

MIGRATION AND MASS CHANGE OF WHITE-RUMPED SANDPIPERS IN NORTH AND SOUTH AMERICA

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ABSTRACT.—White-rumped Sandpipers (*Calidris fuscicollis*) migrate between Canadian Arctic breeding areas and “wintering” areas in Patagonia, one of the longest animal migrations in the Western Hemisphere. Migrant White-rumped Sandpipers employ both long-distance, nonstop, and short-distance multiple-stop flights. Southbound migrants fly over the Atlantic ocean from northeastern North America to South America. They then gradually move southeast along northeastern coasts before turning inland in trans-Amazonian travel requiring about one month. Northward migration routes from Patagonia evidently are similar, but are traversed in a rapid series of long nonstop flights. Staging zones are unknown in northern South America during north migration, in the Caribbean basin, or on the Atlantic coastal plain of the U.S. A major staging area is identified in the Great Plains, where birds evidently prepare for a last remaining flight to the Arctic. The migration system of this small sandpiper makes the species vulnerable to loss of strategic migration habitats. *Received 11 Dec. 1990, accepted 10 April 1991.*

Studies of avian migration energetics generally have focused on migration before long flights over ecological barriers such as oceans or deserts. There are few studies of energetics in the context of an annual migration strategy, especially in the case of trans-hemispheric migrants. The present study focuses on long-distance migration in the context of a full annual cycle.

The White-rumped Sandpiper (*Calidris fuscicollis*) is one of the longest distance bird migrants in the Western Hemisphere. Studies of its southward migration (McNeil and Cadieux 1972a; McNeil and Burton 1973, 1977; Burton and McNeil 1975) have confirmed long distance, transoceanic routes between eastern Canada and northeastern South America, as first postulated by Cooke (1910). Relatively little is known about how the remaining migration is completed between Canadian Arctic breeding areas and austral wintering latitudes of South America. This paper gives an annual perspective of distribution, use of migration staging areas, timing, and mass change during north and south migrations.

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The energetics of long flights have been investigated by Odum (1958) and others, studying passerine migrants, and by McNeil (1970), McNeil and Cadieux (1972a), Davidson (1984), and Castro and Myers (1988, 1989), studying shorebirds. These studies found that birds accumulate fat which is later metabolized to fuel long, over-water flights. Methods were developed for estimating flight-distance capacities based on the amounts of fat birds had accumulated. More recent studies (e.g., Davidson and Evans 1988) suggest that metabolism of muscle protein may also contribute a small amount to migration energy requirements. We provide data on fluctuations in the mass of White-rumped Sandpipers during migration and winter and use formulae (McNeil and Cadieux 1972b, Castro and Myers 1988) to estimate flight-distance capabilities at different seasons. We combine this information with observations of seasonal distribution to provide an integrated picture of this small sandpiper's hemispheric migration strategy.

METHODS

White-rumped Sandpipers from different locations and years in both North and South America (Table 1) provide data for this study. All birds were captured either with mist nets or walk-in traps and later released or were collected under permit (McNeil 1970). Mass to the nearest gram was measured with Pesola spring scales or with an Ohaus balance. Although we assume that the masses we recorded are representative of each locality, we cannot assess this as data were not available over a series of years. Where listed in text, mean values are given with \pm one standard deviation.

Wing lengths usually were measured by flattening and straightening the primaries before measuring. However, Harrington measured unflattened wing chord lengths. These have been adjusted by adding 3 mm to measurements, this value being intermediate to those used for similar adjustments applied to Dunlin (*Calidris alpina*, 4 mm, Pienkowski et al. 1979) and Semipalmated Sandpipers (*Calidris pusilla*, 2.6 mm, Harrington and Morrison 1979).

