

The migration system of the Red Knot *Calidris canutus rufa* in the New World

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Morrison, R.I.G. & Harrington, B.A. 1992. The migration system of the Red Knot *Calidris canutus rufa* in the New World. *Wader Study Group Bull.* 64, Suppl.: 71-84.

The main features of the migration system of the Red Knot *Calidris canutus rufa* in the New World have now been determined from distributional and banding studies carried out on an international scale. The North American population appears to consist of two main groups. The largest, estimated to involve some 100,000 - 150,000 birds, breeds in the central Canadian Arctic and winters in the southern parts of South America, principally in Tierra del Fuego and Patagonia. Its southward migration route may be traced through James Bay, the eastern seaboard of the U.S.A., and northern South America, before it appears on the Atlantic coast of Argentina. The passage northwards occurs up the coast of Argentina to the coastal lagoons in southern Brasil (and perhaps Uruguay), then to northern Brasil, and onwards to Delaware Bay on the east coast of the U.S.A., before heading inland through James Bay. The second, smaller group, consisting of a few tens of thousands of birds, winters mainly in Florida, with smaller numbers being found around the Caribbean and parts of the north coast of South America. Less is known about the movements of this group, though it appears likely that its members move northwards through the interior of North America during the spring and may occupy the western end of the breeding range; southward migration occurs through the eastern seaboard of the U.S.A. Banding studies have provided information on various aspects of the biology of Knots, including where the birds moult, and the changes in mass that occur at some of the important stopover areas, enabling estimates of potential flight range to be made.

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INTRODUCTION

The New World race of the Red Knot, *Calidris canutus rufa*, is one of three major groups of Knots found in the North American Arctic. Knots breeding in the northeastern Canadian Arctic (see Godfrey 1986, 1992) belong to the race *islandica* (Roselaar 1983), which migrates to European wintering grounds (see Morrison 1975, 1984; Davidson & Wilson 1992). Knots migrating through Alaska, some of which may breed in the Russian Arctic (Kessel 1989), as well as the Alaskan breeding population itself, have been referred to the race *rogersi* (Portenko 1972, but see Tomkovich 1992); this group may winter in Australasia (unpublished data, Bird Banding Laboratory; see Morrison 1984). *Rufa* occupies breeding grounds in the central Canadian

Arctic (Godfrey 1986) and the majority migrate to wintering areas in the southern part of South America along the coastlines of Tierra del Fuego and Patagonia (Morrison 1984; Harrington 1986; Morrison & Ross 1989). A smaller part of the population winters in Florida and around the coasts of the Gulf of Mexico and northern South America (Harrington *et al.* 1988; Morrison & Ross 1989). This review summarizes knowledge that has been obtained through various international studies on the migration system and distribution of the birds, and draws attention to some of the gaps in information which remain. Movements of the two main wintering groups of *rufa* are treated separately. Banding and colour-marking studies are not reviewed in detail, though significant records are included as appropriate.

TAXONOMY

Rufa is distinguishable from *islandica* and the nominate *canutus* in breeding plumage, being much paler in appearance, especially on the back (Conover 1943). Details of differences may be found in Cramp & Simmons (1983) and Tomkovich (1992). Although most *rufa* in breeding plumage are notably pale, birds with darker cinnamon breasts have been seen in areas ranging from southern Argentina to James Bay. Conover (1943) commented on the variability in the colouration of the underparts. The significance of these observations is not currently understood.

Measurements of museum specimens of known sex show that *rufa* is quite similar in bill size to *canutus*, and larger than *islandica*, which is larger again than *rogersi*. There appears to be less difference in wing length between *rufa*, *islandica* and *canutus*, with *rogersi* again being smaller (Table 1). Measurements from mixed sex samples caught in the field from various parts of the birds' ranges again show that *rufa* and *canutus* are similar in bill length and larger than *islandica* (Table 2). Within the *rufa* group, there does not appear to be any major morphometric difference between the populations wintering in Argentina and Florida (Table 2, Harrington *et al.* 1988).

Genetic analyses, involving protein electrophoresis to investigate enzyme polymorphism, and restriction mapping and polymerase chain reaction methods to analyse differences in nuclear and mitochondrial DNA, have indicated that *islandica* from breeding grounds on northern Ellesmere Island are distinct

Table 1. Summary of mean wing (maximum chord, uncorrected for variation between observers), bill (exposed culmen) and tarsus measurements of museum specimens of Red Knots *Calidris canutus*. All measurements in mm. Compiled from Cramp & Simmons (1983) and Godfrey (1986).

Race	Wing		Bill		Tarsus	
	male	female mixed	male	female mixed	male	female mixed
<i>islandica</i>	169	173	32.6	34.4	30.5	31.4
		171		33.5		31.0
<i>canutus</i>	167	170	34.7	36.6	31.4	31.6
		169		35.8		31.5
<i>rufa</i>		170		35.6		32.2
<i>rogersi</i>	163	168	31.5	33.9	30.0	31.5
		166		32.7		30.8

Table 2. Mean bill lengths of mixed-sex field samples of Red Knots.

Race/ Location (year)	mean (mm)	(n)	SD	Refer- ence
<i>rufa</i>				
James Bay 1978	35.3	(32)	1.73	1
James Bay 1979	35.2	(43)	1.76	1
James Bay 1982	35.5	(34)	1.59	1
Surinam 1978	35.6	(35)	1.68	2
S. Brasil 1985a	34.9	(20)	1.97	3
S. Brasil 1985b	35.9	(20)	2.15	3
Massachusetts	35.6	(751)	1.94	4
New Jersey	35.6	(439)	1.78	4
Florida	36.3	(238)	1.94	4
Argentina	36.2	(273)	1.92	4
<i>islandica</i>				
Iceland 15 May 1970	33.1	(146)	-	1
Iceland 19 May 1971	34.0	(118)	-	1
Iceland 2 May 1972	32.3	(156)	3.19	5
Iceland 23 May 1972	32.4	(517)	2.10	1
Alert 1974	32.0	(23)	1.47	5
Alert 1986	33.0	(40)	2.07	6
Norway 1985	33.0	(96)	1.81	7
Greenland	32.2	(25)	-	8
Teesmouth	32.5	(59)	1.72	7
Morecambe Bay/Wash	33.0	(163)	-	9
<i>canutus</i>				
Mauritania	35.1	(280)	1.78	10
W. France	35.7	(583)	1.85	10
Germany	35.1	(291)	1.86	10

References: 1: Morrison (unpubl. data); 2: Morrison & Spaans (unpubl. data); 3: Antas & Morrison (unpubl. data); 4: Harrington *et al.* (1988); 5: Morrison (1975); 6: Morrison & Davidson (1990); 7: Davidson & Evans (1986); 8: Cramp & Simmons (1983); 9: Dick *et al.* (1976); 10: Piersma *et al.* (1987).

from *rufa* sampled on migration and wintering areas (Baker 1992). *Rufa* and *islandica* can also be distinguished by the species of parasitic nematode worms inhabiting the birds' proventriculus (R.C. Anderson, University of Guelph, pers. comm.).

