TABLE 1. NUMBER OF CITATIONS OF THE MOST EXTENSIVELY STUDIED SHOREBIRDS IN THE WORLD (THOMAS ET AL. 2003).

Species	Number of citations in title only	Number of citations in text
Eurasian Oystercatcher (*Haematopus ostralegus*)	112	292
Dunlin (*Calidris alpina*)	58	137
Northern Lapwing (*Vanellus vanellus*)	51	125
Red Knot (*Calidris canutus*)	36	132
Redshank (*Tringa totanus*)	29	88
Ruff (*Philomachus pugnax*)	22	57
Eurasian Curlew (*Numenius arquata*)	20	43
Black-bellied Plover (*Pluvialis squatarola*)	18	73

around 17,200 in 2006. The work has involved a diverse selection of people and organizations, government and non-government from Argentina, Chile, Brazil, and Canada as well as all East Coast states of the U.S. from Florida to Massachusetts and the U.S. Fish and Wildlife Service (USFWS). From the beginning, shorebird ecologists from outside the Americas have also been involved, especially from the United Kingdom, The Netherlands, and Australia, several of whom have contributed to this review.

Studies of *C. c. rufa* have focused on determining the cause of the population decline and whether anything can be done to reverse the situation. With limited resources, they have sought to cover the whole of *C. c. rufa*'s latitudinal range of over 120° from Tierra del Fuego (54° S) to King William Island (68° N) and the whole of its annual cycle from one arctic breeding season to the next. More specifically, a large proportion of the effort has been directed at measuring demographic rates and identifying where in the annual cycle the problems lie. All this has proved very challenging and we do not yet know all the answers. Nevertheless, considerable progress has been made, due in no small part to the use of modern and sometimes innovative techniques as well as much hard work and the support of many people and organizations.

Worldwide, the main organization concerned with research and conservation science in relation to the world's 221 species of shorebird is the International Wader Study Group, which organized a workshop attended by 132 specialists from 20 countries in 2003 to determine if shorebird populations worldwide are

in decline. The conclusions show that of those shorebirds whose population trend is known, 48% are declining and only 16% increasing (International Wader Study Group 2003). Many of the declining populations were found to be those of long-distance migrants and *C. c. rufa* was cited as a prime example. Problems identified as common to several long-distance migrants were their high dependency on a very limited number of key stopover sites making them particularly vulnerable to habitat loss (as in the Yellow Sea where huge areas of intertidal habitat have been lost to reclamation) and declining food resources at stopover sites arising from the unsustainable exploitation of natural resources. In the latter case, the prime examples worldwide were considered to be unsustainable shell-fish harvesting in the Dutch Wadden Sea and the exploitation of horseshoe crabs (*Limulus polyphemus*) in Delaware Bay.

As a result of *C. c. rufa*'s decline, in November 2005 the parties to the Convention on the Conservation of Migratory Species of Wild Animals, also known as the Bonn Convention (which include Argentina and Chile, but not the U.S., Brazil, or Canada), determined that *C. c. rufa* was endangered and as such added it to appendix 1 of the convention which commits the parties to strive towards protection of the species and the conservation of its habitat. In April 2007, the Canadian government's Committee on the Status of Endangered Wildlife in Canada determined that *C. c. rufa* was endangered following completion of a status review. In Brazil the Red Knot is being proposed for listing as endangered.

A problem arising from the continuous nature of the *C. c. rufa* studies over the past nine years has been a lack of time and resources to write up and publish results. All too often, data have been analyzed and partly written up only to be overtaken by the accumulation of more data. We therefore greatly welcome the opportunity that this status review affords to take stock and set out a full account of our current knowledge. We describe *C. c. rufa* in the context of worldwide Red Knot populations and assess its status, its general natural history, its habitat, its breeding system, its migrations, and its feeding ecology. We address especially the threats it faces and the conservation actions that may lead to its recovery.

