurrence of extra-pair copulation; however, they appear to be unlikely given the apparent monogamous mating system and the vigorous territorial defense shown by males.

Nest sites

Nests are cup-shaped depressions, often with well-defined rims, lined with dried leaves, grasses, and sometimes lichens, averaging 11.9 cm across, 11.1 cm wide, and 4.4 cm deep. The lichens, which Red Knots use for nest lining are species that form hollow tubes thus providing an excellent insulating layer above the cold ground. On Southampton Island, nest cups were most often lined with the small leaves of mountain avens (*Dryas octopetala*) and rarely lined with lichen; nest cups averaged 11.1 cm wide and 5.7 cm deep (L. J. Niles *et al.*, unpubl. data).

Males prepare three–five nest scrapes in their territory before females arrive. Vegetation is removed by pulling with the bill and by sitting in the nest depression and pivoting on the breast while kicking backwards with the feet. Once in the nest, the female removes vegetation from under her breast, placing it at her side or tossing over her back while kicking backwards with her feet.

Red Knot nests may be scraped into the main body or edges of mountain avens patches or in low, spreading vegetation on hummocky ground containing lichens, leaves, and moss. Selection of nest sites may vary with snow or other conditions when individuals arrive in breeding areas. Knots generally use nest sites on dry, slightly elevated tundra locations often on wind-swept ridges or slopes with little vegetation. Isolated patches of stunted willow (*Salix* spp.) and/or mountain avens often dominate the vegetation in the area. The majority of nests found on Southampton Island were within 300 m of wetlands >2 ha in area, which allows suitable foraging habitat for parents and young after the eggs hatch (L. J. Niles *et al.*, unpubl. data).

On Southampton Island, nests were most often found on small patches (~0.5 m dia.) of mountain avens. Nests were located in exposed areas of glacial, shattered rocks, and mudboils. The amount of vegetative cover averaged 33% within 1 m of the nest and 25% within 10 m of the nest (L. J. Niles *et al.*, unpubl. data).

Red Knot nests are located principally at elevations <150 m, often in damp habitats, though they may nest in drier sites, but not far from damp areas. Nest sites are often on higher ground where little winter snow accumulates and/or where spring snowmelt is earliest. Twenty-one nests on Southampton Island were found, on average, to be within 360 m of a glacial ridge/esker and within 200 m of a wetland (L. J. Niles *et al.*, unpubl. data). Red Knot nests also tend to be widely separated, located between 0.75 km and 1.5–15 km apart. Nests evidently are located within the display flight areas.

Number of broods

Red Knots lay only one clutch per season and, so far as is known, do not lay a replacement clutch if the first is lost.

Clutch size

The usual clutch size is four eggs, though three-egg clutches have been recorded. It is estimated that the clutch of four eggs is laid over 4–6 d. The average egg size measured on Southampton Island (N = 90) had a length of 42 mm (range = 37.8–44.5 mm) and a width of 29 mm (range = 26.6–31.3; L. J. Niles *et al.*, unpubl. data) and is similar to other Red Knot studies (Harrington 2001). Fresh egg mass is estimated to be 18–19 g on Southampton Island (M. Peck, unpubl. data).

Incubation period

The incubation period lasts approximately 22 d from the last egg laid to the last egg hatched. Both sexes participate equally in egg incubation.

Nestling period

Hatching occurs within the first half of July and within clutches is apparently quite synchronous, occurring within the same day. The fledgling period is estimated to be 18 d.

Young birds leave the nest within 24 hr of hatching. Broods have been observed to move 300 m within 24 hr of leaving the nest. No published measures of growth and development exist, in part because broods are extremely cryptic, recognize and respond to parental alarm calls by freezing, and are difficult to follow.

After hatching, families quickly move away from high nesting terrain to lower, wetland habitats. Although information conflicts, typically only the male parent stays with the brood once the chicks leave the nest. Male parents

brood and defend the young. No information is available on how long young require brooding. Young forage for themselves and are not fed by their parents.

Nesting success

Annual variation of hatching success is unknown. It probably varies in parallel with snow-cover conditions at nest sites in spring, particularly the timing of snowmelt.