Flight ranges (FR) were calculated using the formula of McNeil and Cadieux (1972b) as follows:

$$\text{Flight Range} = \frac{[\text{FW} - \text{Y}] \times \text{S} \times 9.1 \text{ kcal}}{\text{Antilog}(\log 37.151 + 0.744 \times \log \text{W})}$$

where FW = total mass in grams, S = flight speed (km/h) for the species (80 km/h for White-rumped Sandpipers), W = total mass in kg, Y = 6.44 + 2.55 (wing length in cm, adults and immatures) or Y = 5.66 + 2.63 (wing length in cm, adults only). Flight range capacity was calculated for each locality based on the mean of the ten highest FR values. We assume that the ten highest values represent birds having attained departure mass, but cannot test this assumption. We also expect that some individuals leave at lower fat levels as appears true in other sandpipers (Dunn et al. 1988). The FR's of Magdalen Island birds and a few from coastal Venezuela were calculated using data from fat extraction (McNeil and Cadieux 1972a, b), but substituting the value of 9.5 with 9.1 kcal/g of fat (Johnston 1970, Blem 1990) to be consistent with the above formula.

Regression analysis was used to determine whether body size (as indicated by wing length) influenced the regression of mass or FR values against date. Mass change through time is

TABLE 1
NAMES AND LOCATIONS OF SITES USED IN THIS REPORT

Site name	Location	Years	Source
Magdalen Islands, Quebec, Canada	47°30'N; 61°50'W	1969, 1971	McNeil
Venezuela (coast)	10°25'N; 63°50'W	1966–1967, 1984–1986	McNeil
Venezuela (inland)	8°31'N; 67°35'W	1982–1984	Thomas
Suriname (coast)	5°55'N; 54°55'W	1975, 1978, 1980	Spaans
S. Brazil, Lagoa do Peixe	31°20'S; 51°00'W	1984 1986–1987	Harrington Resende and Leeuwenberg
Kansas	38°30'N; 99°05'W	1978, 1985, 1987	Martinez

depicted by linear regression of mass against date. Weight change was not determined for individual birds due to low numbers of recaptures.

During northward migration in 1989 and 1990, Castro measured fat levels of 21 White-rumped Sandpipers at Cheyenne Bottoms, Kansas (Castro 1990). Using this same sample as a basis for comparing flight distance capacity, as estimated by two different formulae, we determined fat content, following the methods of McNeil and Cadieux (1972b), and compared the results to Castro's measured fat levels (Castro, unpubl. data).

We also estimated how many hours White-rumped Sandpipers could fly by first calculating fat-free, wet mass of individuals using the formula of McNeil and Cadieux (1972b), and then subtracting this value from the known mass to estimate the amount of fat. This was converted to kilojoules (kJ) assuming 39.5 kJ/g of fat (Blem 1990). Then we estimated hourly energy expenditure in kJ according to formula *b* of Castro and Myers (1988). We used the latter values for estimating the time the available fat could fuel flight. The maximum ten values at each site were used for comparisons among sites.

We used molt terminology of Humphrey and Parkes (1957). Statistical tests of mass differences between sites were by analysis of variance. Rates of mass change between sites were compared by linear regression of mass against date and then testing for heterogeneity between the slopes (SAS GLM procedure; SAS 1985, 1986).

RESULTS

Flight range estimates.—The McNeil and Cadieux (1972b) formula consistently overestimated ($\bar{x} = 9.47 \pm 1.69$ g, $N = 21$) Castro's measured lean mass levels at Cheyenne Bottoms. We have no way to resolve which values were correct. Differences of estimates by the two methods were lowest in heaviest birds. Because our study focuses on heaviest birds, the difference between the methods is not important to our evaluations.

Southward migration, Magdalen Islands, Canada.—Adult White-rumped Sandpipers arrived principally during August and early September. Few were caught after 11 September, presumably because most had migrated. At about this same time, increasing numbers of juveniles began