BREEDING GROUNDS

Rufa breeds in the central Canadian Arctic from Victoria Island southeastwards to Southampton Island and Coats and Mansel islands in northern

Hudson Bay, as well as on the east coast of the Foxe Basin (Godfrey 1986) (Figure 1). It also breeds on at least some of the islands of the Foxe Basin (e.g. Rowley Island, R.I.G. Morrison unpubl. data). Details of the breeding range, however, are poorly known. Little information is available for the extensive areas between Southampton Island/Foxe Basin and southern Victoria Island, and the eastern and western extremities of the range are unclear. For instance, do Knots breed on the west coast of Baffin Island in the Foxe Basin, and does their breeding range in the west extend to northern Victoria Island and Banks Island, where they were not seen during extensive surveys by Manning *et al.* (1956)? It is also not known whether there is any overlap between the ranges of *rufa* and *islandica*. The dividing line appears to be around Lancaster Sound (approx. 75°N), though this must be regarded as only approximate: *islandica* appears to occupy northern Prince of Wales Island and Somerset Island (Manning & Macpherson 1961; Godfrey 1986, 1992).

MOVEMENTS OF POPULATIONS WINTERING IN SOUTH AMERICA

Southward migration

Little is known about how *rufa* (or other races) depart from the Arctic following their breeding attempt. Do they need to accumulate fat reserves for a flight to the first known migration areas (as do arctic-breeding geese), and, if so, do they depend on tundra food resources or can they make use of intertidal resources at arctic premigratory gathering points or staging areas? There are reports of large numbers of shorebirds occurring during late summer at areas with extensive tidal flats, such as Cresswell Bay on the east side of Somerset Island (Alliston *et al.* 1976) and Bay of God's Mercy on the south coast of Southampton Island (F.G. Cooch pers. comm.). Whether large numbers of Knots occur in these flocks is not clear, though the dates involved have generally been later than the main period of adult Knot migration southward.

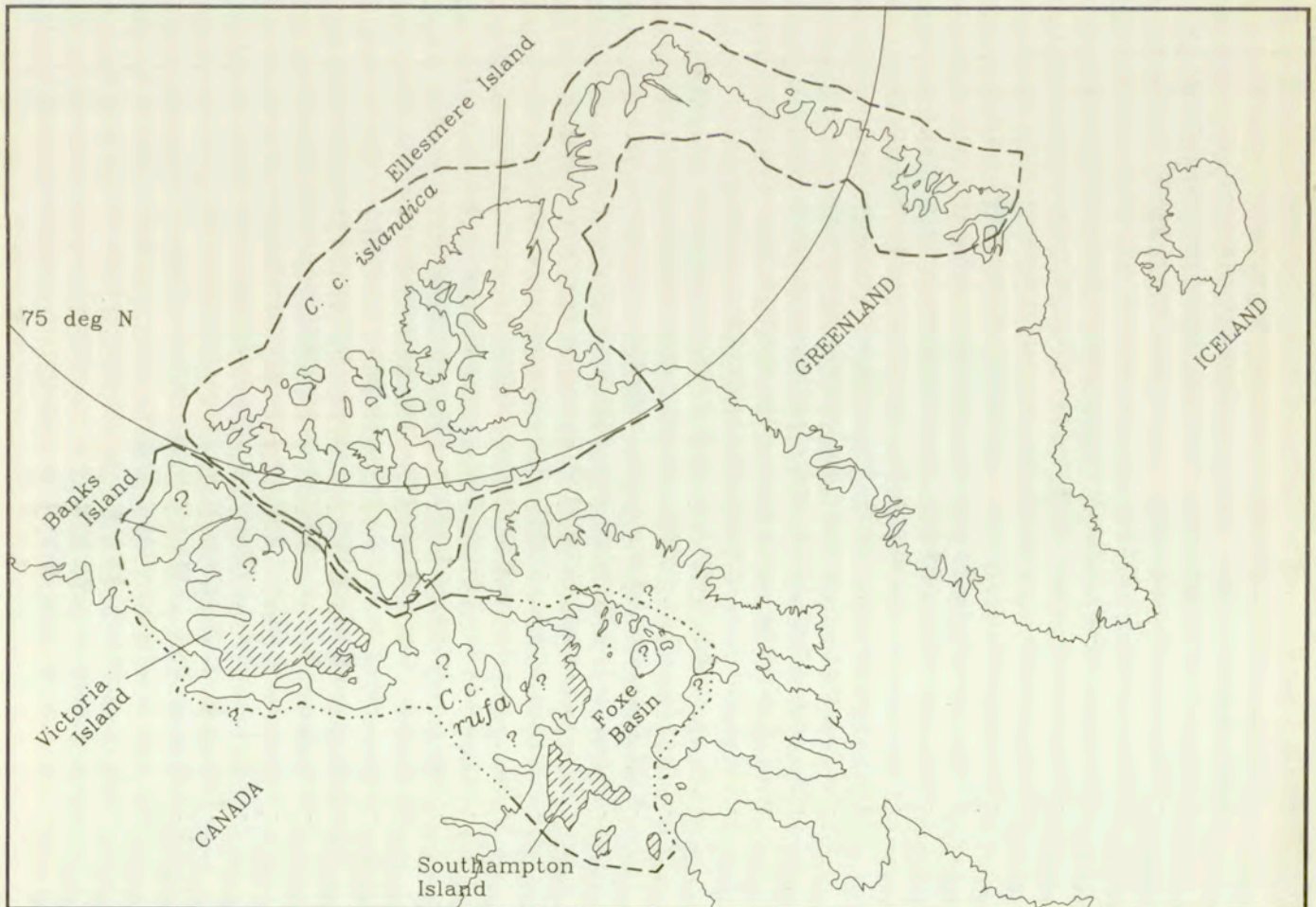


Figure 1. Breeding range of Red Knots *Calidris canutus rufa* (shown with broken shading) and *C. c. islandica* in the Canadian Arctic.