TAXONOMY

Red Knots are currently classified into six subspecies, each with distinctive morphological traits, migration routes, and annual cycles. Available evidence from long-term banding
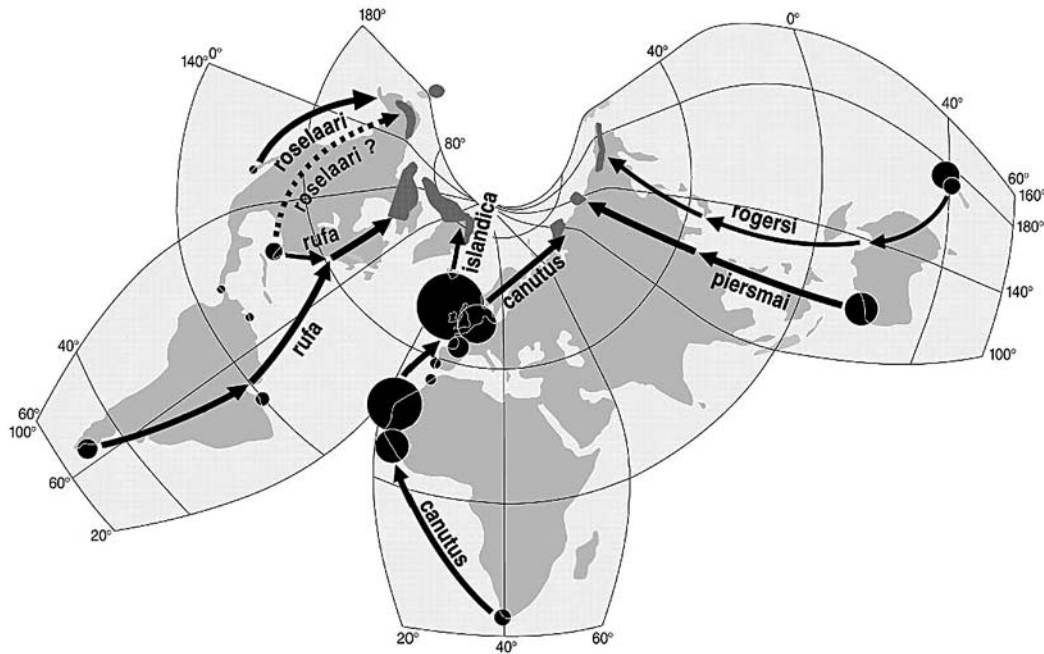
FIGURE 1. Worldwide distribution of the six recognized subspecies of the Red Knot. All breeding areas (dark gray shading) are on high-arctic tundra where the adults spend June–July. After their long-distance migrations (arrows), they spend the non-breeding season (August–May) mainly in intertidal soft-sediment habitats (dots, which are scaled according to population size). This map was prepared in 2003 and revised according to recent studies described in this review. Note that it is uncertain whether the Red Knots that winter in Northern Brazil and/or Florida are *Calidris canutus roselaari*, but some birds presumed to be *C. c. roselaari* winter on the coast of California and Baja California (map drawn by Dick Visser, provided by Jan van Gils, and reproduced with their permission).

programs indicates that distinct flyways exist (Piersma and Davidson 1992) and six separate breeding areas are known to host different populations, all of which are now formally recognized as subspecies based on body size and plumage characteristics (Tomkovich 1992, Piersma and Baker 2000, Tomkovich 2001; Fig. 1; Table 2). *C. c. roselaari* is thought to breed in northwest Alaska and Wrangel Island. Its wintering areas are unknown, but museum skins studies by Tomkovich (1992) indicate that this subspecies may migrate down the Pacific coast of North America and winter in the Gulf of Mexico. Because Red Knots wintering in Florida, Georgia, and South Carolina have a different molt schedule, and they do not migrate to southern South America, they have been referred to *C. c. roselaari*. The breeding grounds of the southeastern U.S. wintering Red Knots have not been confirmed. *C. c. rufa* breeds in the central Canadian Arctic and winters in southern Patagonia and Tierra del Fuego. Another group wintering in northern Brazil and possibly Venezuela is presumed to belong to this subspecies. *C. c. rogersi* breeds on the Chukotski Peninsula in eastern Russia and winters in

TABLE 2. POPULATION ESTIMATES OF THE SIX SUBSPECIES OF THE RED KNOT (*CALIDRIS CANUTUS*).