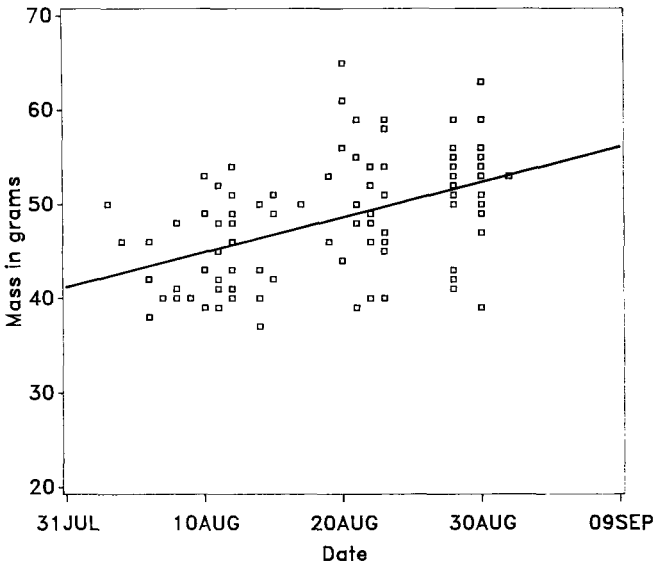


FIG. 1. Regression plot of adult White-rumped Sandpiper mass during August at the Magdalen Islands southern migration staging area in Quebec, Canada. The regression line formula is $Y = 2.15 + 0.20X$, $P < 0.001$.

to be captured. Weekly average mass of adults increased steadily (0.2 g/day, Fig. 1) between mid-August and mid-September. Average mass of juveniles increased steadily between mid-September and early November. Adults and juveniles gained mass at similar rates, as indicated by similar regression line slopes ($P = 0.895$).

We did not find differences of wing lengths among adult birds caught on different dates ($R = 0.014$, $P = 0.893$). We found no primary feather molt nor any significant correlation between mass and wing length ($R = 0.033$, $P = 0.77$). Therefore, we conclude that the relationship ($R = 0.461$, $P < 0.0001$) between date and mass increase was caused by increased mass through accumulation of fat and protein (Davidson and Evans 1988, McNeil and Cadieux 1972a), rather than by some other factor such as arrival and departure of different sized birds.

The ten highest flight range capacity (FR) values of White-rumped Sandpipers in the Magdalen Islands (Table 2) ranged from 3200 to 4050 km for adults and from 3450 to 4150 for juveniles. Mean values of the two age groups did not differ significantly ($P > 0.05$). Energy expenditure estimates (Castro and Myers 1988) suggest that the heaviest individuals were capable of sustaining flight for 40–45 h (Table 3), assuming that only lipids are metabolized. This translates to distance estimates of 3200–3600

TABLE 2
TEN HIGHEST FLIGHT RANGE (FR) ESTIMATES OF WHITE-RUMPED SANDPIPERS DURING
SOUTHWARD MIGRATION, ROUNDED TO NEAREST 50 KM

Place	Magdalen Islands ^a		Venezuela coast ^b	Suriname coast	L. do Peixe Brazil
N	30 (Juveniles)	56 (Adults)	18	28	24
Period	7 Oct– 5 Nov	20 Aug– 6 Sep	1 Aug– 3 Nov	20 Aug– 20 Sep	29 Oct– 21 Nov
	4150	4050	1950	1900	2400
	4100	3800	1250	950	2100
	4100	3700	450	400	1800
	4000	3650	400	100	1350
	3900	3600	300	100	1150
	3700	3550	250	0	850
	3600	3550	100	0	850
	3550	3250	0	0	750
	3500	3250	0	0	650
	3450	3200	0	0	650

^a FR estimate based on extraction from collected birds.

^b Flight range estimate based on fat extraction on collected birds; otherwise values were calculated using formulae of McNeil and Cadieux (1972b) on live birds.

km which is very similar to the estimates derived from the FR values, assuming an 80 km/h flight speed.

Northeastern South America. — White-rumped Sandpipers pass through Suriname between mid-August and late September (Spaans 1978). Mean mass of adults was not different between Suriname and Venezuela (ANOVA, $P = 0.3633$) but was substantially lower than at the Magdalen Islands, Canada (ANOVA, $P < 0.01$). We did not have enough juveniles for

TABLE 3
ESTIMATED POTENTIAL DURATION OF FLIGHT^a FOR WHITE-RUMPED SANDPIPERS AT
DIFFERENT LOCATIONS DURING MIGRATION

	Southward migration period			Northward migration period		
	Quebec, Canada	Venezuela	Suriname	Southern Brazil	Venezuela	Kansas
Hours (mean) ^a	43.14	0.05	4.73	41.31	9.80	40.02
SD	2.07	0.16	8.45	1.52	9.00	1.17

^a Based on the ten highest individual estimates for each location, using fat data of Table 2 and an hourly colloidal fat metabolism rate derived from Castro and Myers (1988).

comparison. Only three of the 46 White-rumped Sandpipers in Suriname/Venezuela had FR values greater than 1000 km (Table 2), and there was no correlation between mass increase and advancing date ($r^2 = 0.03$, $P = 0.25$; Table 2).

