DISTRIBUTION AND GEOGRAPHICAL ORIGINS OF KNOT *CALIDRIS CANUTUS* WINTERING IN EUROPE AND AFRICA

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CONTENTS

1. INTRODUCTION

The Knot *Calidrus canutus* has a circumpolar distribution, breeding in the Canadian Arctic (Bent 1928, Snyder 1957); Greenland, north of Melville Bay in the west and of Scoresby Sound in the east (Salomonsen 1950); Spitzbergen (Dalgety *et al* 1931, 1949, Løvenskiold 1964); and parts of Siberia including the Taimyr Peninsula, the New Siberian Archipelago and Wrangel Island (Walter 1902, Birula 1907, Pleske 1928, Portenko 1939, Dementiev and Gladkov 1951, Kozlova 1962). Information from the Severnaya Zemlya Archipelago is not available. Birds from the north Canadian Arctic (including Ellesmere Island, and islands immediately to the west of this), Greenland, Spitzbergen and Siberia (apart from Wrangel Island) form the nominate race. Birds from the southern part of the Canadian breeding range (including Victoria, Somerset and Southampton Islands) have been separated as *C.c. rufa* and those from Wrangel Island, more controversially, as *C.c. rogersi.*

Knots winter in South East Asia, Australia, and New Zealand, (presumed to be the birds from Wrangel Island, Dementiev and Gladkov 1951), South America (presumably *rufa*), West Europe and parts of Africa. The European

distribution in winter is relatively well known (Spitz 1969, Prater in press), but in all other areas little is known of their numbers and distribution and new wintering sites continue to be discovered. Witherby *et al* (1940) assumed that West European wintering birds were of Siberian origin and despite some suggestions that North Canadian and Greenlandic birds might move to the East Atlantic, (e.g. Godfrey 1953, Snyder 1957), authors of recent handbooks (e.g. Bannerman 1961, Hollom 1968) have assumed that most European wintering birds are indeed from Siberia. Hollom (1968), referring only to birds wintering in Britain, stated "the race concerned *Calidris canutus* breeds mainly in Siberia, wintering south to the Mediterranean and West African coast, also Australia. Another race occurs in North America". We believe this to be incorrect and aim to show that Knots wintering in Britain and elsewhere in Western Europe are mainly, if not totally, from the breeding populations of Greenland and the north Canadian Arctic. We shall attempt to clarify the African distribution and suggest that these birds are from Siberia. This paper aims also to clarify the patterns of migration of the nominate race.

2. METHODS

Bill-lengths of Knots caught for ringing using rocket-, cannon- or mist-nets were measured from the edge of the feathering to the bill-tip. Measurements by different observers were consistent, most of those from Iceland and Mauritania being made by the same observer. Knots were caught in the following localities:

(a) On the west coast of Iceland principally between Halsvadall (64°55'N, 23°20'W) and Stokkseyri (63°50'N, 21°03'W).

(b) In Britain, at The Wash (52°47'N, 0°17'E) and Morecambe Bay (54°00'N, 2°54'W).

(c) In Morocco, at a number of localities but mainly at Puerto Cansado (28°02'N, 12°15'W).

(d) In Mauritania, at the Banc d'Arguin between Cap Timiris (19°22'N, 16°30'W) and Cap Iouik (19°53'N, 16°17'W).

(e) In South Africa, principally at the Langebaan Lagoon, Cape Province (33°05'S, 18°02'E).

A small number of specimens in the British Museum (Natural History) were also measured. There may be some shrinkage of museum material so these measurements cannot be equated with those of live birds.

3. WINTER DISTRIBUTION

3.1 EUROPE

Since Spitz's (1969) report, more recent international censuses have further clarified the West European winter distribution. Prater (in press) reported a mid-winter total of 609,000, of which 97.5% were found in

Ireland, the British Isles, France, and the Netherlands, and 2.5% in Iberia. Mid-winter distribution is therefore restricted, with few birds being found between the North Sea area and south Morocco/Mauritania (see below).

The Knot is most often found in large concentrations in a few major estuaries, the smaller estuaries holding very few birds (e.g. Prater 1971).

3.2 AFRICA

The importance of West Africa as a wintering area has been recognised only recently (e.g. Roux 1959, Blondel & Blondel 1964, Westernhagen 1968). Witherby *et al* (1940) and Heim de Balzac & Mayaud (1962) described Africa as of little importance to Knot while Bannerman (1961) stated "the Knot has no winter quarters anywhere in Africa". The distribution in Africa is still poorly known, but Knots probably occur abundantly only on two parts of the continent: south Morocco/Mauritania and southern Africa.

In Morocco, the principal wintering area is at Puerto Cansado in Tarfaya Province, where Blondel & Blondel (1964) noted 10—12,000 in January 1964. In December 1973 only 1,700 were counted there (Pienkowski & Knight 1976) and in January 1974 only 500, although more may have been present amongst 14,500 unidentified waders seen on that date (Johnson & Biber 1974). Pienkowski & Knight (1976) have discussed the reasons for the considerable annual variation in winter numbers of many species in Morocco.

Further south, Pététin & Trotignon (1972) estimated 50,000 Knot at the Banc d'Arguin in Mauritania in December 1971 and January 1972. A more comprehensive survey in October 1973 gave a total of 130,000 between Cap Timiris (19°22'N, 16°30'W) and Iouik (19°53'N, 16°17'W) (Knight & Dick 1975), and this census was considered to be complete. Further north, the stretch of coast between Nouadhibou (20°55'N, 17°03'W) and Iouik contains an area of mudflats, small relative to the area counted in October 1973, and Pététin and Trotignon (1972) observed few waders there. Between Puerto Cansado and Nouadhibou there are very few areas of intertidal mudflat on the Spanish Saharan coast, but no systematic counts have been reported. Thus, on the north west African coastline between Tangier and the Senegal River there is a winter population of at least 135,000 Knot in some years, mostly on the Banc d'Arguin. There is almost certainly a summering population of at least 10,000 (Westernhagen 1968), but it has not been fully counted.