MORTALITY

Despite little information from the breeding grounds, the Long-tailed Jaeger (*Stercorarius longicaudus*) is prominently mentioned as a predator of chicks in most accounts. Also mentioned are Parasitic Jaeger (*S. parasiticus*) and arctic fox (*Alopex lagopus*), and it is likely that other arctic predators, including Pomarine Jaegers (*S. pomarinus*) commonly take chicks and eggs. Herring Gulls (*Larus argentatus*) and Glaucous Gulls (*L. hyperboreus*) may also be predators of chicks.

Away from the breeding grounds, the most common predators of Red Knots are Peregrine Falcons (*Falco peregrinus*), harriers (*Circus* spp.), accipiters, Merlins (*Falco columbarius*), Short-eared Owls (*Asio flammeus*), and Great Black-backed Gulls (*Larus marinus*). Knots' selection of high-tide resting areas on the coast appears to be strongly influenced by raptor predation, something well demonstrated in other shorebirds.

A full account of diseases and parasitic infections recorded in *C. c. rufa* is presented in the Threats section of this review.

LONGEVITY

To our knowledge, the oldest Red Knot ever recorded worldwide was one that was originally banded on The Wash, southeastern England, in August 1968 as an adult and recaptured there in September 1992 (Wash Wader Ringing Group 2004). Given that it could not have been hatched later than July 1967, it was at least 25 yr old when it was recaptured. The oldest recorded *C. c. rufa* was banded as a juvenile at Punta Rasa, Argentina, in October 1987 and recaptured on the wintering grounds at Bahía Lomas, Tierra del Fuego, in February 2003, making it 16 yr old (L. J. Niles et al., unpubl. data). Although these records demonstrate that the potential lifespan of a Red Knot is considerable, most live much shorter lives. Annual adult survival in stable populations has been estimated at around 80% and the survival of juveniles is about half that (Boyd and Piersma 2001). Therefore, very few Red Knots live for more than about 7 yr.

SITE FIDELITY

Red Knots, especially males, appear to exhibit high breeding site fidelity. They are also very faithful to specific migration and wintering staging sites. Banding studies indicate that no mixing occurs between Red Knots wintering in Florida and those wintering in Argentina, suggesting that Red Knots are also faithful to wintering sites.

MIGRATION

Red Knots are long-distance migrants and have one of the longest-distance migrations in the animal kingdom. Those that breed in the Western Hemisphere, migrate from breeding grounds in the middle- and high-Arctic to wintering sites on the eastern and western Atlantic coasts, including southernmost South America. Knots are jump migrants, flying many thousands of kilometers without stopping. In between these jumps, high proportions of entire populations may use a single migration stopover site. In some Red Knot populations, including *C. c. rufa*, a substantial number of birds remain south of the breeding grounds throughout the breeding season, many but not all of which are 1-yr-old birds.

Red Knots tend to migrate in single-species flocks, largely because of species-specific migration habits. Departures tend to occur in the few hours before twilight on sunny days. Size of the departing flocks tends to be large (>50 birds). Configuration of departing flocks may vary from v-formations to echelons, clusters or bunches.

As Red Knots prepare to depart on long migratory flights, they usually have a mean body mass 50–55% greater than estimated fat-free mass. At stopover sites, 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 arrive as light as 89 g (32% below fat free weight), whereas near departure a few exceed 240 g (85% above fat free weight) (L.J. Niles et al., unpubl. data). In addition to acquiring fat, Red Knots undergo physiological changes on arrival and shortly before departure including substantial changes in metabolic rates, organ size, and muscle mass. Before departure, these changes include substantial decreases in mass and size of the gizzard, liver, kidneys, and guts, and increases in flight muscle and fat mass (Piersma and Gill 1998).

Red Knots arriving from lengthy migrations are not able to feed maximally until their digestive systems regenerate, a process that may take several days (Piersma et al. 1999). This

exacerbates the situation of time-constrained migrants and underscores the need for stopovers that are rich in easily digested food resources.