Southern South America.—Small numbers of White-rumped Sandpipers begin arriving in southern Brazil about two weeks after the main departure from the Guianas. At Lagoa do Peixe, numbers increase gradually in September and October and sharply between mid-November and December (Resende 1988). The same pattern was observed on the mid-Atlantic coast of Argentina (International Shorebird Surveys, unpubl. data).

Average mass and FR index values at Lagoa do Peixe, first measured a number of weeks after some White-rumped Sandpipers had been present, were higher than values from Venezuela and Suriname (Tables 2, 3). This suggests that some were capable of further southward migration and/or that they retained substantial reserves following flights from northeastern South America.

Austral summering period.—White-rumped Sandpipers are found commonly in southern Brazil between October and May (Belton 1984, Harrington et al. 1986, Resende 1988). Mass ($\bar{x} = 37.2 \pm 4.5$ g, $N = 297$) remained relatively low and stable during the austral summer. However, for unidentified reasons, during the first 15 days of February 1987, average mass was substantially lower ($\bar{x} = 32.4 \pm 3.3$ g, $N = 39$, $P < 0.001$) than in other 15-day periods.

White-rumped Sandpipers finish pre-basic molt soon after returning to austral latitudes. The pre-alternate molt of many birds is virtually completed by mid-March (Resende 1988) before northward migration begins. We evaluated whether there were differences of mass at different stages of the molt but found no significant trends. No explainable patterns of mass change were identified until mid-April, when White-rumped Sandpipers began premigratory fattening (see below).

Northward migration, southern South America.—At Peninsula Valdez, Argentina, numbers of White-rumped Sandpipers begin gradually declining in late February (International Shorebird Surveys, unpubl. data). In 1980, numbers declined sharply during late March but remained high until 5 April in 1981 (International Shorebird Surveys, unpubl. data).

In southern Brazil, numbers of White-rumped Sandpipers declined gradually during February 1988 and more sharply during March (Resende and Leeuwenberg, unpubl. data). During an unusual drought in 1989, when Lagoa do Peixe dried almost completely, White-rumped Sandpipers departed in early January (Resende and Leeuwenberg, unpubl. data).

No substantive change of mass occurred in White-rumped Sandpiper

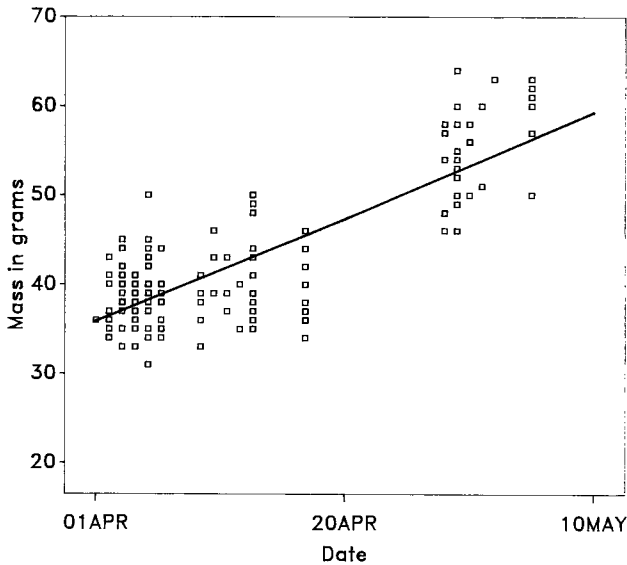


FIG. 2. Regression plot of adult White-rumped Sandpiper mass between 1 April and 5 May at the Lagoa do Peixe migration staging area, Rio Grande do Sul, Brazil. The regression line formula is $Y = -18.81 + 0.60X$, $P < 0.001$.

during two seasons at Lagoa do Peixe before mid-April (Resende 1988, Harrington et al. 1986). Mean mass then increased sharply ($R = 0.85$, $P < 0.0001$; Fig. 2) during late April and early May 1984. Frequent resightings of marked individuals and the steadily increasing average mass (Fig. 2) indicate that the lagoon was being used as a pre-migration staging area (Harrington et al. 1986). This pattern was not seen during the 1989 drought.