The principal areas for Knot in southern Africa are Langebaan (33°05'S, 18°02'E), where 4,000 birds were estimated in March 1973 and 1974 (Pringle & Cooper in press), and Sandwich Harbour (23°20'S, 14°20'E), with an estimated number of 650 birds in February 1972 (Berry & Berry in press). Smaller populations of up to 100 have been reported from Walvis Bay (22°59'S, 14°31'E), Veldrift (32°45'S, 18°10'E), Breede Rivermouth (34°13'S, 20°40'E), Port Elizabeth (33°58'S, 25°42'E) and Durban Harbour (29°52'S,

31°01'E). It is doubtful if other wintering grounds as important as Langebaan and Sandwich Harbour will be found in southern Africa, but the extent of the other sites suggest that not more than the same number are likely to be found elsewhere. Therefore at least 5,000 and probably not more than 10,000 Knot winter in southern Africa between Walvis Bay and Durban. Earlier surveys between 1950 and 1966 (Broekhuysen 1956 & 1971) found lower numbers but possibly the apparent increase is due to improved coverage.

Despite increased coverage in recent years, few Knots have been recorded between these main wintering areas of north-west and south-west Africa (e.g. Brunél & Thiollay 1969, Erard & Etchécopar 1970, Fry 1961, Grimes 1974, Wallace *in litt.*); or in east Africa (see section 4.2.3. "Migration in southern Europe and Africa"). However, many areas have not been adequately surveyed, for example the Archipel des Bijagos in Guinea Bissau, which has a considerable area of mudflat possibly suitable for Knots.

4. GEOGRAPHICAL ORIGINS AND MIGRATION

4.1. BILL-LENGTHS

Bill and wing lengths proved useful in determining the origins of several wader species, e.g. Dunlin *Calidris alpina* (see Evans 1964, Griffiths 1970, Pienkowski & Dick 1975) and Redshank *Tringa totanus* (see Hardman 1966, Hale 1971, 1973). Pienkowski & Minton (1973) showed that wing lengths of individual Knots change by abrasion during the year, thus invalidating earlier analyses (Minton 1969 a, b, Pienkowski *et al* 1971) which suggested that the wing lengths of Knots wintering in Britain were longer than those of birds present during the autumn. We shall not make use of wing lengths in this analysis.

Figure 1 presents bill-lengths from various localities at different times of the year. Clearly the measurements fall into two distinct groups with those from Britain and mid-winter in France being similar to those from Iceland, but measurements from South Africa, Mauritania, Morocco and the Camargue during spring migration being significantly larger ($P<0.001$). Differences in bill-lengths could be due to a number of factors including changes in bill-lengths of individuals, and differences due to age and sex composition of samples as well as to geographical variation. We examine these in turn below.

4.1.1. Seasonal Variation

The largest series of measurements of adults, from The Wash, show a seasonal variation with peaks in September/October and February/March. Measurements of juveniles from The Wash and of birds from South Africa show similar patterns. At The Wash, for which most information is available, the variation can be accounted for totally by seasonal changes in the bill-

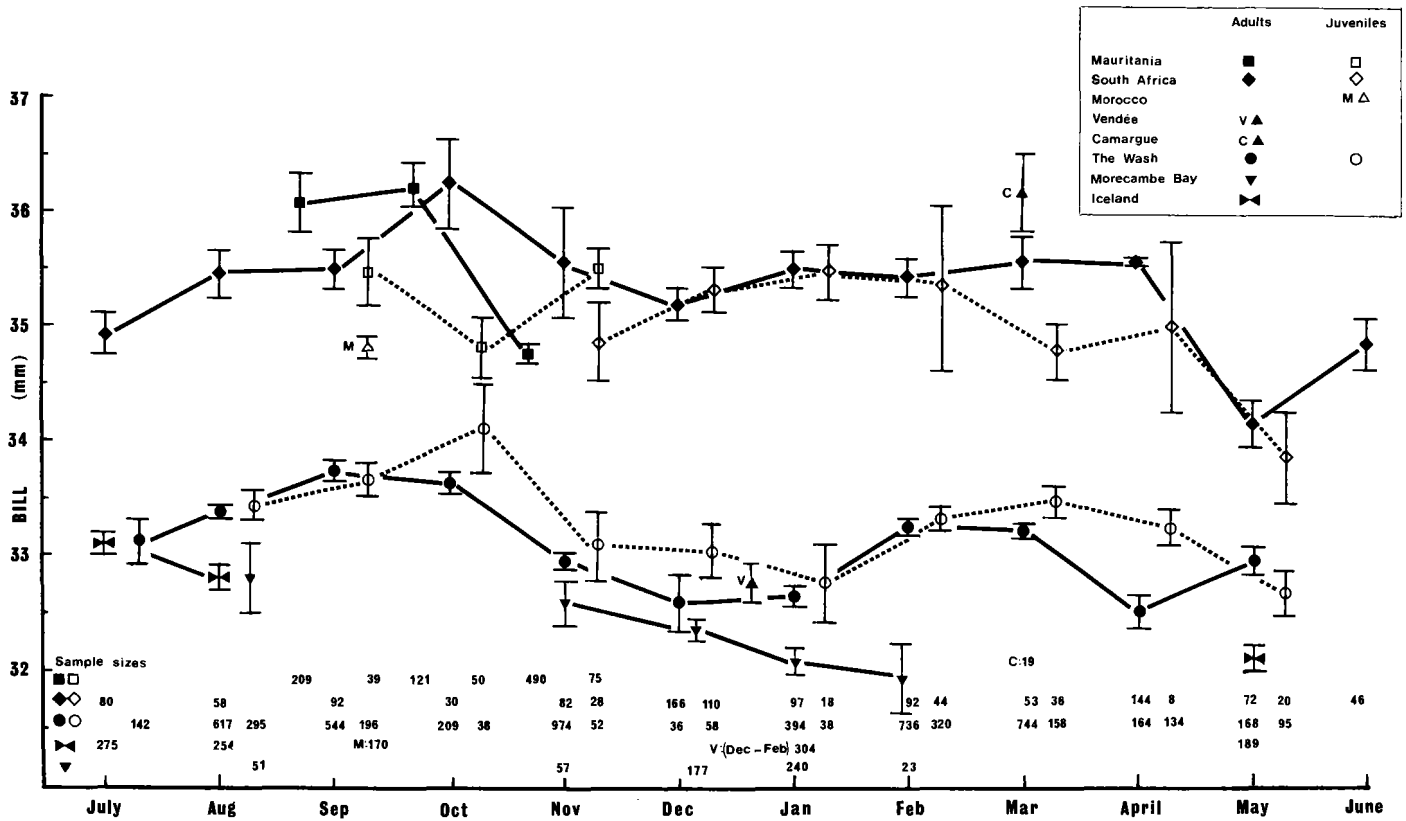

Figure 1. Mean monthly bill lengths of Knots from various localities. Shown as mean ± standard error.
(data for Vendée from Fournier & Spitz (1970); for Iceland from Morrison (1975) and for Camargue A. R. Johnson (pers comm.)