Subspecies	Estimated population size	Source
C. c. canutus	400,000	Wetlands International (2006)
C. c. islandica	450,000	Wetlands International (2006)
C. c. rogersi	90,000	C. D. T Minton (unpubl. data)
C. c. piersmai	50,000	C. D. T Minton (unpubl. data)
C. c. roselaari	35,000–50,000[a]	Wetlands International (2006)
C. c. rufa	18,000–35,000	This review

[a] As discussed elsewhere in this review, *C. c. roselaari* almost certainly has a much smaller population than that suggested by Wetlands International (2006).

southeast Australia and New Zealand. *C. c. piersmai* breeds on the New Siberian Islands in northcentral Russia and winters in northwest Australia, and *C. c. islandica* breeds in northern Greenland and northeast Canada and winters in northwest Europe. The nominate subspecies *C. c. canutus* breeds on the Taymyr Peninsula in western Siberia and winters in west and southwest Africa. Earlier work failed to distinguish geographically isolated groups indicating apparent panmixia caused by a late Pleistocene bottleneck (Baker et al. 1994, Piersma 1994). This analysis, however, was limited by an extreme lack of genetic variability making it difficult to distinguish between genetic variation inherited from a common ancestral stock following a recent bottleneck and current gene flow between current populations.

GENETIC EVIDENCE FOR RED KNOT SUBSPECIES

To detect possible genetic differences among Red Knot subspecies, Buehler and Baker (2005) assayed genetic variation by sequencing 675 base pairs of the fast-evolving control region of the mtDNA molecule in 91 individuals sampled worldwide. Most haplotypes in the Red Knot network differ by a single base change, producing a star-like pattern characteristic of a species that has undergone a recent bottleneck with subsequent expansion (Fig. 2). Despite the apparent lack of sorting of haplotypes into discrete genetic lineages in each subspecies, Red Knots showed low but significant population differentiation using both conventional F-statistics and exact tests. Four genetically distinct groups were found corresponding to *C. c. canutus, C. c. piersmai, C. c. rogersi,* and a North American group containing *C. c. roselaari, C. c. rufa,* and *C. c. islandica* (see Table 3 for FST summary; pooled exact test, P < 0.001).

Genetic differences between subspecies are also apparent in nuclear DNA. A genomic scan of 836 loci using amplified fragment length polymorphisms (AFLP) detected different frequencies of these dominant markers at 129 loci, and showed significant genetic differentiation
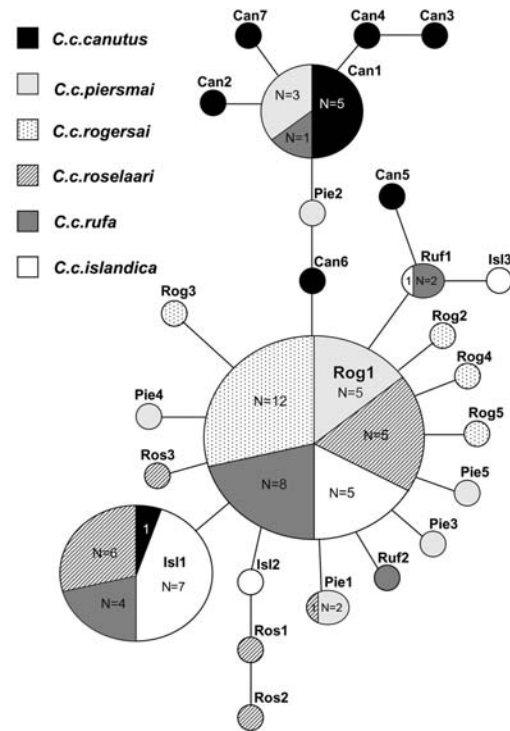