Northern South America and the U.S.—The principal northward migration of White-rumped Sandpipers in Venezuela and Suriname is between late April and mid-May (McNeil 1970, Spaans 1978, Thomas 1987). Individuals caught in Venezuela between early April and early June ($\bar{x} = 35.1 \pm 4.00$ g, $N = 203$) were substantially lighter than those caught during April/May in Brazil ($\bar{x} = 55.9 \pm 5.27$ g, $N = 39$), and their FR values (Table 4) were consequently much lower. At both the inland and coastal sites in Venezuela, there was no consistent mass increase with advancing date ($P = 0.794$ inland; $P = 0.859$ coastal).

In contrast to Venezuela, numbers of White-rumped Sandpipers at Cheyenne Bottoms, Kansas, gradually increased between late April and late May (Fig. 3). Maximum counts during seven years generally were

TABLE 4
TEN HIGHEST FLIGHT RANGE (FR) ESTIMATES^a (ROUNDED TO NEAREST 50 KM) OF
WHITE-RUMPED SANDPIPERS BASED ON MASS DURING THE NORTHWARD MIGRATION

Place		
Cheyenne Bottoms 12 May–2 June	Venezuela coast 20 Apr–1 June	So. Brazil 13 Apr–4 May
3750	1900*	4600
3650	1800*	4200
3650	1650	4200
3650	1550	4000
3550	1500*	4000
3450	1500*	3950
3350	1450*	3750
3350	1250*	3750
3350	1250*	3750
3250	1250*	3550

^a Estimates calculated according to McNeil and Cadieux (1972b) except as indicated.

* FR estimate based on fat extraction from collected birds.

during the last ten days of May (Fig. 3), about ten days after the peak in Venezuela (McNeil 1970, Thomas 1987). The Kansas peak is later than the peak of much lower numbers near Decatur, Alabama, where D. Hulse censused shorebirds for eight years for the International Shorebird Surveys (Fig. 3).

The buildup of White-rumped Sandpiper numbers at Cheyenne Bottoms during late May suggests immigration with little emigration of migrants before a threshold date, a pattern characteristic of migration staging areas used for fattening. Therefore, it is no surprise that average mass increased steadily and markedly (Fig. 4, $P < 0.001$), resulting in high FR capacities (Table 4).

DISCUSSION

Southward migration. — White-rumped Sandpiper southward migration happens later than for many congeners. In the Bay of Fundy, Canada, numbers do not increase appreciably until mid-August, after the peak of Semipalmated (*C. pusilla*) and Least (*C. minutilla*) sandpiper migration is past (Hicklin 1987). The species is less common in New Brunswick and Nova Scotia (Hicklin 1987, Maritimes Shorebird Survey, unpubl. data) than farther north and east (Todd 1963, Morrison 1984). Studies at the Magdalen Islands and at Sable Island (McNeil and Cadieux 1972a, McNeil and Burton 1973, Burton and McNeil 1975, this study) show that White-