Table 1. Mean changes in bill length of Knots caught twice within one year at the Wash, E. England, grouped for different periods of the year.

Period 1 Period 2	August Sept.-Nov.	within Sept.-Nov.	Sept.-Nov. Dec.-Feb.	August Dec.-Feb.	within Dec.-Feb.	Dec.-Feb. Mar.-May.	Sept.-Nov. Mar.-May	within Mar.-May	Mar.-May August
number of birds	6	10	13	10	6	35	17	11	9
[1]mean of changes in bill length (mm)	1.3	—1.0	—0.2	—1.3	1.3	—0.2	—1.2	1.0	1.2
[2]t	3.18	6.32	1.39	2.63	6.32	0.71	5.50	4.35	8.31
[3]p	<0.05	<0.002	n.s.	<0.05	<0.002	n.s	<0.001	<0.002	<0.001

Notes: 1. The mean change is given as from period 1 to period 2 in each case, but changes from period 2 to period 1 are included in the calculations.
Notes: 2. Difference from zero change tested by t-test for paired comparisons.
Notes: 3. n.s. indicates not significantly different from zero change.

lengths of individual retrapped birds (Table I). This variation could be due to either:

(a) Seasonal changes at the feather margin at the base of the upper mandible associated with abrasion and moult; or

(b) seasonal changes in the growth or wear of the rhampotheca, perhaps related to feeding conditions (e.g. Davis 1951, Stettenheim 1972).

The latter may occur in Oystercatchers *Haematopus ostralegus* (White & Gittins 1964) and Turnstones *Arenaria interpres* both of which have rhampothecae extending well beyond the bone structure; but this is not the case in the Knot and so cannot cause the variation (Dr. P. J. K. Burton *in litt.*). Changes in the feather margin are a more likely cause as the apparent bill lengthening coincides with the wear and loss of feathers prior to autumn and spring body moults.

4.1.2. Differences due to age and sex

Mean bill-lengths of juveniles did not differ significantly from those of adults in either Britain or South Africa (Figure I), so growth would appear to be complete before autumn migration.

Birds sexed by dissection at Morecambe Bay (A. J. Prater *in litt.*) and The Wash (M. W. P. pers. obs.) show mean bill-lengths of 32.2 ± S.E. 0.2 mm. (n=92) for males and 34.0 ± S.E. 0.2 mm. (n=71) for females during the winter months. Knots from South Africa show similar dimorphism, with males 34.5 ± S.E. 0.2 mm. (n=26) and females 35.9 ± S.E. 0.3 mm. (n=17) (Dr. R. Summers pers. comm.). This difference, although significant, is so small in relation to the accuracy, class interval, and variance of the measurements that for practical purposes the bimodality cannot be detected in a mixed population using, for example, the probability paper methods of Harding (1949).

4.1.3. Geographical variation

There are few published bill-lengths from the breeding areas and these have usually been given as means and ranges, without standard errors. Further, the methods of measurement and state of the specimens (e.g. fresh or long dead) have often not been stated.

Skins in the British Museum (Natural History) have provided 20 measurements from or near the breeding grounds in Greenland (mean 32.5 ± S.E. 0.3 mm.) and 6 from Siberia and Eastern Europe, the latter being almost certainly of Siberian origin, (mean 34.2 ± S.E. 0.7 mm.). Despite the small size of the samples, this difference is statistically significant (t_{24}= 2.403, $P< 0.05$). While museum skins are liable to varying degrees of shrinkage and measurements cannot be compared directly with those of live birds (Vepsäläinen 1968, Green & Williams 1972), the relative difference in size should be similar to that in live specimens.

This difference receives some support from the limited information in the literature. Knots of the nominate race collected in various parts of Greenland and Ellesmere Island (Manniche 1910, Pedersen 1930, Løppenthin 1932, Schaanning 1933 and Parmelee & MacDonald 1960) had range of bill-lengths 30—34 mm. (mean 31.8) for 22 males and 32—36 mm. (mean 33.7) for 13 females. The ranges for Siberian birds of the nominate race, given by Kozlova (1962), were 29.0—35.2 mm. for 19 males and 31.5-38.5 mm. for 12 females.

In view of the geographical position of Iceland and numerous ringing recoveries (see below) we conclude that the shorter billed group in Figure 1 are of Greenlandic and north Canadian origin, and museum specimens and literature records suggest that the larger billed birds came from Siberia.

We cannot, however, decide from our analysis of bill-lengths whether the winter populations are each derived from single breeding areas or, if not, what proportions of each breeding population are present in each wintering area, because the difference between the two populations is too small to allow separation of the modes in a mixed sample. Similarly, small changes in the proportions of the two populations in a mixed sample cannot be detected since such changes are likely to be smaller than seasonal variations. However the lack of intermediate mean bill lengths at sites between the two wintering groups suggests little mixing in the places investigated.

4.2. RINGING RECOVERIES AND VISIBLE MIGRATION

The frequency of ringing recoveries relating any two areas on the migration route of a species depends on numbers ringed, the periods of ringing and the greatly differing chances in different areas of reporting of ringed birds. Table 2 summarises ringing recoveries and ringing totals in various countries. The use of ringing recoveries and observations of visible migration enables the migration of the two populations between breeding and wintering areas to be described.

4.2.1. North Canadian/Greenlandic breeding population

Since Nørrevang's (1959) review of recoveries, there have been many more which show movement between West European coasts, Iceland, Greenland and Arctic Canada (Pienkowski *et al* 1971, Morrison & Wilson 1972, Spencer & Hudson 1974, Morrison 1975). Prater (1974) reviewed observations on timing of passage in Europe and traced the main movement of this population through Iceland in July/August, to and through Denmark in August, and to the Waddensee from August onwards. The return passage occurs through Denmark and Iceland in May. Most Greenlandic/Canadian Knots (represented by Icelandic ringed birds) have been found to winter on the coasts of the Irish Sea, North Sea and Bay of Biscay (fig. 2a). Within this

Table 2. Summary of available information on international movements of ringed Knots.