C. c. rufa undergoes a lengthy migration, with wintering grounds on the southern coasts of the Chilean and Argentinian sectors of Tierra del Fuego (Fig. 14). Two other populations are of uncertain subspecific status, but which might be *C. c. rufa*. One winters in the southeastern U.S. (mainly the western and northeastern coasts of Florida, but also the coasts of Georgia and South Carolina), the other in the Maranhão region of northern Brazil. Generally, northward migration begins in February for birds wintering in Tierra del Fuego, though a few leave before the end of January. They reach Brazil in April and depart in early May. Relatively few individuals were thought to use the southeastern Atlantic coasts of the U.S. during migration. However, recent spring surveys on the Atlantic coasts of northern Florida, Georgia, South Carolina, North Carolina, and Virginia indicate that Red Knots stopover in these states in May and early June with numbers ranging from tens to >9,000 (P. Leary, pers. comm.; B. Watts, pers. comm.; B. Truitt, pers. comm.). The length of stopover at these locations is generally believed to be brief and reliant on ephemeral food resources such as mussel spat (B. Truitt, pers. comm.) and small clams (*Donax spp.*; B. Winn, pers. comm.). *C. c.*

rufa becomes abundant in the northeastern U.S. in early May, especially on Delaware Bay where the highest numbers occur. Some Red Knots use the interior flyway from Texas–Louisiana via Saskatchewan to the Arctic during spring and to a lesser extent during autumn migration (Skagen et al. 1999). Although up to 2,500 Red Knots were recorded in both Texas and Saskatchewan in spring during 1980–1996, we do not know of any more recent record of substantial numbers using this flyway. Nevertheless recent observations of a Red Knot on the Texas coast color marked in Argentina in May 2004 and a Red Knot color marked on Delaware Bay in August 2005 indicate that the flyway is still being used.

During southbound migration, *C. c. rufa* begin to stage in mid-July on Hudson and James Bays and on the Atlantic coast of the U.S., especially at sites in Massachusetts and New Jersey. Several studies suggest that adults fly directly to South America from the eastern seaboard of North America, departing U.S. staging areas and arriving in northern South America in August. Passage continues across Amazonia, towards wintering (non-breeding) areas in southern Argentina and Chile. Recent observations show that Red Knots banded in South America (mainly Argentina and Chile) start to move through Georgia in July and are gone by November (B. A. Harrington, unpubl. data; B. Winn, pers. comm.). This suggests that some portion of the Red Knot population migrates down the Atlantic coast of the U.S. and departs to South America from southern U.S. staging areas. Most adult Red Knots pass through Suriname during the latter half of August and first half of September (Spaans 1978). Knots wintering in southern Argentina and Chile generally arrive by late September through October (Baker et al. 2005a). *C. c. rufa* are uncommon on the western coasts of the North and South American continents.

Another subspecies, *C. c. roselaari*, breeds in Alaska and Wrangel Island. At least some of these birds winter in California and Baja California, others probably winter farther south, but, as discussed in the population size and trends section of this document, known winter numbers are far less than those thought to occur in Alaska in late spring.

FEEDING HABITS

Knots use three main foraging methods: pecking, plowing, and probing. Pecking is generally used when foraging on epifauna, such as horseshoe crab eggs, small snails, and mussels. Probing and plowing may be involved in

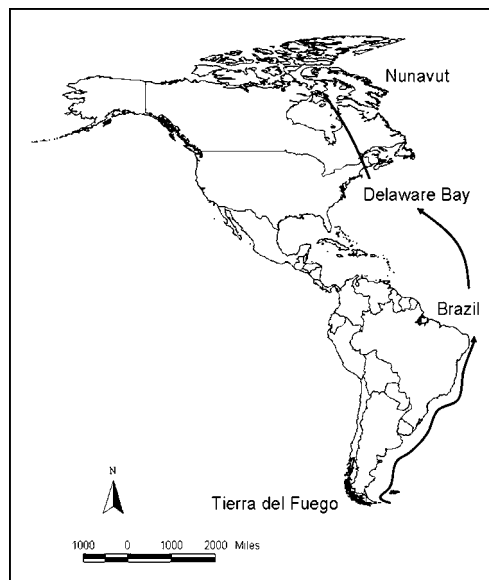


FIGURE 14. Migration route of *Calidris canutus rufa* between its wintering grounds on Tierra del Fuego, South America, stopover areas along the Patagonian Coast of Argentina, and in the northeastern United States, and breeding grounds in the Canadian Arctic.