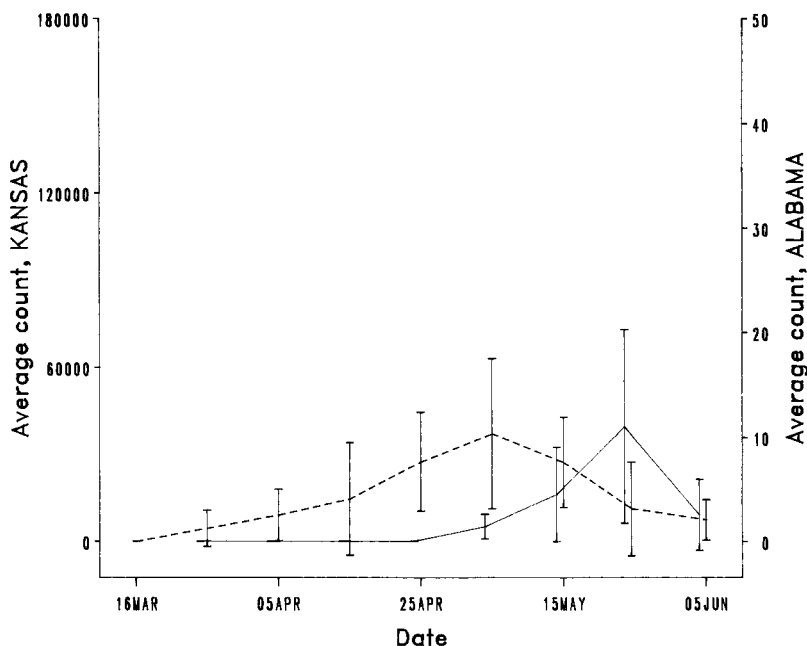


FIG. 3. Average counts (± 1 SE) of White-rumped Sandpipers per 10-day period during northward migration at Cheyenne Bottoms, Kansas (left scale, solid line) and at Decatur, Alabama (right scale, broken line) based on five or more years of censusing at each site. Data are from the International Shorebird Surveys.

rumped Sandpipers fly directly over the Atlantic Ocean from eastern Canada to northeastern South America. They arrive principally in the Guianas during late August, where they remain through mid-September (Spaans 1978).

Ours and earlier work (see below) show that White-rumped Sandpipers employ low altitude, "short-hop" flights during the next migration stage along the Guyana and Suriname coasts (Spaans 1978). This is in accordance with our low flight range (FR) index (Table 2); few birds were capable of flying more than a few hundred kilometers without stopping. Coastwise migration probably continues along the northwest Brazilian coast to areas east of the Amazon River mouth (Antas 1983).

The next portion of southward migration is not well known. Antas (1983) indicates there is an overland trip between northern and southern Brazil, with short flights and frequent stops on river bars and banks during September/November when water levels are low. Our summary for the timing of this leg of the migration (about a month) supports the Antas

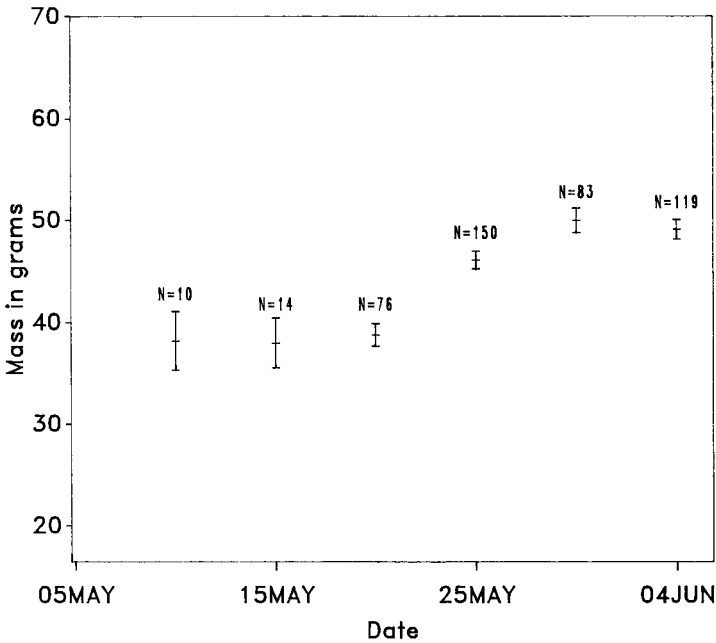


FIG. 4. Average mass per 5-day block of White-rumped Sandpipers (± 1 SE) at Cheyenne Bottoms, Kansas, 1 May–4 June, based on data from 450 birds captured for banding during three years.

hypothesis. The alternative possibility, a coastwise migration around eastern Brazil, is not supported by data from routine censuses of suitable coastal habitat near Recife, one of the easternmost points of Brazil, where the species is rare (Severino de A. Júnior, in litt.).