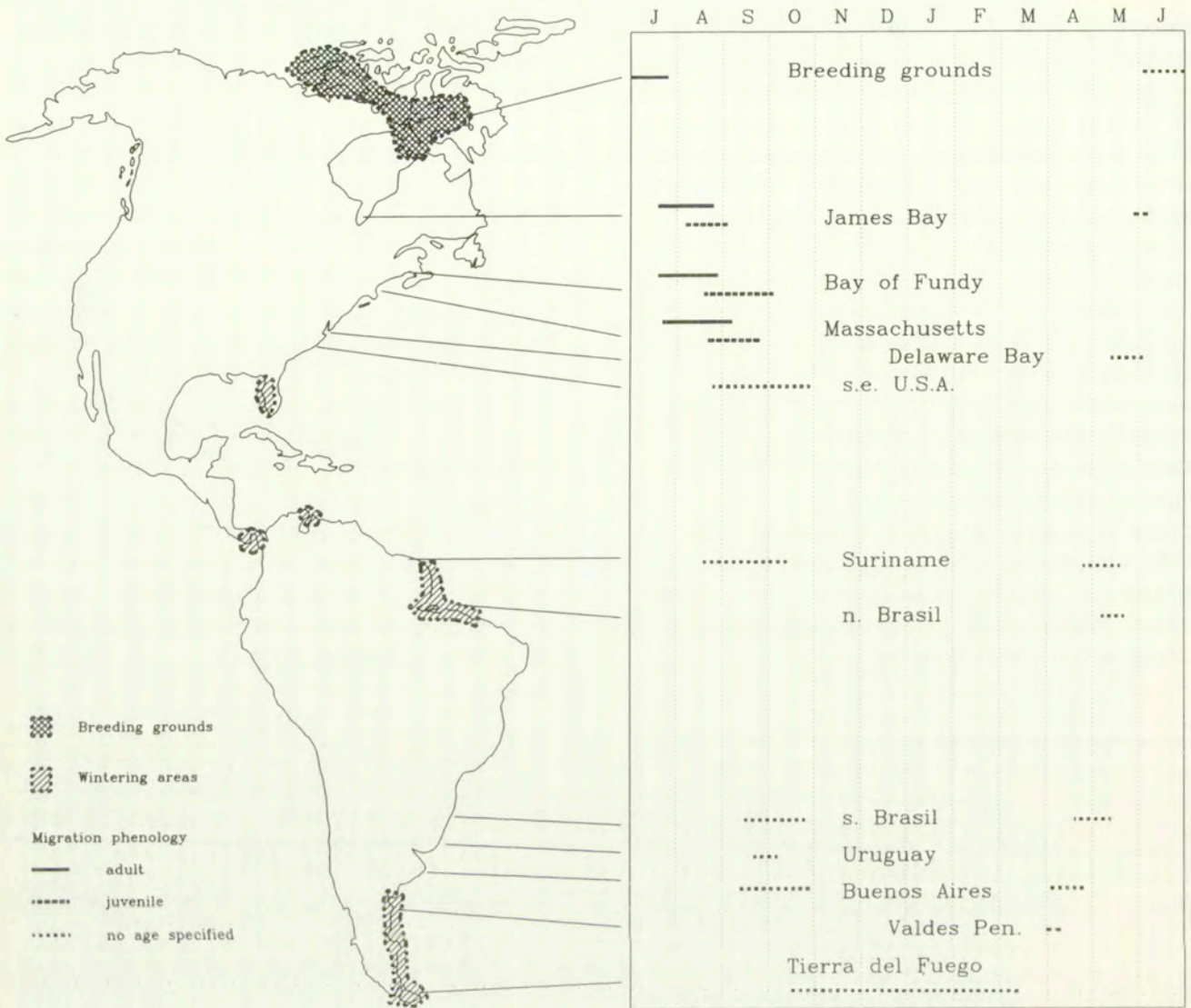


Figure 2. Key stopover and wintering areas and migration phenology of Red Knots *Calidris canutus rufa* in North and South America.

The first known major autumn stopover area for *rufa* (key areas and migration phenology are illustrated in Figure 2) is along the west coasts of James Bay and Hudson Bay (Hope & Shortt 1944; Morrison & Harrington 1979). Numbers of adults build up from around mid July, reaching a peak in late July or early August, with some persisting into the latter half of August. Juveniles appear later, usually towards the end of the first week in August, in lower numbers, and their passage continues through August. Some Knots, mainly juveniles, occur much later; there are records of flocks well into October (R.I.G. Morrison & C.C. Rimmer, unpubl. data).

Aerial surveys of the Ontario coastlines of James Bay and Hudson Bay in late July/early August in the late 1970s produced totals of some 7,000 - 10,000 Red Knots, with more recent surveys reporting 5,000

- 15,000 (Morrison & Harrington 1979; Morrison 1984; R.I.G. Morrison & R.K. Ross unpubl.). Most Knots were concentrated in a few favoured areas, a phenomenon which occurs throughout their migration and wintering areas. In southern James Bay, for instance, about 40% of the birds occurred on only 11% of the coast, and this proportion rose to about 70% on approximately 22% of the coast (Morrison 1983). Knots in James Bay prefer the lower intertidal areas for feeding, usually occurring in areas characterized by extensive sandflats; such areas are found in both the southern and northern parts of James Bay, as well as along the southwestern coast of Hudson Bay. The distribution of the birds appeared to be related to the preferred size class of their principal prey, the bivalve *Macoma balthica* (Morrison 1983).

Knots start appearing on the Atlantic coast staging grounds at around the same time as in James Bay, i.e. from mid July onwards (Harrington 1986), suggesting that initial migration southwards from the breeding grounds is rapid or that different parts of the breeding population may be involved. In the Canadian Maritime Provinces, adult counts peak in late July/early August, with maximum numbers of juveniles occurring between late August and mid September (Morrison 1976). Counts of adults at the east coast U.S.A. sites have risen markedly by the end of July, though peak numbers do not usually occur until mid August; most adults have departed from the northeastern U.S.A. seaboard by late August and early September (Harrington & Leddy 1980; Harrington 1986).

On the northeastern U.S.A. seaboard, Knots are concentrated between Chesapeake Bay and Cape Cod Bay. Peak counts at International Shorebird Survey sites in the mid to late 1970s were in the range 6,000 - 9,000 (very similar to survey totals in James Bay/Hudson Bay). Between 1975 and 1978, 60-90% of the birds occurred in two states, Massachusetts and New Jersey; the top five sites in any given year accounted for 75-85% of the total, although the relative importance of the major sites varied from year to year (Morrison *et al.* 1980).

