Alternatively, the Maranhão population could be an easternmost part of the *C. c. roselaari* population which is also speculated to winter in Mexico. If that is true the southeastern U.S. population would have a census population size of about 7,500 birds, based on counts in winter in western Florida, Georgia, and South Carolina in 2005 implying that the effective size of the southeastern U.S. population is approaching the critical population size for persistence in the longer term and is in danger of extinction from the perspective of stochastic ecological risk factors in the near future. These ecological risk factors caused the severe decline in the Tierra del Fuego population (Baker et al. 2004).

The third possibility is that all three Red Knot populations (Tierra del Fuego, Maranhão and southeastern U.S.) really belong to one subspecies (*C. c. rufa*). This seems implausible biologically, because the aggregate evidence from genetic, ecological, morphological, and banding data clearly document differences among these populations. Furthermore, these differences equate with those used to recognize the other four subspecies of Red Knots worldwide (Tomkovich 1992, 2001). Risk-averse management should take as the absolutely minimum position that each of these three populations are distinctive population fragments of *Calidris canutus*, and that two subspecies are probably represented.

In summary, clarification of the taxonomic status of these populations will require further genetic research using a larger battery of high-resolution microsatellites and AFLPs. Additionally, we need to better understand their migration pathways, breeding ranges, and population vital rates. The status of the Red Knots seen staging in South Carolina and Georgia and wintering in Florida and the Caribbean cannot be assumed to be C. c. *roselaari* until their breeding range is discovered and further genetic studies are completed. Of the six currently recognized subspecies of Red Knots in the world, three breed in the U.S. and Canadian Arctic (*rufa, roselaari,* and *islandica*) and only the first two will be discussed throughout this document except where studies of other subspecies apply to Red Knots worldwide. Within the Americas taxonomic uncertainty exists about small population segments in Maranhão in northern Brazil and on the Pacific coast of Mexico. These segments along with the southeastern U.S. wintering population are each less than 10,000 birds and are apparently in decline, but by far the most alarming decline is in the long-distance migrant population in Tierra del Fuego which has fallen from 67,000 in the 1980s to about 17,200 in 2006.

PHYSICAL DESCRIPTION

Essentially, the plumage of all Red Knots is mainly chestnut-red or salmon-colored during the breeding season and white and gray for the remainder of the year. The differences between the subspecies are largely confined to breeding plumage and size. In the detailed account of the subspecies below, we concentrate on male plumages because they show the most pronounced differences. We also focus on *C. c. rufa* and the critical difference (for some of the issues discussed in this review) between *C. c. rufa* and *roselaari*. In addition, we outline the plumages of the other subspecies to give an idea of the general nature of subspecific variation in the species. We also present biometric data from Harrington (2001) covering wing-chord and culmen length (Table 4) and mass (Table 5), although differences noted by these data may possibly be attributed to phenotypic plasticity rather than inter-subspecific ones.

The upperparts (crown, mantle, tail, and scapulars) are plain ash gray, with light fringes (when newly molted) on the scapulars and median wing coverts. The underparts are dull white. The underwing, rump, lower back and axillary feathers are light gray to dirty white with dark subterminal chevrons. The upper breast is dirty white with faint, suffused, dark or gray to brown, fine vertical streaking, which may extend laterally to the flanks. The head has dull patterning: the crown, chin, throat, hindneck, and neck sides are plain to light gray with an indistinct whitish supercillium. The greater upperwing coverts and inner primary coverts have white tips, which appear as a white wing-line when in flight. The primaries are dark brown to black on the outer webs, more pale on the inner webs, and white at the base. The proximal primaries have light borders on the outer webs. The distal primary coverts and alula are dark brown-black. The secondaries and tertials and remaining greater and lesser wing coverts are ash gray, broadly tipped with white. The rectrices are gray with narrow white fringes; the outer rectrices often have a dark subterminal band. The feather rachises are dark (Hayman et al. 1986, Harrington 2001).

First Basic Plumage

This is similar to the definitive basic plumage, except for retained back to upper tail coverts, some rectrices, and a few tertials or median upper wing coverts, all of which may occasionally be replaced. Birds wintering in South America may also replace primaries (Harrington 2001).

TABLE 4. MEAN WING CHORD AND CULMEN MEASUREMENTS FROM MUSEUM SPECIMENS OF RED KNOTS TAKEN FROM WESTERN HEMISPHERE LOCATIONS.