FIGURE 2. Minimum spanning network showing the relationships between haplotypes from the mitochondrial control region of Red Knots. Ovals represent haplotypes and connecting lines represent a single base pair change between haplotypes. Small open circles on lines represent multiple base pair changes between haplotypes.

among subspecies (Fst = 0.089). The genetic distance between *C. c. roselaari* and *C. c. rufa* is small (0.1) but similar to the genetic distance between *C. c. rogersi* (southeastern Australia and New Zealand) and *C. c. canutus* (Eurasia).

The demographic history of Red Knot populations can be deduced from the genetic signature in the control-region sequences, providing they are selectively neutral (which appears to be the case in Red Knots) and can be done by computing the number of mutational differences

TABLE 3. ESTIMATES OF F_{ST} FOR POPULATION DIFFERENTIATION IN RED KNOTS (BELOW DIAGONAL) CALCULATED USING MtDNA CONTROL REGION SEQUENCES.

	C. c. canutus	*C. c. islandica*	*C. c. piersmai*	*C. c. rogersi*	*C. c. roselaari*	*C. c. rufa*
C. c. canutus	0	+	+	+	+	+
C. c. islandica	0.19	0	+	+	–	–
C. c. piersmai	0.07	0.12	0	+	–	–
C. c. rogersi	0.27	0.20	0.07	0	+	–
C. c. roselaari	0.17	–0.04	0.08	0.15	0	–
C. c. rufa	0.23	0.005	0.07	0.05	0.002	0

Note: Above the diagonal + indicates the relationship was significant (P = 0.01) and - indicates not significant (P > 0.01).

between each pair of sequences in individual birds. These pair-wise differences in Red Knot subspecies have a single peak pattern expected when a population expands after a recent bottleneck (i.e., most birds have haplotypes that differ by only one–three mutations; Fig. 3).

Coalescent modeling of the sequence variation using a rate of molecular evolution calibrated for shorebirds estimated that divergence times of populations representing all six subspecies of Red Knots occurred within the last 20,000 yr (95% CI: 5,600–58,000 yr ago), thus corresponding to the Last Glacial Maximum 18,000–22,000 yr ago. This basal split separated *C. c. canutus* in central Siberia that migrated to western Africa from a lineage that expanded into eastern Siberia and began to migrate to Australia (the ancestor of *C. c. rogersi* and *C. c. piersmai*).

As the ice retreated the latter lineage eventually expanded across Beringia into Alaska and established the North American lineage about 12,000 yr ago (95% CI: 3,300–40,000). At this time an ice-free corridor had opened between the ice sheets covering the Rocky Mountains to the west and the Great Plains to the east, which served as a dispersal route for an assortment of organisms including humans, other mammals, and probably birds. This corridor was oriented northwest–southeast, and thus may have guided the evolution of a new migratory pathway between Alaska or the western Canadian Arctic and the southeastern U.S. As the ice sheets retreated further eastward across the high Arctic of Canada the ancestral population was fragmented sequentially within the last 5,500 yr into three breeding populations, corresponding today to *C. c. roselaari, C. c. rufa* and *C. c. islandica*. If this is correct, then the present wintering flocks in the southeastern U.S. are properly attributed to *C. c. roselaari* and we would predict that they return annually to their ancestral breeding grounds in arctic northwestern North America. Furthermore, the migration pathways of *C. c. rufa* and *C. c. islandica* are newly evolved responses to the eastward expansion of their breeding ranges. The divergence of *C. c. piersmai* and *C. c. rogersi* was estimated to have occurred about 6,500 yr ago (95% CI = 1,000–23,000), probably as a consequence of their isolated breeding ranges in the New Siberian Islands and the Chukotski Peninsula in Russia.