After mid August, the pattern of migration in eastern North America changes: juveniles make their appearance - in much lower numbers than adults and scattered over a much wider area, including many at inland sites where adults are not generally found. Peak counts of juveniles tend to occur in early September in Massachusetts. While numbers in the northeastern U.S.A. decrease after mid August, they tend to increase in the mid Atlantic states, and increase throughout September and October in the southeastern and Gulf coast states (Harrington & Leddy 1980; Harrington 1986). Taken together, these count data indicate that after mid August, juvenile Knots fly on a broad front to coastal sites south of New England, where they mix with adults that have not yet migrated to South America.

From the eastern U.S.A., *rufa* launches a trans-oceanic flight that takes the birds through the Guianas on the north coast of South America. The main passage period appears to be the second half of August and first half of September, with another peak in the first half of October (Spaans 1978). Up to 900 Knots were observed during fieldwork in Surinam in mid September 1978 (Morrison & Spaans

1979), and aerial surveys of the Guianas in late August/early September 1982 produced records of some 2,450 Knots (Harrington & Leddy 1982). Very few Knots appear to remain in Surinam during the northern winter: Spaans (1978) reported very few during ground work, and none was identified on aerial surveys in January 1982 (Morrison & Ross 1989). Knots appear to move through Surinam during southward migration fairly rapidly: observations have been made of many shorebirds, including Knots, passing eastwards along the coast of Surinam during September (Spaans 1978; R.I.G. Morrison & A.L. Spaans unpubl.), and it seems likely that the birds move on to staging areas, perhaps in northern Brasil, before heading south across Amazonia.

The southward journey onwards from the northern/northwestern coast of South America appears to take the birds directly across Amazonia, a flight of some 4,000 km, to the southern parts of Brasil or the coastal areas of Buenos Aires Province in Argentina near the Rio de la Plata. Knots have been observed passing down the coast of Rio Grande do Sul in southern Brasil in good numbers in some, but not all years, usually in October (W. Belton pers. comm.). Specimens of adults have been collected in this area from mid September and several juveniles have been taken in southern Brasil in September, as well as in Uruguay from September onwards. Adult male Knots have been collected in Uruguay between 21 September and 1 October (R.I.G. Morrison unpubl. data). Myers & Myers (1979) observed Knots in Buenos Aires province, Argentina, by late August. Blanco *et al.* (1988) reported arrival in Buenos Aires Province at Punta Rasa at the southern end of Bahia Samborombon in late August/early September; there was no clear peak of southward migrants and some 40-60 Knots were observed throughout the northern autumn/southern spring. Passage down the coast of Argentina occurs during October (Harrington 1986).

Populations wintering in South America

In Argentina, Myers & Myers (1979) reported that Knots were seen regularly in Buenos Aires province during the northern winter/austral summer, generally in flocks of 10-30; the species was almost exclusively maritime in habitat use, being found on sandy beaches and mudflats.

The most important wintering grounds of the Red Knot are in Tierra del Fuego and along the coastlines of Patagonia between the Valdes Peninsula and Tierra del Fuego in Argentina (Morrison & Ross 1989). The most important individual site yet identi-

fied is Bahia Lomas, in the Chilean sector of Tierra del Fuego, at the eastern end of the Strait of Magellan. Bahia Lomas contains vast expanses of mudflats, backed by grasslands. In January 1985 it held some 42,000 Red Knots, or about 55% of the South American total of 76,400 counted during the Canadian Wildlife Service Shorebird Atlas Project aerial surveys (Morrison & Ross 1989). Other important areas included the enormous bay system of Bahia San Sebastian and the intertidal restinga areas along the Atlantic coast of Argentinian Tierra del Fuego (see also Devillers & Terschuren 1976). Altogether, Tierra del Fuego held some 53,000 Red Knots, or about 70% of the South American survey total (Morrison & Ross 1989). Most of the remaining large concentrations in the south of the continent occurred between Tierra del Fuego and the Valdés Peninsula.

No comparable concentrations of wintering Knots have been found elsewhere in South America. Some were found on the north coast of the continent, mostly in north-central Brasil, with smaller concentrations near Lake Maracaibo in Venezuela. No Knots were identified on the Pacific coast of South America during the aerial surveys, although small numbers have been reported south to Peru and Chile (e.g. Hughes 1976; Sallaberry 1989).

Many juveniles move south to wintering grounds in Argentina, as shown by the recovery of a juvenile banded in September in Massachusetts in southern Brasil in November the same year, by the presence of juveniles in museum specimens collected in southern Brasil in the autumn (some as early as September) and winter (R.I.G. Morrison unpubl. data), and the observation of juveniles in wintering flocks in Tierra del Fuego (Harrington & Morrison 1980a, b).

Northward migration

After spending the northern winter/southern summer between November and February in the south, Knots begin their northward migration during March. At the Valdés Peninsula, Argentina, 5,000 - 6,000 Knots were observed during peak migration in early April 1980 (Brayton 1986) and some 20,000 occurred in early April 1981 (B.A. Harrington unpubl. data). At Punta Rasa, over 1,000 Knots were observed during the peak of northward migration in 1988, which again occurred in early April, the passage finishing around the end of April (Blanco *et al.* 1988). Myers & Myers (1979) reported Knots up to 22 April 1974 in Buenos Aires province, and 110 at the Valdés

Peninsula as late as 27 May 1974 (the date suggesting these were 'summering' birds?). The migration continues northwards to the coastline of Rio Grande do Sul Province in southern Brasil. Little is currently known of the importance of the coast and associated coastal lagoons in Uruguay, some of which are important for wintering Nearctic shorebirds (Morrison & Ross 1989). Up to 5,000 Knots have been recorded near Chui, near the border of Uruguay and Brasil, and 85 Knots were observed at the Laguna da Rocha on 16 March 1986 (R. Vaz-Ferreira, pers. comm.). The Rio Grande do Sul coast comprises one of the longest (over 600 km) ocean beaches in the world and is backed in places by shallow, brackish lagoons. The most important of these is the Lagoa do Peixe, where over 11,000 Knots were found on migration during late April 1984; a further 10,000 Knots occurred on ocean beach habitats north of the Lagoa do Peixe at Pinhal (Harrington *et al.* 1986). Knots reach very high weights, some of the highest ever recorded (see below), at the Lagoa do Peixe, and the area appears to provide the last major stopover sites before a direct flight across Amazonia at least as far as the north-central coast of Brasil, where flocks of up to 5,000 Knots were found in mid May in 1987, including birds which had been colour-marked at the Lagoa do Peixe (R.I.G. Morrison, R.K. Ross & P. Antas unpubl. data).