Source	Wing-chord length (mm)	Culmen length (BAH)
Adults		
Females	164[a] ± 22 (78)	36.3[b] ± 3.1 (78)
West[c]	167[e] ± 21 (11)	37.0[f] ± 6.0 (11)
Northeast[d]	161[e] ± 23 (29)	35.9[f] ± 2.8 (29)
Males	161[a] ± 17 (97)	34.9[b] ± 2.2 (97)
West[c]	162[g] ± 23 (18)	35.8[h] ± 1.8 (18)
Northeast[d]	160[g] ± 19 (35)	34.9[h] ± 2.6 (35)
Juveniles		
Females	160[a] ± 16 (35)	34.4[b] ± 4.9 (35)
West[c]	161[e] ± 15 (13)	36.0[f] ± 4.7 (13)
Northeast[d]	159[e] ± 15 (13)	33.4[f] ± 2.6 (22)
Males	154[a] ± 27 (37)	32.6[b] ± 5.6 (37)
West[c]	158[g] ± 13 (9)	33.7 ± 6.8 (9)
Northeast[d]	159[g] ± 15 (22)	32.2 ± 4.9 (28)

[a] Not significantly different between sexes (adults, F = 1.32, P = 0.10, juveniles, F = 1.65, P > 0.05).
[b] Significantly different between sexes in adults (F = 1.45, P < 0.05) but not in juveniles (F = 1.15, P > 0.05).
[c] West includes Alaska, Alberta, British Columbia, and California.
[d] Northeast coast includes North Carolina and coastal points north and east.
[e] West and northeast wing lengths were significantly different (adults: t = 3.52, P < 0.001; juveniles: t = 2.06, P < 0.05).
[f] West and northeast bill lengths were significantly different (adults: t = 1.67, P < 0.05; juveniles: t = 4.01, P < 0.001).
[g] West and northeast wing lengths were not significantly different among adults (t = 1.27, P > 0.05), but were significantly different in juveniles (t = 1.96, P < 0.05).
[h] West and northeast were not significantly different (t = 1.57, P > 0.05) among adults but were significantly different among juveniles (t = 1.96, P < 0.05).
Note: Data given as mean ± SD (N); adult Red Knots measured between April and June, juvenile Red Knots during fall migration; taken from Harrington (2001).

TABLE 5. BODY MASS OF WESTERN HEMISPHERE RED KNOTS AT DIFFERENT STAGES OF NORTH AND SOUTH MIGRATION.

Location	Date[a]	Body mass (grams)	Significance[b]
Winter			
Sarasota, FL	283	124.9 ± 7.1 (103–140, 101)	G
	6	136.5 ± 8.9 (112–158, 120)	F
	10	139.7 ± 9.1 (123–160, 25)	F
North migration			
Punta Rasa, Argentina[c]	98	138.9 ± 16.6 (105–167, 30)	F
Península Valdés, Argentina[c]	101	151.3 ± 13.1 (114–182, 102)	E
	110	148.2 ± 17.0 (104–185, 162)	E
Lagoa do Peixe, Brazil[c]	119	199.9 ± 17.6 (135–246, 139)	A
	123	204.4 ± 21.6 (150–289, 141)	A
Delaware Bay, NJ	133	159.2 ± 12.7 (129–198, 221)	CD
	138	153.6 ± 16.8 (91–205, 385)	DE
	143	175.4 ± 18.1 (107–210, 278)	B
	148	162.4 ± 24.1 (105–198, 24)	C
South migration			
Scituate, MA	209	148.4 ± 19.2 (101–206, 608)	E
	215	169.3 ± 18.7 (135–205, 23)	B
	220	172.4 ± 20.2 (103–225, 659)	B
	232	168.9 ± 20.2 (128–207, 32)	B
Plymouth, MA	235	124.2 ± 16.1 (90–149, 18)	G

[a] Dates are Julian dates.
[b] Means sharing the same letter were not statistically different (P > 0.05) according to a general linear means model (SAS PROC GLM) and a Duncan's multiple range test (SAS Institute, 1985).
[c] Samples do not include birds recorded as in basic plumage. Definitive basic (non-breeding, or winter plumage.
Notes: From Manomet Center for Conservation Sciences (unpubl. data) given as mean ± SD (range, N). Taken from Harrington (2001).