Given the recency of these divergence times, it is not surprising that the level of genetic differentiation in these neutral mtDNA sequences and nuclear AFLP is small. Time has not been sufficient for mutations to accumulate in these DNA regions to track evolutionary changes operating in the more immediate scale of ecological time. In such cases, conservation geneticists have cautioned that these apparent small genetic differences in neutral DNA sequences should not be misinterpreted in defining subspecies (Avise
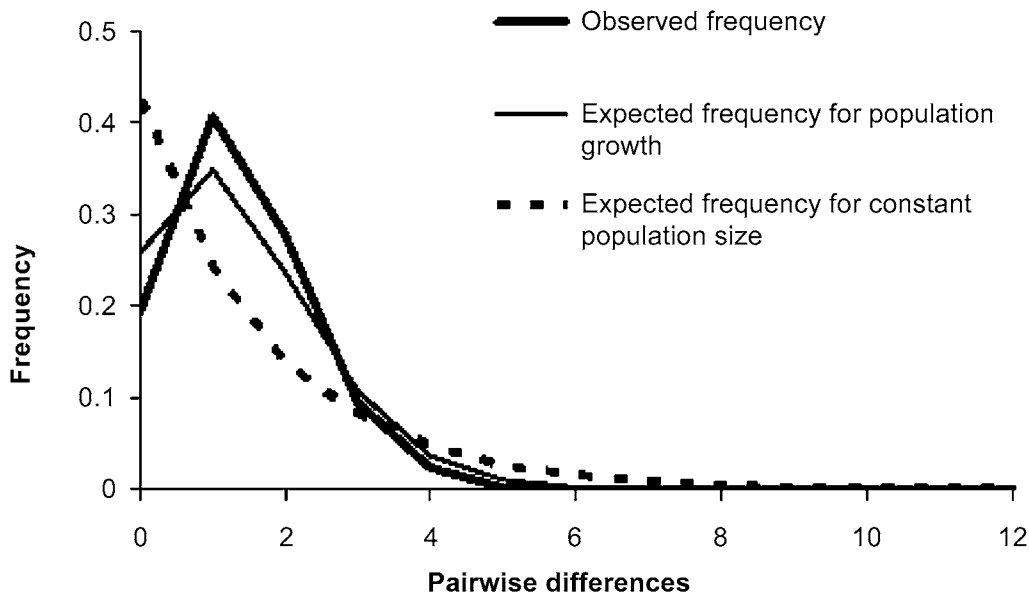

FIGURE 3. Observed and expected mismatch distributions of mitochondrial control region sequences in Red Knots. Red Knots closely match the pattern expected under population growth in the recent past.

1989). Instead, more emphasis should be placed on morphological and ecological differences because they likely track more immediate adaptive changes that are much more rapid responses to positive natural selection.

Despite the lack of fixed genetic differences among subspecies, the population divergence time of the Red Knots that winter in the southeastern U.S. (presumed to be *C. c. roselaari*) and those that winter in Tierra del Fuego (*C. c. rufa*) is estimated to be about 1,200 yr ago (Buehler and Baker 2005). Therefore, these populations have not been exchanging a significant number of individuals per generation for a long time, and clearly are independent units for conservation. This conclusion is supported by other biological information such as different primary molt schedules and, as described below, the lack of exchange of color-marked individuals.