detecting buried bivalve prey. On the breeding grounds, the diet of Red Knots consists mostly of terrestrial invertebrates, though they will also eat plant material especially early in the season. During the rest of the year, at stopover sites and on their wintering grounds in Tierra del Fuego, Chile, Maranhão, Brazil, and the southeastern U.S., they feed almost exclusively in intertidal habitats, particularly on mudflats and beaches and, on the coast of Argentina, on restingas (broad, wave-cut platforms extending across the intertidal zone) where they specialize on bivalves which are swallowed whole. Common bivalves consumed include *Mytilus*, *Mulinex*, *Donax*, *Macoma*, *Tellina*, *Myadora*, *Nucula*, and possibly *Gemma*. They will also take gastropods, such as *Hydrobia*, *Littorina*, and *Heleobia*, amphipods, and occasionally polychaetes.

When stopping over in Delaware Bay, they feed almost exclusively on the eggs of horseshoe crabs. Feeding on horseshoe crab eggs on Delaware Bay, however, is a major departure from the prey usually taken.

HABITAT

Red Knots use very different habitats for breeding and wintering and migration. Breeding habitats are located inland, but close to arctic coasts. Wintering and migration habitats are similar—generally coastal with large areas of intertidal sediments.

PREFERRED MICROHABITATS

Selection of preferred microhabitats on breeding grounds may vary depending on the amount of snow cover individuals encounter when they arrive. Nests are usually located on sparsely vegetated, dry, sunny, elevated, wind-swept ridges or slopes. Nest locations are also usually located near wetlands and lake edges, which then become the preferred microhabitat after hatching.

Preferred wintering and migration microhabitats are muddy or sandy coastal areas, more specifically, the mouths of bays and estuaries, unimproved tidal inlets and tidal flats (Table 6; Fig. 12).

BREEDING HABITAT

As described above, Red Knot breeding habitat is principally at elevations of <150 m and includes small wetlands where the chicks can feed. At the landscape scale, a model of potential breeding habitat was developed by New Jersey Department of Environmental Protection Division of Fish and Wildlife Endangered and

Nongame Species Program (NJENSP) and Rutgers University using remotely-sensed land-cover characteristics. The model showed that Red Knot breeding habitat is generally found at elevations <150 m above sea level, <50 km from the coast and where vegetation cover is <5%. Red Knots and their chicks and fledglings forage in shallow sedge meadows and on sparsely vegetated lake edges proximate to nest sites.

MIGRATION AND STOPOVER HABITAT—CANADA

The critical staging areas for Red Knots during spring and fall migration in Canada are along sandy beaches and tidal mudflats in James Bay and tidal mudflats and salt marshes in the northern Bay of Fundy (R. I. G. Morrison, unpubl. data; M. Peck, unpubl. data; K. Ross, pers. comm.). In the Bay of Fundy, Red Knot migrants are rare in spring, but relatively common in the fall (Hicklin 1987).

MIGRATION AND STOPOVER HABITAT—NORTHEASTERN U.S.

It is not believed that large numbers of Red Knots occur during migration in Maine (L. Tudor, pers. comm.), New Hampshire (C. Raithel, pers. comm.), Connecticut, and Rhode Island (J. Dickson, pers. comm.; D. Varza, pers. comm.). In the northeastern U.S. (New Jersey–Maine), the principal Red Knot staging areas are along the New Jersey, New York, and Massachusetts coastlines. In Massachusetts, Red Knots use sandy beaches and tidal mudflats during fall migration near Scituate, Duxbury, and Plymouth Beach, and along the shoreline in Cape Cod south to Monomoy (B. A. Harrington, unpubl. data). New York's Jamaica Bay Wildlife Refuge has a concentration of migratory Red Knots during spring and fall along sandy beaches and most commonly within the impoundment (K. Tripp, pers. comm.). Along the Atlantic coast of New Jersey, Red Knots utilize sandy beaches during spring and fall migration for foraging (K. Clark, unpubl. data; D. Hernández, unpubl. data; L. J. Niles, unpubl. data; H. P. Sitters, unpubl. data).

MIGRATION AND STOPOVER HABITAT—DELAWARE BAY, U.S.

Delaware Bay is the most important staging area during northbound migration and is normally used by the whole or a large proportion of the *C. c. rufa* population which spends 2–3 wk staging there in the latter half of May. Beaches typical of the Delaware Bay shore are a mixture of sand and smooth gravel, and shorebirds