Wetmore (1927) observed White-rumped Sandpipers in Paraguay on 6 September, about the same time as first arrivals in southern Brazil (Belton 1984). Numbers at Lagoa do Peixe, Rio Grande do Sul, increased rapidly between mid- and late-October (this study). Although some individuals remained there through the austral summer (Resende and Leeuwenberg 1987, Resende 1988), the principal “wintering” area is in southern Argentina and Chile (Wetmore 1927). First arrivals appear at Peninsula Valdez, on the central Atlantic coast of Argentina (latitude 42°S) during mid-September; numbers continue increasing through October and November (International Shorebird Surveys, unpubl. data). In Tierra del Fuego, numbers also begin increasing during September (Humphrey et al. 1970).

Northward migration.—Early northward White-rumped Sandpiper migration is not conspicuous. At Peninsula Valdez, departures evidently began in late March (International Shorebird Surveys, unpubl. data); in 1981 we recorded sharply reduced numbers during the first ten days of April. Myers and Myers (1979) noted departure from drying habitats in Buenos Aires Province (latitude 37°S) during late March and early April but not until early May in suitable wet habitats. Wetmore (1927) reported northward migration during early March in western Buenos Aires Province.

Antas (1983) notes the northward migration of White-rumped Sandpipers in Brazil happens when water levels of rivers are high. He concludes that birds must either follow a long coastal route, or use non-stop flights to traverse a shorter, overland route between southern and northern South American coasts. The latter possibility would require large fat deposits. During our work in 1984, we found exceptionally heavy individuals in southern Brazil during late April/early May. This was followed by an exodus of migrants between 1–8 May (Harrington et al. 1986). Our FR estimates argue that nonstop flights to the north coast were possible. If our flight speed estimate of 80 km/h is low (see McCabe 1942), then the flight distance capacity would be greater.

In northeastern Venezuela, numbers of White-rumped Sandpipers during northward migration are five times higher than during southward migration (McNeil 1970). This pattern is reversed farther east, in Suriname, where Spaans (1978) found lower numbers in April–May as compared to September (Spaans 1978).

In the llanos of Venezuela, far from the coast, there apparently were two migration “waves” in 1984, one 26 April–4 May, and another 13–16 May (Thomas 1987). The variability of routine counts, and the low masses of White-rumped Sandpipers in the Venezuelan llanos (Thomas 1987), indicate high turnover rates.

At a coastal site in eastern Venezuela, Francine Mercier’s weekly counts (unpubl. data) showed fluctuating numbers between mid-April and late May. There was no gradual buildup characteristic of migration staging sites. The low FR values from the Venezuela coast also did not indicate staging behavior. In short, we found no direct evidence of staging for non-stop flights to the United States. Nevertheless, comparison of migration dates in Venezuela and Kansas (see below) suggest a rapid passage. In addition, three individuals marked by Thomas in Venezuela between 25 April and 14 May were seen in Texas and Kansas between 14 and 23 May.

Distributional evidence also suggests a nonstop flight from South Amer-

ica to North America. The White-rumped Sandpiper is rare in Colombia (Remsen 1977), in Central America (Ridgley 1976, Slud 1964), and on Caribbean Islands (Raffaele 1989; International Shorebird Surveys, unpubl. data). It also is unusual in peninsular Florida and on the U.S. Atlantic coast during spring (Longstreet 1934; International Shorebird Surveys, unpubl. data). Peak but low numbers farther west, in Alabama (Fig. 3), occur at about the same time as peak numbers in Venezuela (McNeil 1970, Thomas 1987) but considerably earlier than peak numbers in the Great Plains (see below).

The principal northward migration of White-rumped Sandpipers in North America is through the Great Plains (Bent 1927). The species is scarce in the east, for example Delaware Bay (Dunne et al. 1983), New England (Forbush 1925), James Bay (Harrington, unpubl. data), and the Canadian Maritimes (Hicklin 1987). Although seen regularly in southern Canadian prairies between late May and mid-June (Colwell et al. 1988), the timing and low numbers suggest "fallout" from an overhead migration rather than buildup characteristic of staging areas. Farther north and west, for example near Edmonton, Alberta, White-rumped Sandpipers are rare in spring (Sadler and Myres 1976).