ECOLOGICAL AND MORPHOLOGICAL EVIDENCE FOR SUBSPECIES IN NORTH AMERICA

Because *C. c. islandica* has a completely separate breeding range in northeastern Canada and Greenland, winters in western Europe, and has brighter breeding plumage and considerably shorter average bill length than other Nearctic-breeding Red Knots, it clearly warrants subspecies status (Roselaar 1983). Knots attributed to *C. c. rufa* and *C. c. roselaari* are much paler by comparison and have much longer average bill length. To our knowledge no one has adequately compared morphological variation in *C. c. rufa* and *C. c. roselaari* populations. To address this inadequacy, bill length and body weight were measured in samples of Red Knots from Bahía Lomas in Chile (the Tierra del Fuego population [TDF]), Maranhão in northern Brazil (MA population) and Florida (southeastern U.S. population). The samples were selected because all specimens were sexed molecularly (Baker et al. 1999a.), and thus the sexes could be analyzed separately. Additionally, they were taken in January or February which reduces variation in body weight due to different periods of the annual cycle. As in all Red Knots, sexual dimorphism in both bill length and body weight is apparent, with females having longer bills (Fig. 4a) and higher body mass (Fig. 4b) on average than males in all three populations. Comparisons among localities for each sex separately showed highly significant geographic variation. Analysis of variance followed by HSD post hoc tests for unequal sample sizes revealed that average bill length is significantly longer in Red Knots from both Florida and Maranhão in northern Brazil than from Bahía Lomas in Tierra del Fuego (females,

P < 0.001; males, P < 0.01) indicating that these populations are discrete (but no significant difference was found between the bill lengths of birds from Florida and Maranhão). Conversely, controlling for differences in mass related to sex, size (using bill length), and whether a bird is in primary molt, Red Knots wintering in Bahía Lomas have significantly lower mass than those wintering in Florida (P < 0.001), and knots wintering in Maranhão have significantly lower mass than knots wintering in the other two sites (P < 0.01) (Niles et al. 2006; Fig. 4b). However, lower body weight in more tropical wintering populations of Red Knots is also demonstrated in Australia (C. D. T. Minton, unpubl. data).

In addition to the significant differences in these ecologically important biometrical variables, a small but apparently diagnostic difference occurs in winter plumage in Florida Red Knots. All 26 collected specimens from western Florida have more heavily marked flanks and throats, and have more pronounced brown flecks and vermiculations extending further distally on the background white plumage of the breast and belly. Knots from Maranhão closely resemble the ventral plumage of the Tierra del Fuego population.

EVIDENCE FOR DISCRETE WINTERING POPULATIONS

In addition to these morphological and ecological differences, discrete wintering populations are evident. Color-banding studies have been conducted where individuals are banded with color-marked flags based on the wintering grounds where they were captured. Based on re-capture and resighting data, individuals from the two northernmost populations in Florida and Maranhão have not been recaptured or re-sighted in Tierra del Fuego, and vice versa. Moreover, extensive searches of the Maranhão flocks in the austral summers of 2004 and 2005 failed to find any Red Knots marked from Tierra del Fuego, or any birds with southeastern U.S. color combinations, indicating that they are a completely separate population (Baker et al. 2005a). However, 15 of the 46 Red Knots marked in Maranhão with individually inscribed blue flags were resighted in Delaware Bay in May–June 2005, showing that at least some of these birds pass through the bay each spring.