Country of ringing:	Ellesmere Island	Greenland	Iceland	Finland	Sweden	Poland	E. Germany	Norway	W. Germany	Denmark	Netherlands	Belgium	British Isles	France	Morocco	Mauritania
Total no. ringed:	23	14	?	325	?	510	52	6188	?	?	1575	109	43033	1092	181	998
No recovered in:																
Canada			1					1			1		2			
Greenland			7					2			2		41			
Iceland													187	1		
Siberia														1		
White Sea								1								
Finland																
Sweden				1												
Poland													3			
W. Germany			2		1			3					11			
Norway					1	1							3	1		
Denmark			1	1	5			46			1		21			
Netherlands			13					7					24	1		
Belgium								1					1			
British Isles	2		63		3			37			6			6		
France			6	3	11		2	27		1	2	1	25			
Spain								1					2	1		
Portugal			1		1			2				1	1			
Italy								1								
Mauritania						1	1	1					1			
Senegal													4			
Liberia													1			
Ivory Coast								1								
Mozambique													1			
South Africa							1					1	1			
Barbados													1			

area Knots tend to move progressively westwards during the winter (Branson 1971, 1973, Pienkowski *et al* 1971, Prater 1971, Stanley 1971).

4.2.2. Siberian breeding population

There have been no recoveries in Siberia of British ringed Knots, despite the large numbers ringed, but we do not know the relative chances of recovery in Greenland/Canada and Siberia. However, British-ringed waders of other species have been recovered in or near similar breeding ranges (Table 3). This suggests that few, if any, Siberian Knots occur regularly in the British Isles.

An autumn migration to the west from breeding grounds in the Taimyr Peninsula and the New Siberian Islands was well documented by Birula

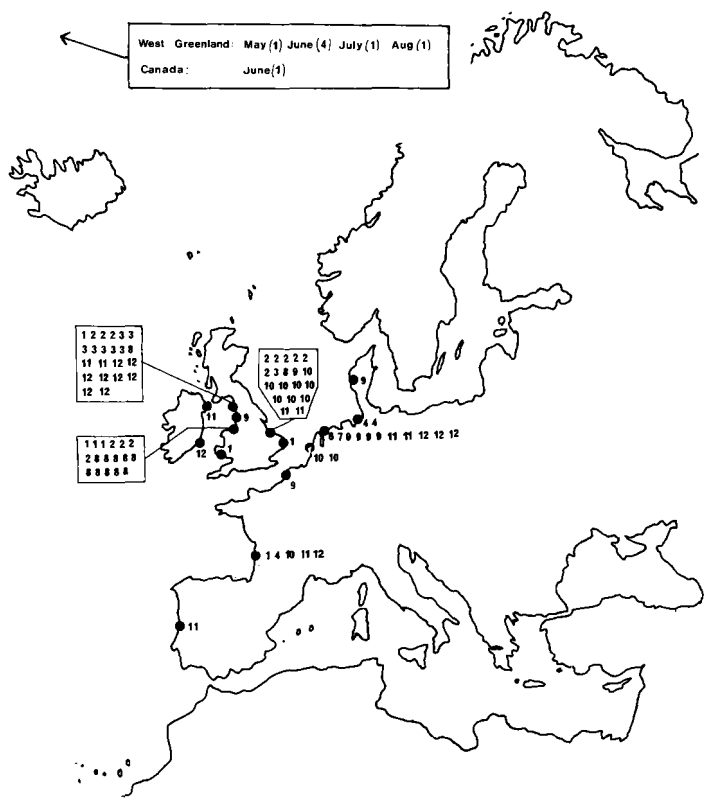

Figure 2(a). International recoveries of Knots ringed in Iceland. (numbers refer to the month of recovery.)

Table 3. Numbers of waders ringed in Britain and recovered in the U.S.S.R. up to December 1973.

	Number ringed	Number recovered	%
Charadrius hiaticula	12,606	1	0.008
Pluvialis squatarola	1,819	1	0.055
Arenaria interpres	6,109	0	0
Limosa lapponica	1,142	3	0.263
Calidris canutus	43,033	0	0
C. minuta	674	0	0
C. alpina	121,793	19	0.016
C. ferruginea	877	3	0.342
C. alba	9,226	2	0.022

(1907, translated by Pleske 1928). For example during the night of 27-28 August 1900 in Middendorff Bay, West Taimyr (75°00' N, 92°59' E) „... a flock of Knots... came in from the north or north-east and was chiefly composed of adult birds beginning their [body] moult. These flocks stayed but a very short while on the sand beach, and were succeeded one after another by new flocks coming from the north... I should add that the western coast of Taimyr, which in these latitudes has an almost north-easterly direction, represents a very important flight line, especially during the autumn migration." And while not excluding the possibility that birds may have also departed in other directions, Birula reported that in autumn 1902, „I have several times had occasion to note that in leaving the Island of New Siberia the flocks of young Knots headed directly west or southwest." Dementiev & Gladkov (1951) and Kozlova (1962) summarise available records of Knot along the north Russian coast and Kozlova suggested (in translation) „that the Knot passes from a given area of Siberia to the west, keeping over the Polar Sea at some distance from the mainland, so that they are not [commonly] found on the coast between the Karsk and Barents Seas, and thus reach the White Sea-Baltic flyway." In view of the Knots' tendency to make long non-stop flights in other areas (see below), it is also feasible that the Knots simply overfly the coast, a possibility also noted by Kozlova.

The migration of the Knot through southern Finland (Lilja 1964, Kaukola & Lilja 1972), South Sweden (Edelstam 1973), and Denmark (Nettlestrøm 1970, Meltofte *et al* 1972), reaches a peak at the end of July for adults and in late August for juveniles. Arrivals of Knots at Ottenby, Sweden, coincided with arrivals of Curlew Sandpipers *Calidris ferruginea* and Bar-tailed Godwits *Limosa lapponica,* which breed only in Siberia and north Europe and not in north east America or Greenland, suggesting a common geographical origin for all three species, since weather conditions are likely to influence the migration of all of them in a similar way.

Some migration also takes place over the north and west coasts of Scandinavia; Kozlova (1962) referred to small but regular migrations along the Murman coast and Miss C. M. Lessells (pers. comm.) reported adult Knot in breeding plumage at Varanger Fjord in the extreme north-east of Norway on 24 and 30 July, 1974. In central Norway, Folkestad (1975) reported that Knots may occur in some numbers on autumn migration, particularly at times of westerly or south-westerly winds. These could be from Greenland but most waders passing through this area are of north-eastern origin, and the Knots may have appeared on land only when meeting opposing winds.

Recoveries of birds ringed in autumn in the Baltic (fig. 2b) clearly indicate a migration along the west European seaboard in August/September and a return in May, with only six recoveries in Europe during the winter. This pattern differs markedly from recoveries of Icelandic and British ringed birds.