The increasing numbers and masses of White-rumped Sandpipers in Kansas during May and early June (Fig. 3, 4) indicate a major staging zone where birds obtain sufficient fat to fuel non-stop flights to central Arctic Canadian breeding areas. According to unpublished data in the International Shorebird Survey, more White-rumped Sandpipers can sometimes be found at Cheyenne Bottoms in Kansas than from the combined spring counts at more than 300 other locations that were censused at the same time. White-rumped Sandpipers typically arrive in breeding areas between late May and mid-June (Parmelee et al. 1968), very soon after numbers decline in the Great Plains (Fig. 3).

Comparison of mass gain rates in northward and southward migration.—Our data show variable patterns of mass gain by White-rumped Sandpipers during migration. In some cases, the patterns appear related to whether samples are from staging sites where individuals remain for days and add fat, for example the Magdalen Islands, Lagoa do Peixe, or Cheyenne Bottoms, or whether they are from areas where individuals visit briefly. Examples of the latter are the Venezuela and Suriname sites which were characterized by fluctuating numbers of White-rumped Sandpipers (Thomas 1987; Francine Mercier, unpubl. data) and by low masses (see above).

Seasonal differences in rates of mass increase at major staging sites also exist. We compared rates of mass gain at the three staging sites by charting daily averages against time. To ensure comparability, we restricted eval-

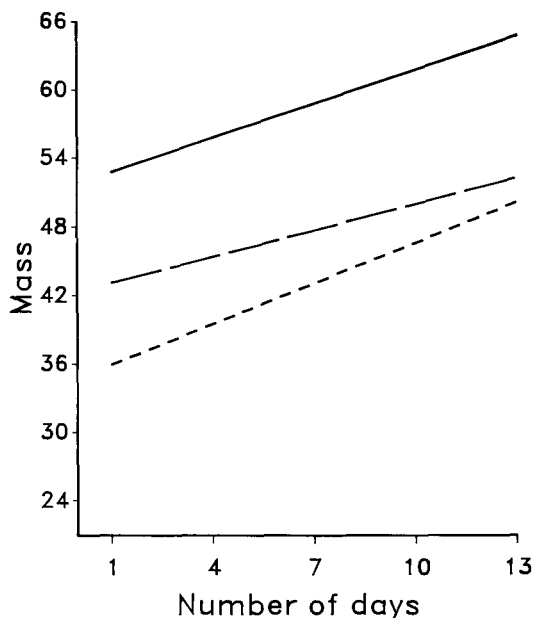


FIG. 5. Rates of White-rumped Sandpiper mass gain during 15 days of the maximum mass-gain period at three widely separated migration staging areas in North and South America, including southern Brazil during April–May (solid line), Kansas in the United States during May (dotted line), and in eastern Canada during August/September (broken line). The slope for Canada is statistically different from the others (see text).

uations to the 15-day period of maximum mass gain at each site. This analysis (Fig. 5) suggests that mass increase rates, illustrated by the r -values, were similar during northward migration at Lagoa do Peixe in Brazil and at Cheyenne Bottoms, United States, even though the birds in Brazil were, on average, substantially heavier than in Kansas. The slopes of these two lines were not statistically different from each other ($P > 0.05$). In contrast, the rate of mass increase during autumn was lower ($P < 0.001$) at the Magdalen Islands in Canada.

Our census and the available literature suggest that the overall timing of northward White-rumped Sandpiper migration is more rapid than the southward migration, even if comparisons are restricted to adult birds. For example, peak southward migration of adults in the Magdalen Islands is during August/September, about two and one-half months before major population buildup south of the Equator. On the other hand, major emigration from southern latitudes begins just a month and a half before spring settlement in breeding areas. The limited information presented

here (Fig. 5) also suggests that the fat deposition needed for rapid migration also occurs more rapidly during northward than during southward migration. For many, and perhaps most birds, this fattening occurs at widely separated, strategic sites which are potentially critical to the world populations of this remarkable migrant (cf. Myers et al. 1987).

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