A small spring passage occurs in Surinam (Spaans 1978), but it appears that the largest concentrations are found to the east of the mouth of the Amazon River. The migration northwards is very rapid, and the stopover in northern Brasil is probably rather short (up to a week?), as indicated by the observation of marked birds from the Lagoa do Peixe in Delaware Bay, New Jersey, just 13 days after the first Knots had been seen leaving the lagoon, some 8,700 km to the south (Harrington 1986).

Knots pass northwards along the Atlantic coast of the U.S.A. from the middle to the end of May (Harrington 1986). In some years, major flights have been observed passing along the coasts of Georgia and North Carolina, e.g. over 12,000 in Georgia on 22 May 1971 (Harrington 1982), but in most years landfall is apparently made on the mid Atlantic coast. The most spectacular staging area currently known is on the New Jersey shoreline of Delaware Bay, where concentrations of Knots have averaged around 60,000 birds in the latter part of May in recent years, with a reported maximum of up to 95,000 birds (Dunne *et al.* 1982), more *rufa* than have been found anywhere else in the Western

Hemisphere. The timing of migration of Knots in Delaware Bay coincides with the egg-laying period of the Horseshoe Crab *Limulus polyphemus*, the eggs forming the major food of the birds at this site.

The major exodus from Delaware Bay occurs in the last few days of May or first few days of June. The migration route strikes inland and northwards, and large flights of Knots have been observed in southern James Bay, again in the last few days of May and in early June (R.I.G. Morrison unpubl. data). In 1982, the first major arrivals were observed in James Bay on the day following a mass exodus from Delaware Bay; the flight between the two areas would take in the order of 20 hours (1,400 km at 65-75 km/h, see Zwartz *et al.* 1990). In some years, quite large concentrations have been found at locations around Lake Ontario, e.g. 400 on 18 May 1969 at Presqu'île Provincial Park, 1,500 at Prince Edward Point on 30 May 1979, and 1,000 near Amherstview on 21 May 1985 (McRae 1982; Weir 1989). Such birds probably represent weather-induced dropouts from the main migration overhead (McRae 1982). Knots pass rapidly through southern James Bay in spring, stopping only briefly (less than one day) on the coastal marshes to feed (the mudflats are still covered with ice) before resuming their flight northwards to the breeding grounds, where they arrive in the first half of June.

MOVEMENTS OF FLORIDA-NORTHERN HEMISPHERE WINTERING POPULATIONS

A second, much smaller segment of the New World population winters well to the north of the main Tierra del Fuego/Patagonian group. Largest numbers have been reported from west Florida, where about 10,000 birds winter (Harrington 1982; Harrington *et al.* 1988), with smaller numbers occurring around the Gulf of Mexico, Caribbean, and possibly further east along the northern coast of South America. The largest numbers reported from the north coast of South America involve a possible 8,200 Knots on the north-central coast of Brasil, with smaller groups of 120 on the north coast of Brasil between the Amazon River and French Guiana and another 520 near the mouth of Lake Maracaibo, Venezuela (Morrison & Ross 1989). Harrington & Leddy (1980) list winter records for other U.S.A. Gulf of Mexico states, which include high counts of 752 in Alabama on 15 February 1971, 40 in Mississippi on 23 February 1979, 120 in Louisiana on 12 January 1972, and up to 1,440 in Texas in November, although

numbers in the latter state in the period December-February generally fall in the range 100 - 300. Little information is available from Mexico. In central America, Smith & Stiles (1979) indicated that between 250 and 500 Red Knots wintered on the Pacific coast of Costa Rica between February and March.

The spring migration route of this population can be traced around the west coasts of the Caribbean and Gulf of Mexico and northward through the Prairie Provinces of Canada. Reports of up to 1,700 Knots have been made in early May on the beaches west of the mouth of Lake Maracaibo (Casler & Lira 1979). A distinct passage occurs along the Gulf coast of Texas from late April to mid May, with peak counts of 2,000 - 2,500 birds at Padre and Mustang islands and 2,000 in the Galveston area. Spring numbers in the interior of the U.S.A. south of the U.S.A./Canadian border are generally scanty, but there are reports of up to 2,500 Knots in Saskatchewan (Last Mountain Lake, 21 May 1972, Lahrman 1972) and 'hundreds' in Alberta in the latter half of May (Harrington & Leddy 1980).

At least some Knots wintering in Florida travel north through the interior as shown by records of a bird banded in Florida in November being found on northward migration in Manitoba in May, and the sighting of another Florida bird on northward migration in Alberta (B.A. Harrington unpubl. data). Part of the Florida wintering population migrates north along the Atlantic coast of the U.S.A., since Florida birds have been sighted at the major stopover area in Delaware Bay in spring, though the extent of overlap is thought to be small (Harrington *et al.* 1988). Their proportional under-representation at this site may reflect the use of the interior route by part of the population.

In autumn, some Knots wintering in Florida return southwards via the Atlantic coast, where limited mixing may occur with the population wintering in Argentina. There is a passage of Knots through the Texas coast in September/October, with a second peak in November (Harrington & Leddy 1980). Some birds from the 'northern' wintering population apparently pass through James Bay, as indicated by the recovery of a Knot banded in James Bay on 31 July 1976 on the Pacific coast of Panama on 10 January 1977 (R.I.G. Morrison unpubl. data).

The breeding origin of the Florida/Gulf/Caribbean wintering group is not precisely known. The interior

migration route suggests that they occupy the western end of the range, and it is possible that some may migrate to breeding areas in northern Alaska, though northern Alaskan birds are generally referred to the Pacific population (Cramp & Simmons 1983). There appears to be a gap in the breeding distribution of Knots between Victoria Island and northern Alaska (Cramp & Simmons 1983; Godfrey 1986).

POPULATION SIZES

Current estimates for the size of the South American wintering population are in the range 100,000 - 150,000 birds. Harrington *et al.* (1988) indicated that the Patagonian population consists of about 100,000 birds; recent estimates from resighting data suggest a population of $150,000 \pm 100,000$ (B.A. Harrington unpubl. results). Morrison & Ross (1989) reported an overall South American aerial survey total of 76,400, with a Patagonian total of 67,500. The average peak spring migration number at Delaware Bay in recent years has been $60,000 \pm 40,000$, with an estimated maximum of 95,000 (Harrington *et al.* 1988; Dunne *et al.* 1982; Wander & Dunne 1982; Kochenberger 1983). These figures are in reasonably close agreement considering the different observers and methods involved.