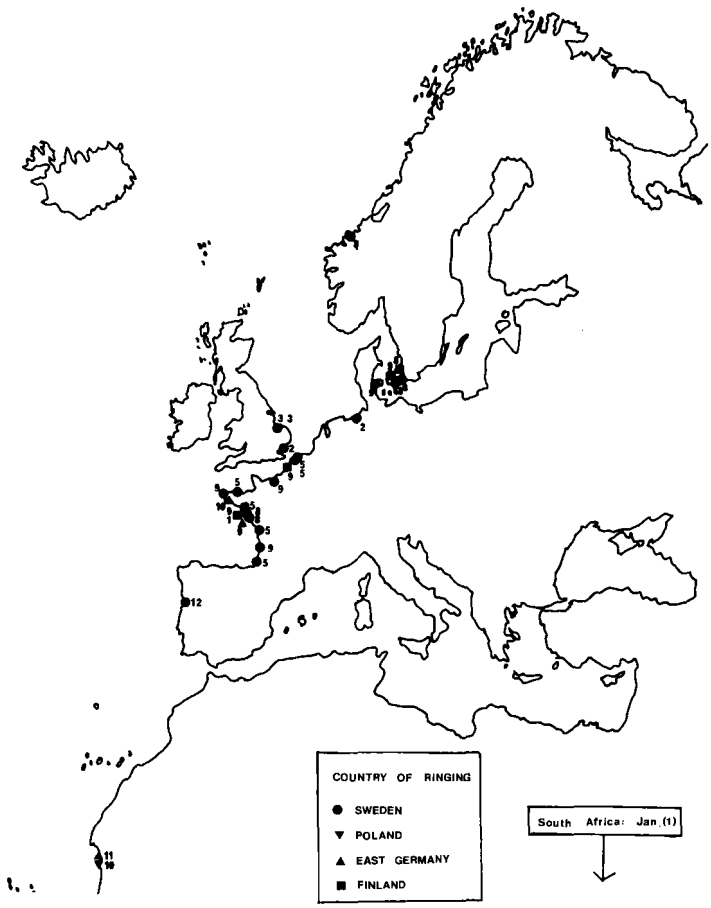

Figure 2(b). International recoveries of Knots ringed in the Baltic. (numbers refer to the month of recovery.)

As mentioned earlier, Prater (1974) has reviewed observations of timing of passage of Knot in Europe and traced the movement of the Greenland and Canadian breeding populations through Iceland to the Waddensee and Britain. The timing of two sets of observations were inconsistent with this pattern. Firstly, the passage periods in Finland were somewhat later both in autumn and in spring, and were compatible with those noted on the breeding grounds by Birula (1907). Secondly, numbers of Knot in the German Waddensee were surprisingly high in May. The timing of both autumn and spring migration in Scandinavia of presumed Siberian birds was slightly later than that of Greenlandic birds.

In Vendée, West France, which forms the southern limit of the wintering area for most Greenlandic/Canadian birds, O. Fournier (pers. comm.) has

observed large influxes of Knots in breeding plumage during May. These flocks were observed to depart in a north-easterly direction. A Siberian destination is suggested by the recovery at Udachnyi, Jakutsk, Siberia (66°29' N, 112°15' E) in June 1974 of an adult Knot ringed on 5 May 1966 in Vendée (G. Jarry pers. comm.) The southern wintering area of these Knots is supported by the recovery in Gironde, France, on 15 May 1975 of a Knot ringed on 17 November 1973 in Mauritania. Comparison of dates and locations of recoveries of Knots ringed in Norway (fig. 2c) with those of

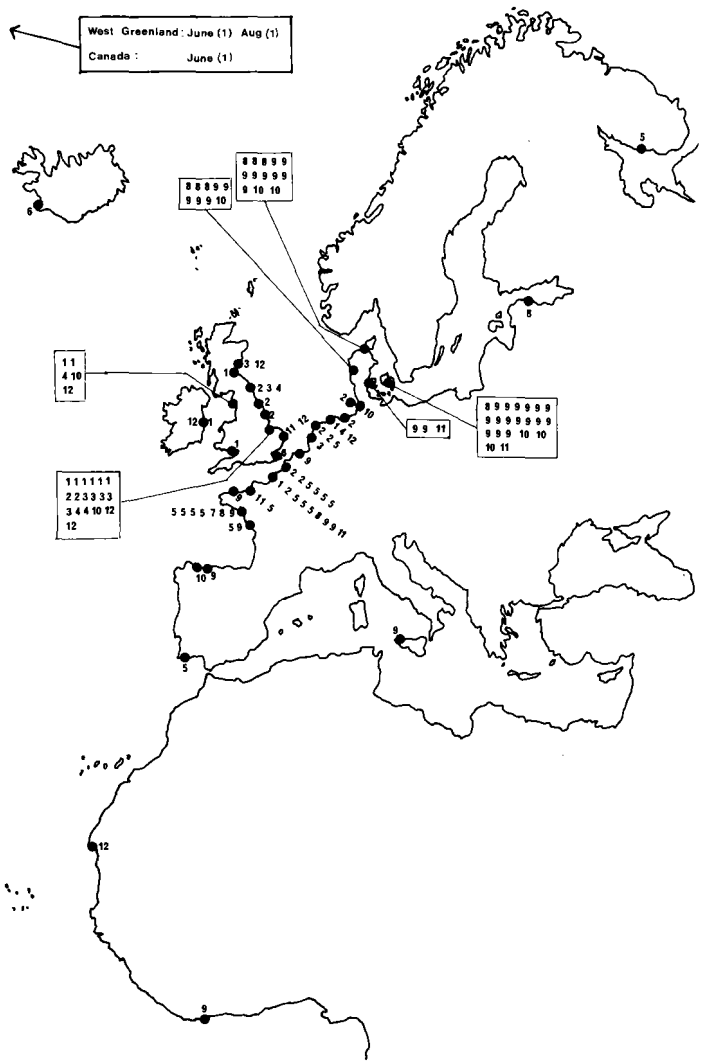

Figure 2(c). International recoveries of Knots ringed in Norway. (numbers refer to the month of recovery.)

presumed Greenlandic/Canadian and Siberian origin (fig. 2a & 2b respectively) make it clear that birds of both populations pass through south west Norway. The assumption by Spencer & Hudson (1974) that British ringed Knots recovered in Norway were necessarily of Siberian origin is erroneous.