One possibility is that both the Maranhão and southeastern U.S. Red Knots are *C. c. roselaari,* in which case the risk of extinction of this subspecies and *C. c. rufa* will be significant, because both have winter range census populations of only 15,000–20,000 (Baker et al. 2005a, B. A. Harrington, unpubl. data; B. Winn, pers.
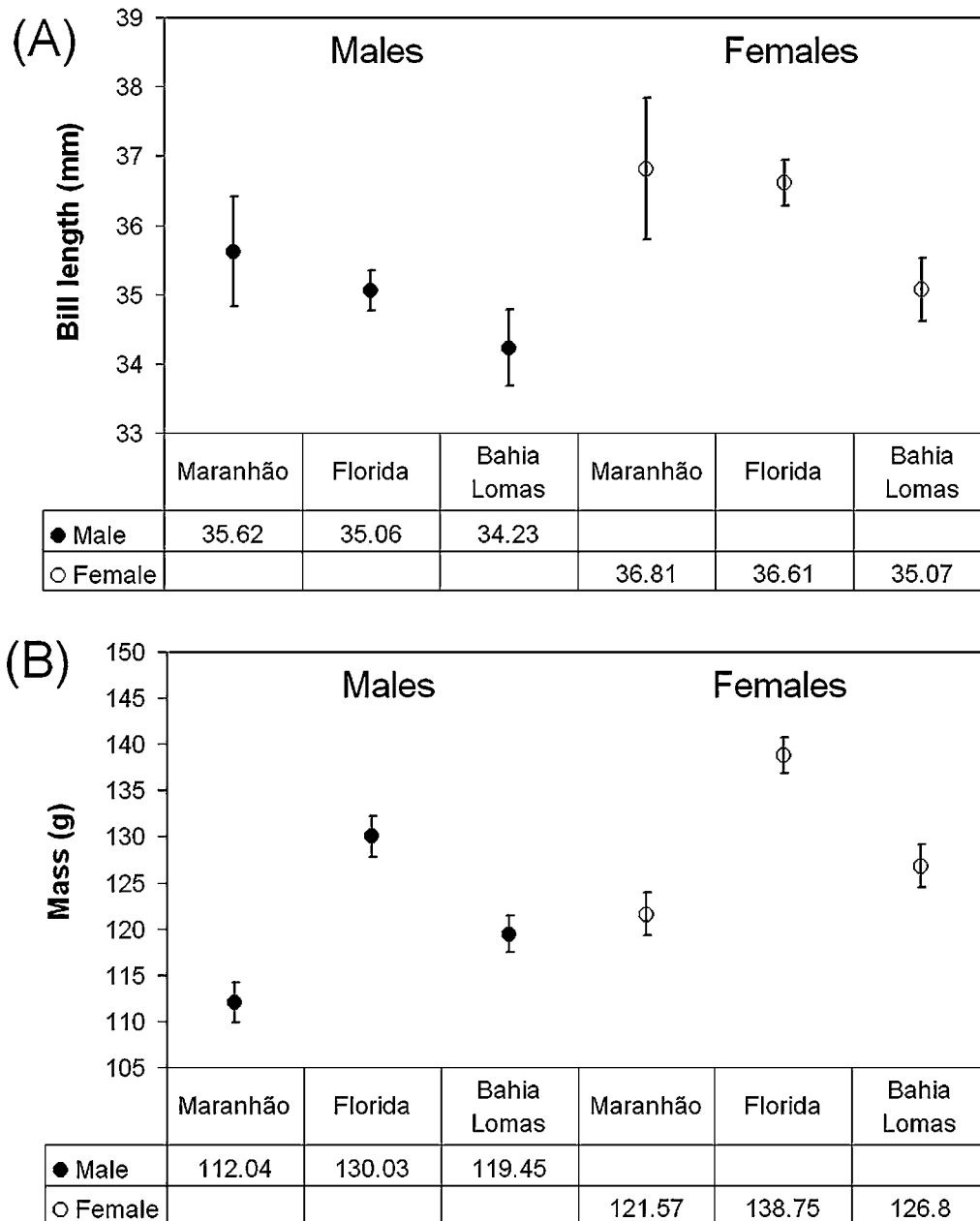
FIGURE 4. Biometrical variation of male and female Red Knots in the wintering populations of Maranhão (Brazil), Florida, and Bahia Lomas (Tierra del Fuego) indicated by (A) bill length and (B) body mass (mean ± 95% confidence intervals (data are from Baker et al. 2005a and Niles et al. 2006).

comm.). Based on genetic data, the effective population size of either subspecies is probably in the order of 1,000–2,000 adult breeders, as the effective number of breeders can be as low as about 10% of the adult population (Whitlock 2000). At this threshold of effective population size, both theoretical modeling and empirical estimates of population genetic parameters predict a much greater risk of extinction both from mutation accumulation in the long term and from the immediate ecological threats to small populations (Whitlock 2000).

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).