Harrington *et al.* (1988) estimated the size of the Florida population as approximately 10,000 birds, based on the mean of $6,300 \pm 3,400$ (mean \pm SD) from four aerial surveys carried out between October and January 1980 - 1982. A minimum of several thousand more Knots apparently winter at other locations around the Gulf of Mexico and the Caribbean. Further information on the status and origins of the 8,200 Knots reported from the north-central coast of Brasil (Morrison & Ross 1989) is needed.

An interesting discrepancy currently exists between population estimates for the Patagonian group made during northward and southward migration. As described above, the estimate using resighting data, counts and aerial surveys from northward migration is 150,000, whereas that from southward migration is 50,000 - 60,000. Similar results have been obtained with other species (e.g. Ruddy Turnstone *Arenaria interpres*, B.A. Harrington unpubl. results). The reasons for this discrepancy are not clear. Possibilities include some birds overflying the east coast of North America and/or higher turnover in flocks in autumn. Numbers in James Bay do not appear to be large enough to suggest that substantial numbers

depart directly for South America, and weights in James Bay indicate that such a flight would only be a borderline possibility for individuals at the highest observed weights based on current understandings of flight range capabilities (Davidson 1984). Turnover does not appear to be especially high in flocks of Knots on autumn migration (B.A. Harrington unpubl. results).

Howe *et al.* (1989) carried out an analysis of population trends of shorebirds using data collected through the International Shorebird Survey (ISS) scheme in the U.S.A. between 1972 and 1983. Although the change in the index of Knot populations was not statistically significant, the mean annual change was -11.7% and the cumulative change over the measured period was -74.6%. Declines in the Knot population may be part of a more general decline in shorebird numbers, since the trend analysis showed three of the 12 species analysed had decreased significantly and a further six (including the Red Knot), while not decreasing significantly, showed mean annual percentage changes of -3% to -12%. Knots are faced by threats from a variety of developmental sources in many parts of their ranges (Morrison 1984; Harrington 1986; Morrison & Ross 1989). Recent counts of Knots on migration in Massachusetts in autumn have remained relatively constant (B.A. Harrington, ISS unpubl.), and updating the trend analysis with data from recent years would be helpful in assessing the current status of the population. Studies of resightings of colour-banded birds by Harrington *et al.* (1988) showed that there was apparently no interchange between the Florida and Patagonian wintering populations, with no direct exchanges of banded birds between the two areas and only four sightings of birds banded in Massachusetts or New Jersey in some 20,000 birds checked in Florida. This result, and the under-representation of Florida birds at migration sites in Massachusetts and New Jersey, indicated that there was also very little overlap on migration.

Another result from the resighting studies of Harrington *et al.* (1988) was the indication that the Patagonian population had a much lower annual survival rate than the Florida population, approximately 35% compared with 76%. Several problems exist, however, with this analysis, although the estimates were made at a time when the population was probably decreasing. A survival rate of 0.35 is well below the level at which the population would be able to sustain itself, and both figures are generally less than

those thought to apply to shorebirds the size of a Knot (Evans & Pienkowski 1984). Estimation of annual mortality from resighting/recapture data is complicated by the likelihood that complete mixing does not occur within the population being studied and because the estimate will include emigration as well as death. Another potential problem with estimation of mortality is loss of colour marks, which was reported to have occurred with cohorts of birds marked in Argentina. Examination of the figure published by Harrington *et al.* (1988) relating resighting rate with months since banding suggests that initial rates of resightings were rather similar for the Florida, New Jersey and Massachusetts birds, and that continued sightings after approximately 30 months were largely responsible for the higher estimates of mortality for the Massachusetts and New Jersey birds. It is unknown whether use of different habitats by the two populations may have caused differential band loss, but the use of hard, rocky restinga habitats by the Patagonian group makes this a possibility.

MOULT

Body feathers

Red Knots start moulting out of breeding plumage before departure from the breeding grounds. An incubating bird caught on 8 July 1987 on Rowley Island, N.W.T., showed heavy moult on head, neck, back and breast feathers, and the scapulars were also in moult. Knots trapped in James Bay on migration had mostly lost an estimated one third to one half or more of their summer plumage by mid August; most did not show any active moult of body feathers, but a few were in active moult (R.I.G. Morrison unpubl. data). Hope & Shortt (1944) commented that the Knots collected in James Bay were mostly in nuptial plumage, though in varying degrees of moult, with females most advanced.

Birds captured on migration in Surinam in mid September were again noted as being in approximately one half breeding plumage; most had suspended body moult but a few were in active moult (R.I.G. Morrison & A.L. Spaans unpubl. data). Examination of a small sample (5) of adults collected in mid September from Rio Grande do Sul, southern Brasil, again indicated that approximately one half summer plumage remained on most birds, with some but not all of the birds showing active body moult. Blanco *et al.* (1988), however, reported that birds arriving at Punta Rasa, Buenos Aires Province, Argentina, in September were in non-breeding plumage.

Body moult is finished on the wintering grounds, and by mid December is mostly complete. Harrington and Morrison (1980a, b) reported that approximately 10% (16/156) of adults examined closely in Tierra del Fuego on 11 December 1979 had some traces of breeding plumage.

Body moult into breeding plumage starts on the wintering grounds. At Punta Rasa, Buenos Aires Province, moult starts in early March and is well advanced by the first week of April (Blanco *et al.* 1988). Migrants observed at the Valdes Peninsula in early to mid April were in breeding plumage. Most birds captured on migration in southern Brasil in the latter part of April at the Lagoa do Peixe were in the last stages of completing body moult into breeding plumage. Of a sample of 119 captured on 22-25 April 1985, 51 (43%) had completed moult into breeding plumage, with the remaining 57% still showing some active moult (R.I.G. Morrison & P. Antas unpubl. data). It appears likely that most, though not necessarily all, Knots stop body moult before departing on migration. Birds at higher mass levels tended to have completed body moult compared to those at lower masses: the median mass range of actively moulting birds was 141 - 150 g, whereas the median range of birds which had completed moulting was 151 - 160 g. Birds at the higher mass levels were more likely to have completed moult: almost 40% of birds which had stopped moult weighed over 160 g, whereas only 22% of birds still actively moulting weighed over 160 g.