4.2.3. Migration in southern Europe and Africa

We have already noted that few Knots winter between the two main centres of Western Europe and West Africa and have suggested that those occurring in Africa are of Siberian origin. W. Tait (in Bannerman 1931) reported large „armies" of Knots on migration in September and October on the Portuguese coast. Relatively few remained during the winter but large numbers reappeared on passage during May. At the Coto Doñana, southern Spain, the Knot is a passage migrant in small numbers (Ree 1973). In the Camargue in southern France Knots occur irregularly during spring migration (A. R. Johnson pers. comm.).

In Morocco, north of Puerto Cansado, records of Knot are usually of small groups, often mainly juveniles, which rarely stay long, during migration. At Puerto Cansado, larger influxes and onward movements of Knots were apparent during August and September 1972 (Pienkowski & Knight 1976).

We have suggested above that the Banc d'Arguin in Mauritania is by far the most important wintering area for Knot in Africa, but only four Knots have been recovered in that area. One ringed at Revtangen, Norway on 28th August 1939 was recovered at Nouadhibou (formerly Port Etienne) on 2nd December 1939. The other three were among 998 Knots caught by the Oxford & Cambridge Mauritanian Expedition 1973. Despite the very large numbers ringed recently in the British Isles, only one (0.1% of birds caught) came from the latter area. Amongst 2,354 Knots caught in Iceland by the Cambridge Iceland Expedition 1972, 5.3% carried British rings, indicating that Knots in Mauritania were not of the same population. The other two Knots recovered in Mauritania, both adults, were ringed in Poland and East Germany, where only about 700 Knots have been marked, providing strong evidence for the occurence in Mauritania of Siberian birds.

To complicate the picture, five juveniles ringed in East England in the first week of September 1963 were recovered between 8 and 37 days later in Senegal and Liberia (Fig. 2d). Early September of 1963 was exceptional in that large numbers of juvenile Knots were present on The Wash (C.D.T.M. pers. obs.). 1963 and the years when other juvenile Knots, ringed on autumn passage in Britain and western Europe, were recovered in Africa, namely 1969 and 1970, were all years noted for heavy autumn passages through Britain of Curlew Sandpipers *Calidris ferruginea* and Little Stints *Calidris minuta,* species which breed only in northern Eurasia. The westward movement of these birds in August and September of some years is associated with persistent north-easterly winds due to atmospheric low pressure systems centred over southern Scandinavia (Nisbet & Vine 1956,

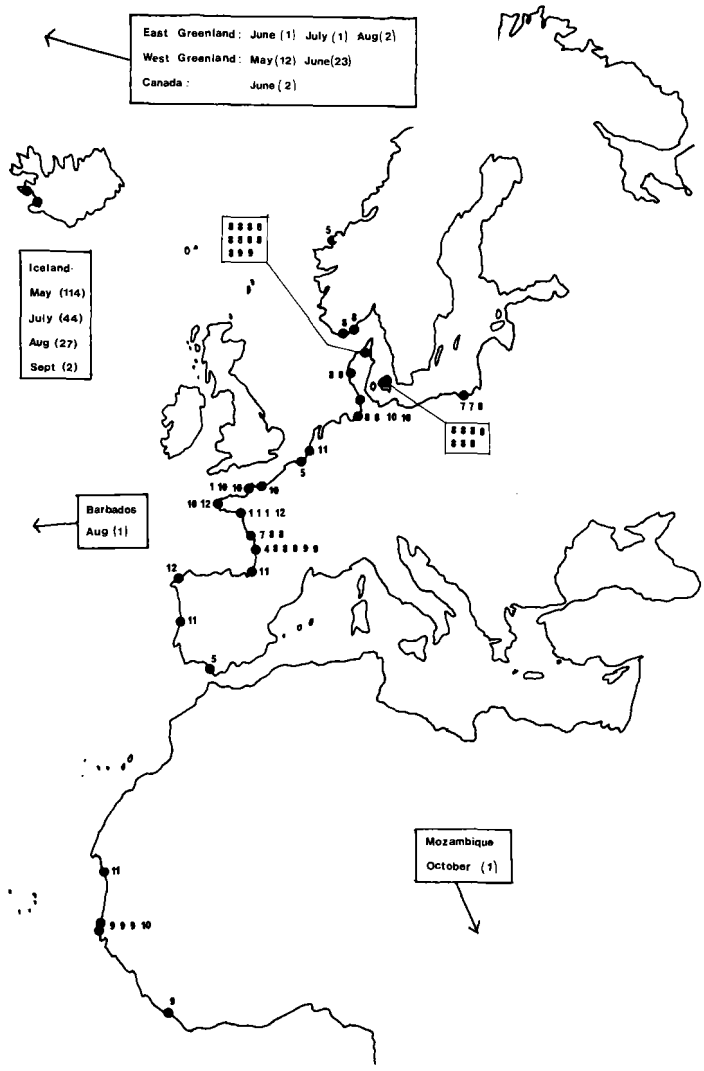

Figure 2(d). International recoveries of Knots ringed in the British Isles. (numbers refer to the month of recovery.)

Stanley & Minton 1972). Such conditions occurred in 1963, 1969 and 1970 and we suggest that some juvenile Knots from Siberia were similarly affected. Similar meteorological conditions prevailed throughout late July 1973 and may have led to a more westward migration than usual in adult Siberian Knots, for an adult ringed in Western Europe was recovered subsequently in Africa (see below). Adult Knots migrate earlier than juveniles and seem to be less prone to westward displacement than juveniles.