DEFINITIVE ALTERNATE PLUMAGE

In definitive alternate plumage the face and underparts are variable chestnut-red, with variable amounts of white and brown on the rear belly and white flecks on the front belly. The lower rump and uppertail are whitish gray. The mantle, scapulars, and tertials have blackish centers, and are edged with rufous and tipped with pale gray. The wing coverts are grayish with white (Hayman et al. 1986).

ALTERNATE PLUMAGE

Alternate or breeding, plumages vary by subspecies and by sex (Harrington 2001). In alternate plumage, *C. c. rufa* is distinguished by its characteristic pale rufous color on the breast, neck and head (Sibley 2000). Back feathers and scapulars have dark brown-black centers edged with faded rufous. Scapulars and tertials are unevenly colored with broad, dark, irregular-shaped centers, widely edged in notched patterns to variable degrees, some with faded rufous and others with bright salmon-red color. Post-breeding adults have a worn mantle and scapulars, which become extensively blackish, rendering the different subspecies indistinguishable (Hayman et al. 1986).

FEMALES

Females are similar to males, though rufous colors are typically less intense with more buff or light gray coloration in the dorsal parts. Females of all subspecies have less evenly and less brightly colored underparts than males and may have scattered white feathers. Females also have more extensive white on the lower belly and may have scattered breast and/or flank feathers with wavy, dark marks at the tips. The supercillium is less pronounced than in males, and may be indistinct from the crown and eyeline. The hindneck is more buff than cinnamon.

MALES—*CALIDRIS CANUTUS RUFA*

Of all races, *C. c. rufa* males have the palest chestnut underparts with more extensive white on the rear belly and a duller underwing area (Hayman et al. 1986). They have a nearly white vent, lower flanks, and under tail coverts (Harrington 2001). Crown and nape are streaked with black and gray and/or salmon. Other features include prominent brick red or salmon red superciliary stripe, auricular region and lores colored as in crown but with finer streaks; chin, throat, breast, flanks, and belly brick red or salmon red, sometimes with a few scattered

light feathers mixed in; undertail white, often including scattered brick-red or salmon-red feathers marked with dark, terminal chevrons laterally. Back feathers and scapulars have dark brown-black centers edged with faded salmon. Scapulars and tertials are unevenly colored with broad, dark, irregular-shaped centers widely edged in notched patterns to variable degrees, some with faded salmon and others with bright salmon-red color. Lower back and upper tail-coverts are barred black and white, with scattered rufous (Paulson 1993). Remiges, rectrices, and about half of the wing coverts are retained from basic plumage. Primaries are dark brown to black, secondaries and remiges gray, and there is a narrow wingbar. Putative younger males tend to be less brightly colored dorsally (Harrington 2001) and have greater numbers of light feathers scattered among ventral feathering (Hobson 1972). Adults passing through James Bay during southward migration show molt of body feathers as well as scapulars (Hope and Shortt 1944). Southward-migrating individuals in Massachusetts during July and early August (mostly *C. c. rufa* bound for austral wintering grounds) show molt of ventral and dorsal body feathers, but do not show any flight-feather molt. Body-feather molt appears to become arrested before departure in mid-August (Harrington 2001). In contrast, data from adults captured later than August in New England and many caught in the southeastern U.S show advanced prebasic molt of primaries, secondaries, and rectrices, suggesting that these individuals may, in fact, be *C. c. roselaari*. This flight-feather molt appears to be virtually completed before *C. c. roselaari* move to Florida winter locations during October and November (Harrington 2001).

MALES—*CALIDRIS CANUTUS CANUTUS*

This subspecies has deep chestnut underparts and dark chestnut fringes on the upper body (Hayman et al. 1986). The vent and under tail coverts are deep rufous (Harrington 2001). The black marks on the upperparts are heavy, with rufous marks small and deeply colored, rounded on tips of scapulars (Harrington 2001).

MALES—*CALIDRIS CANUTUS ROGERSI*

Subspecies *rogersi* appears paler in color than the nominate subspecies (*C. c. canutus*), and the lower belly typically has more white (Hayman et al. 1986). This subspecies also has more coloration on lower belly and under tail-covert region and appears less grayish and slightly

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 submarginal 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