Flight feathers

Moult of flight feathers occurs on the wintering grounds; it has not been observed in migration areas, including James Bay, Surinam, and southern Brasil. The assertion by Prater *et al.* (1977) (quoted in Cramp & Simmons 1983) that *rufa* starts moulting wing feathers in North America and suspends the moult before migration to South America seems to be incorrect, at least as it applies to the Patagonian population. Harrington & Morrison (1980b) were able to obtain data on wing moult of Knots from photographs of flying birds taken at Bahia San Sebastian, Tierra del Fuego, on 11 December 1979. Of 119 birds, 114 (96%) were in active wing moult and only 5 (4%) were not moulting, the latter percentage being very close to the estimated proportion of juveniles in the population (4 of 87 observed closely, i.e. 5%). Most moulting birds had 4-5 unmoulted primaries remaining on the wings, and no gaps were detected in the inner wing for birds with 4 or more old primaries remaining, suggesting that secondary

moult had not yet started. These results indicate moult scores would be in the mid 20s out of a possible score of 50: assuming the moult was approximately one half completed and the duration was 100 days, moult would start in mid to late October and finish in late January/mid February. This period fits well with reported migration dates, and with the observation of Blanco *et al.* (1988) that birds had started wing moult at Punta Rasa by 11 October 1987.

MASS CHANGES DURING MIGRATION

A summary of masses of samples of adult *rufa* caught or collected at various points in their migration range is shown in Figure 3. In both James Bay and Massachusetts, mean masses of catches rose from about 125 - 130 g in the third week of July to maxima in the range 185 - 190 g, at a rate of 3-3.5 g/day. The data suggest that mean masses are slightly lower in James Bay than on the same date in Massachusetts. The mean mass of 35 birds

caught in Surinam in mid September 1979 was 132 g, though the range of 105 - 169 g suggested that some birds had put on weight for further migration while others had only recently arrived. Masses of five adults collected in southern Brasil in mid September ranged from 130 - 166 g, averaging 147 g, indicating the birds were putting on weight for further migration. One adult male in breeding plumage collected in Uruguay at the beginning of October weighed 175 g, suggesting considerable migration was still to take place.

No information is currently available from the wintering grounds in Argentina.

Some of the highest masses ever recorded for Red Knots have been obtained during the northward migration at the Lagoa do Peixe, Rio Grande do Sul, southern Brasil during late April/early May. Mean masses of samples of captured Knots rose from 149 to 164 g between 22 and 25 April 1985 (P. Antas & R.I.G. Morrison unpubl. data) and Harrington *et al.* (1986) reported a mean mass of 202 g for 280

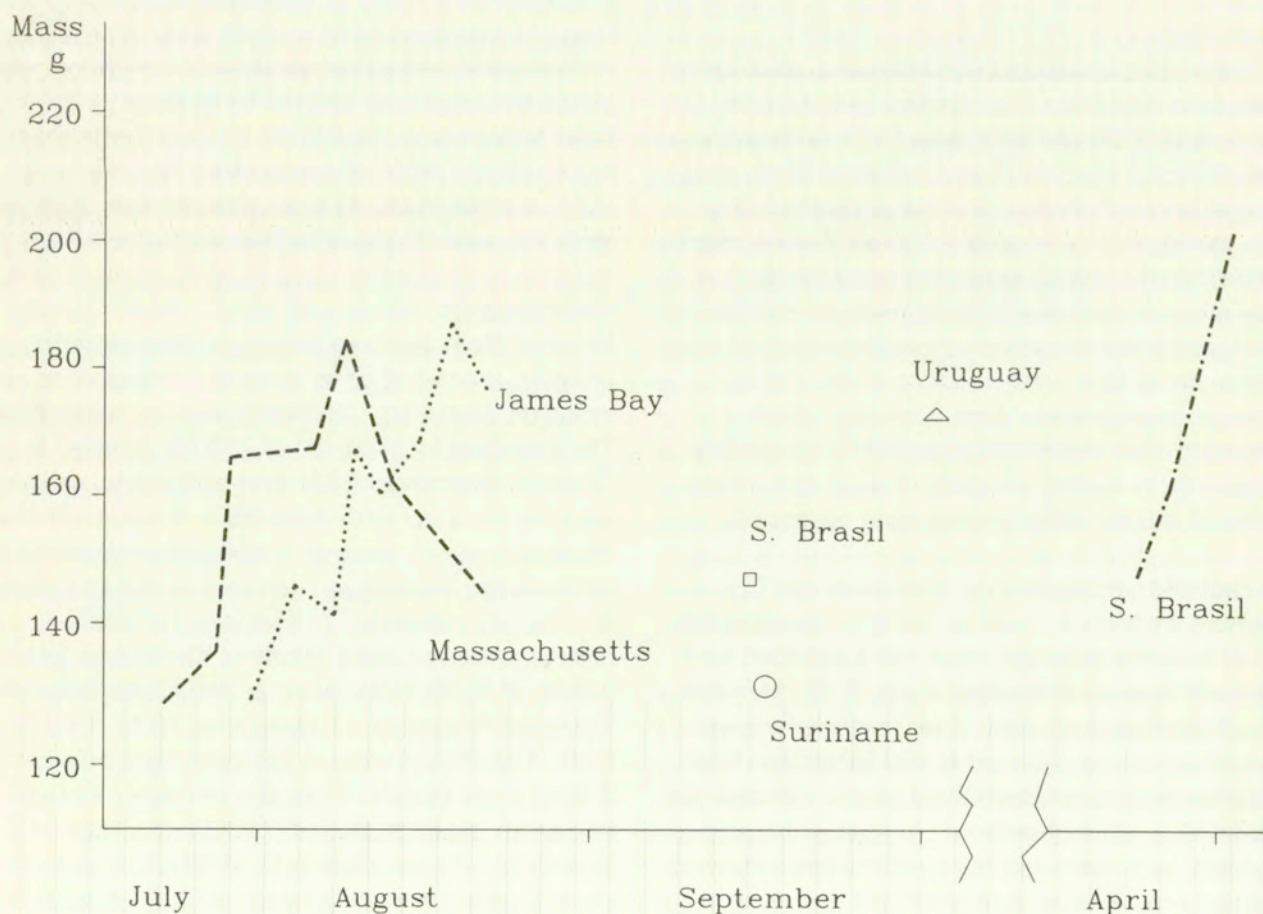


Figure 3. Summary of mass changes of Red Knots *Calidris canutus rufa* at selected areas during the annual migration cycle. See text for further details.