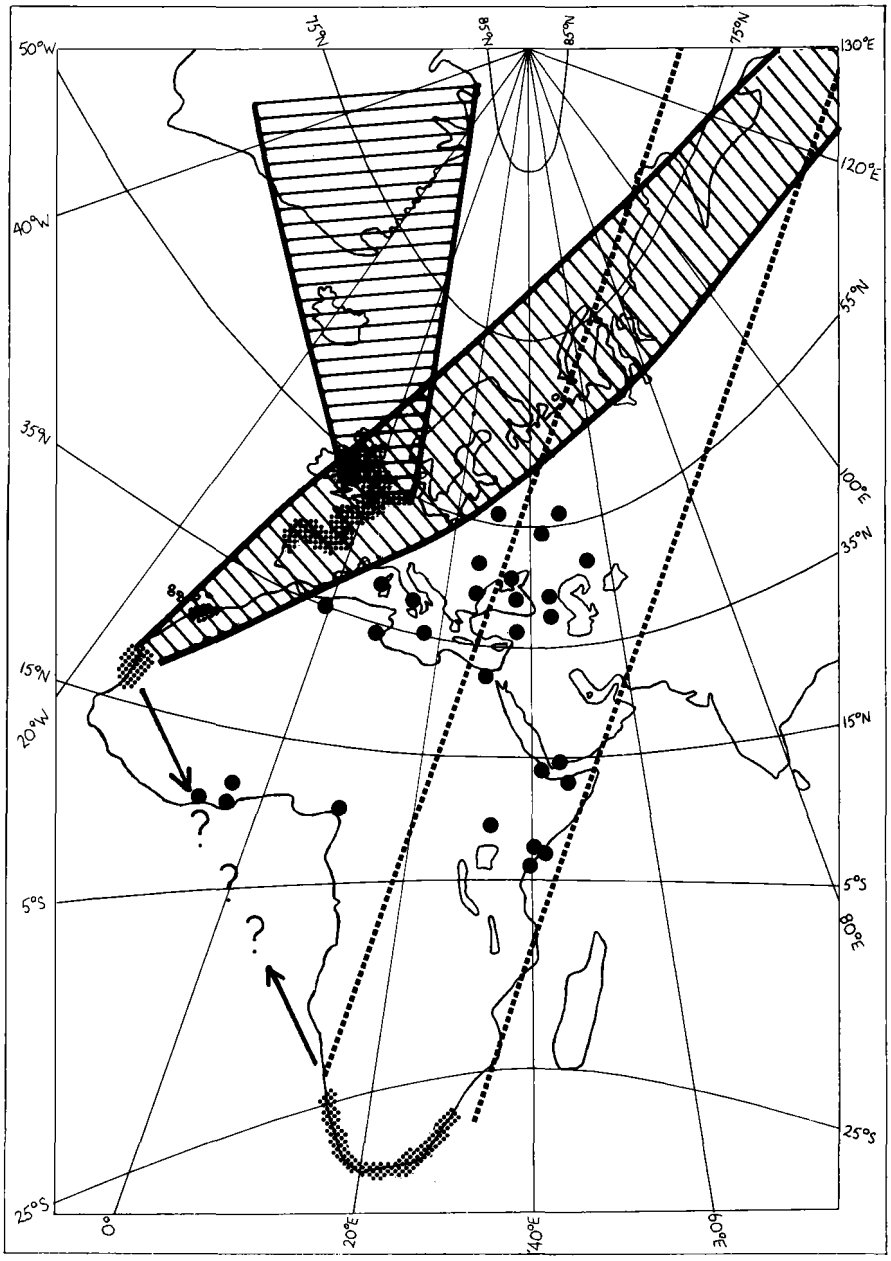

Figure 3. Gnomonic projection showing the main (hatched) and tentative (dashed) migration routes from the breeding grounds to the known wintering areas (stippled). Arrows with '?' indicate movement by an unknown route. Solid dots refer to observations of Knots away from the main migration routes. (Sources: Witherby *et al* 1940, Dementiev & Gladkov 1951, Paige 1960, Kozlova 1962, Fogden 1963).

Finally, one juvenile, ringed in Ireland in September 1973, was recovered in Mauritania by the Expedition. Although numbers of Siberian breeding waders in Britain in that autumn were fairly low, the chance of recovery in West Africa was high due to the presence of the Expedition. The evidence from weather conditions and occurrences of Siberian breeding species in Britain are thus consistent with the suggestion that the few Knots ringed in Britain and subsequently recovered in Africa were birds from Siberia, displaced westwards by adverse winds.

As noted earlier (see section 3 „Winter Distribution") there are few records of Knots seen in Africa other than those in the north-west and the south. As only perhaps 10,000 birds winter in South-Africa (these arriving mainly in November) this is perhaps not surprising. In the west, Wallace (*in litt.*) reports the Knot as principally a late autumn (mainly November) migrant in Nigeria. Germain *et al* (1973) observed a flock of more than 100 in Cameroun, and in Angola Erard & Etchécopar (1970) noted two groups of 30 and 40 individuals in October. In the east, Meinertzhagen (1930) reported flocks of up to 20 at various localities in Egypt and postulated that birds might fly nonstop from there to South Africa. Inland records in Africa and further north in central Eurasia are also very limited, in character with the species' restriction to coastal areas. Most general works on African regions indicate the absence of the Knot or make no mention of it. Scattered records, usually involving single or „a few" individuals in inland Eurasia, Africa and on the East African coast are summarised in figure 3. There is thus a little evidence from observations of migration to and from southern Africa by both West and East Africa.

Despite the low numbers caught in both countries, there has been an exchange of birds in each direction between South Africa and the German Baltic coast, where passage birds are most probably of Siberian origin, and a further recovery in central southern Sweden of a Knot ringed in South Africa. Support for movement to South Africa via Western Europe and West Africa is provided by these and six other ringing recoveries:

(a) Ringed juvenile, 2.9.70 at Revtangen, Norway, to 27.9.70 in Ivory Coast.
(b) Ringed adult, 31.7.73 in Norfolk, England, to 23.12.73 in South Africa.
(c) Ringed ? juvenile, 30.8.69 in Kent, England, to 10.10.70 in Mozambique.
(d) Ringed juvenile, 29.8.69 at Zeebrugge, Belgium, to 2.1.72 in South Africa.
(e) Ringed juvenile, 28.9.72 at Banc d'Arguin, Mauritania to 8.6.75 in South Africa.
(f) Ringed juvenile, 16.12.73 in South Africa, to 17.8.75 in Denmark.

The two birds ringed in 1969 may have been involved in the westward shift of Siberian birds noted in that year (c.f. Stanley & Minton, 1972). It should also be noted that the chance of a ringing recovery on a migration route across East Africa and central Eurasia would be low due to the lack of ringing activity and the tendency of the species to avoid inland areas.

5. DISCUSSION

5.1. WINTERING AREAS OF THE TWO POPULATIONS

Our analysis of bill lengths shows clearly a difference in size between Knots wintering in Western Europe and those in Africa. Further, that the former shorter billed birds are from Greenland and Canada is confirmed by a large number of ringing recoveries. Measurements of a small sample of museum specimens suggest that the longer billed birds are of Siberian origin. This concept is indirectly supported by ringing recoveries and observations of visible migration.