Knots caught in late April/early May 1984, with four birds weighing over 250 g.

Selected mass data and estimated departure masses from various locations are shown in Table 3, along with estimated potential flight ranges. The calculations involved make a number of assumptions, not all of which are likely to be met. An arrival mass of 120 g has been assumed, based on the 'tropical winter mass' derived for the species by Zwarts *et al.* (1990). This may be taken as a reasonable estimate of the mean mass under conditions where the birds are not carrying additional reserves for migration or thermostatic requirements. Calculations are based on the equation of Davidson (1984), and assume that the mass lost represents loss of fat, although it is now known that the percentage of fat in the migratory reserve in shorebirds varies between about 50% and 90% (see Zwarts *et al.* 1990). Ranges were calculated using a flight speed of 75 km/h, though this may be too high. The calculated potential flight ranges are thus likely to be overestimates.

The highest mean mass in James Bay of 186 g and observed masses of individuals of over 200 g indicate flight ranges of 4,500 - 5,000 km, more than enough to reach stopover areas on the eastern seaboard of the U.S.A., but not enough for a direct flight to South America with any margin of safety. Highest mean masses and likely departure masses of over 200 g in Massachusetts indicate Surinam would be within range. For departure masses varying between 186 g (the highest Massachusetts mean) and 210 g, arrival masses predicted by Davidson's (1984) equation are 121 - 139 g, which compares with recorded masses of birds on passage in mid September 1979 of 105 - 169 g, averaging 131 g. The predicted departure mass from Massachusetts for an arrival mass of 105 g in Surinam would be 164 g.

The highest masses recorded in Surinam in mid September 1979 of 160 - 169 g (A.L. Spaans & R.I.G. Morrison unpubl. data) give a predicted range of some 2,800 - 3,300 km, not enough to fly across Amazonia to southern Brasil, suggesting the birds move on to other areas to accumulate fat reserves before the next stage of the flight. Birds departing at the mean mass of 131 g would have a range of about 800 km, approximately the distance to the mouth of the Amazon River.

Table 3. Estimated departure masses and flight ranges of *rufa* Red Knots during migration.

Area of capture	Mass (g)	Flight range (km)	Distance to: (arr. at 120 g)*
James Bay (1)	highest mean (range 156-213)	188 4412	Massachusetts 1300
	? departure	205 5335	Surinam 5500
Mass. (2)	highest mean (range 85-224)	186 4300	Surinam 4200
	? departure	210 5600	
Surinam (3)	mean (range 105-169)	131 815	Amazon R. 1000
	? departure	160 2760	S. Brasil 4100
S. Brasil (4)	southward migration (museum)		
	mean (range 130-166)	147 1920	Valdés Pen. 1600
(5)	? departure	160 2760	Tierra del F. 2900
	northward migration 25 April 1985		
	mean (range 135-190)	164 3000	N.-central Brasil 3300
	? departure	180 3960	Delaware Bay 8700
	'1 May 1984'		
	mean	202 5180	
	? departure	220 6105	
Uruguay (6)	one ad. male, Sept.	175 3670	

* flight range calculated using equation of Davidson (1984), assuming a flight speed of 75 km/h.

1,4,6: R.I.G. Morrison (unpubl. data);

2: Harrington & Leddy (1980);

3: R.I.G. Morrison & A.L. Spaans (unpubl. data);

5: P. Antas & R.I.G. Morrison (unpubl. data).

Masses of the small sample of Knots collected during southward migration in southern Brasil indicate that most would have the range to fly to stopover areas in Argentina.

During northward migration at the Lagoa do Peixe, predicted flight ranges are more than adequate for the birds to reach north-central Brasil (3,300 km) but not adequate for a direct flight to the U.S.A. (8,700 km). Departure masses of 202 g (highest mean), 220 g (estimated departure) and 250 g (exceptional) would give predicted ranges of 5,180, 6,100 and 7,540 km, respectively; note that a tail-wind assisted increase in speed of 15% (to 86 km/h) would bring the U.S.A. within range. For a bird departing southern Brasil at 200 g, the predicted arrival mass in north-central Brasil after a flight of 3,300 km would be 145 g; the required departure mass for the next stage of the journey involving a 5,400 km flight to Delaware Bay would be 206 g, thus requiring a gain of approximately 60 g. The overall journey of 8,700 km between southern Brasil and Delaware Bay would take some 5 days of flying at a speed of 75 km/h, leaving 10 days available for mass gain, if typical departures of approximately 1 May from southern Brasil and arrival of 15 May in Delaware Bay occur. This implies that birds would need to gain mass at a rate of some 6 g/d in north-central Brasil to complete the migration, a high rate compared with those observed elsewhere.

CONCLUSIONS

Despite the great advances in our understanding of the distribution and migration of the subspecies in the last ten years, many important questions concerning *rufa* remain to be answered. For instance, in the Arctic little is known of the extent to which the breeding range of *rufa* may overlap with *islandica*, or of the ranges occupied by the two major wintering groups within *rufa*. Such knowledge will be important in ensuring the conservation of the various populations, especially in view of the genetic variability that has been found between them. Little is known of the major food resources and habitats used by Knots in the Arctic enabling them to reach the first major staging areas in James Bay. Further information is needed on turnover rates in staging flocks in North America, and how this may relate to the differing numbers which can be found during northward and southward migration. A critical evaluation of, and improvement in, current methods of estimating flight range is also needed, especially

in assessing whether birds may be able to make much longer flights than currently suspected. Better knowledge of the physiological condition and composition of body reserves of Knots at different times of the year is needed to enable an annual energy budget to be drawn up and improved estimates of flight ranges to be made. Improved estimates of the annual mortality of the two populations, and of how mortality is partitioned into the annual cycle, are also needed. Rather little is known of the passage of *rufa* through the north coast of South America (especially north-central Brasil), or of the biology of the birds on their wintering quarters in the south of the continent.

ACKNOWLEDGEMENTS

We thank the many people who have been involved in studies of Knots in the New World, including the many participants in the International and Maritimes Shorebird Surveys schemes, and in the banding projects organized by the Canadian Wildlife Service and Manomet Bird Observatory. Special thanks go to Paulo de Tarso Zuquim Antas for his collaboration with surveys and for providing opportunities to take part in banding work in Brasil, and to Arie Spaans for collaborative studies in Surinam; we gratefully acknowledge use of information from both areas. Thanks also to Hugh Boyd and Nick Davidson for their critical comments on the manuscript.

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