Despite the large numbers caught in Britain there have been few recorded movements of individuals between there and eastern Europe and none between Britain and the Soviet Union (Fig. 2d, Table 2). In contrast, the relatively small numbers ringed in eastern Europe and Africa have resulted in four movements between these areas. This comparison suggests that Siberian Knots winter in Southern and Western Africa and few, if any, winter in the British Isles. Equally, as described above, the Knots wintering in Africa are likely to be almost totally, if not entirely, of Siberian origin. The only evidence of mixing in winter quarters of the two populations consists of five Knots caught on migration in Sweden and one in Finland and recovered in winter in Western Europe (Fig. 2b) and the possibility that these were Greenlandic birds cannot be excluded. The two populations clearly occur in the same areas of Western Europe from Norway to France during autumn migration, but there is no evidence from bill length measurements of Siberian Knot occurring at The Wash at this time. However, the situation in the Waddensea, currently subjected to a long-term study by G. C. Boere, is as yet unknown. On the occasions when wind-drifted Siberian birds have occurred in Britain in autumn, onward passage is rapid, as shown by recoveries in West Africa (Fig. 2d) from 8 to 37 days later, and figure 2b also indicates a fairly rapid movement. The two populations may be separated during spring migration by the differences in timing of their passage.

The apparent separation of Knot populations on the winter grounds contrasts with a considerable overlap in Morocco of populations of wintering Dunlin *Calidris alpina* (Pienkowski & Dick 1975) and may arise in part from the more restricted habitat preferences of the Knot. These preferences have been discussed by Wolff (1969), Zwarts (1974), and Pienkowski & Knight (1976), amongst others. Also, it seems probable that the distribution of coastal waders in Africa although little investigated at present, is much affected by the distribution of mangroves in intertidal habitats, and there is a striking inverse relationship in the case of the Knot, a strongly gregarious species in other parts of its migratory and winter range which could be expected to be particularly adversely affected by mangroves. Evans (1974) noted that in South East Australia many waders did not feed on mud-flats covered by mangroves, but only on the open mud.

5.2. POPULATION SIZES

The wintering totals of Knot in north-west and southern Africa are estimated as 135,000 and 10,000 respectively, compared with 609,000 in western Europe.

The apparent difference in population size between Knots from the north Nearctic (wintering in Europe) and from Siberia (wintering in Africa) requires further consideration. Assessment of the size and distribution of breeding populations is difficult, especially as the breeding range is still not fully established and little census work has been undertaken. However, Dementiev & Gladkov (1951) considered that in Siberia the species is „abundant in localities where it nests, but since the bird's nesting region is relatively small, its total numbers by comparison with other shorebirds are also small." The breeding area in Greenland and the north Canadian Arctic appears to be considerably greater (Salomonsen 1950, Snyder 1957) but we do not know the relative breeding densities.

Some information can be gleaned from the numbers seen on migration to and from the breeding grounds. In west Iceland, flocks of several thousand Knot were seen frequently in May 1970 and 1971 and on 16 May 1970 at least 1400 passed over Eyri, Hvalfjordur in 4 hours. Autumn migration in this area was spread from July to September with flocks of a few hundred often noted (P. J. Knight & P. I. Stanley in Pienkowski *et al.* 1971, Morrison and Wilson 1972). In Finland, flocks occurring in late May and June did not exceed 200 birds and the average number of birds seen in a day at the peak of autumn migration was only 20 (Lilja 1964, Kaukola & Lilja 1972). However, comparison of this type of data is possibly unreliable as Knots may be more prone to stopping in Iceland than in Finland.

Further work on the breeding grounds is clearly required before definite conclusions can be drawn on relative population sizes, and it is important to note that Kozlova (1962) recognised the possibility that some Knot from the New Siberian Islands may join the presumed migration of the Wrangel Island birds to Australasia and South East Asia. The Spitzbergen population is small (Løvenskiold 1964).

5.3. MIGRATION ROUTES

The study of the migration routes of the Knot is made difficult by their tendency to make long, non-stop flights between favoured sites and to be seen rarely between them. These flights certainly occur over parts of North America (Bent 1928, Snyder 1957), across the Greenland icecap (Salomonsen 1950) and obviously from Greenland, Iceland and Spitzbergen to Europe. But we have shown that Knots fly over areas where reasonable habitats occur *en route*. Such situations include passage from West Europe to South Morocco and Mauritania, few birds landing at sites in South Iberia or along the Moroccan coast north of Puerto Cansado. Similarly birds leaving the

Siberian breeding ground are rarely sighted between Taimyr and the Baltic. We also tentatively suggest that birds moving between Siberia and South Africa may make extremely long overland migrations.

The map in Fig. 3 is a gnomonic projection on which the shortest route between any two points of the earth (i.e. on a great circle) is represented by a straight line. This feature is not shared by any other map projections, a point frequently overlooked by ornithologists, but well known in aviation. Note, however, that the distance scale varies over the map. The shortest route between north Siberia and Mauritania/South Morocco crosses the Arctic Ocean from breeding areas on the Taimyr Peninsula and further east before following the Atlantic coastline from North Scandinavia to North West Africa (Fig. 3). The suggested movement of Knot away from the north Russian Coast (Kozlova 1962) therefore seems quite reasonable. Lack (1962) cited the Knot as a species that must follow a „dog-leg" [angled] migration from Siberia to account for the radar observations indicating that waders approach Britain in autumn from a N.N.E. direction, a misinterpretation easily arising from the study of Mercator Projections. In fact there is little difference in distance between a migration route following the Norwegian coastline and one following the White and Baltic Sea routes. It is also important to note that Knot from Northern Greenland would pass close to the Norwegian coast if flying on a great circle route to the Waddensee. However, long sea passages would be involved; and there is ample evidence from ringing that the migration route through Iceland is normal for many Knots.

Apart from rare sightings of few Knots in European U.S.S.R., most Knots migrating from Siberia to Mauritania clearly do not follow a single compass direction. Therefore, the route taken by the majority of the population could be due to either (i) movements between intermediate feeding areas on the Baltic coasts, Waddensea, W. France and Portugal, or (ii) migration by the shortest route between breeding and wintering areas by a great circle or a series of compass bearings approximating to this. Both aspects could be important, and we are not able to distinguish between them on present data. However, the observations of movement over the Arctic Ocean and over the north and west coasts of Scandinavia (section 4.2.2.) suggest a migration route approximating to a great circle between the breeding areas and the first major intermediate site at the Waddensea, and were well to the north and west of a compass line between these two areas. This part of the migration route of Siberian Knots (and some other waders) may be a potential situation in which to investigate, possibly by radar, whether compass or great circle navigation is used.

Many map projections exaggerate the distance from North Siberia to Africa compared with those to other potential wintering areas. Distances from the New Siberian Islands to Mauritania and the nearest point of Australasia are in fact 9,500 km. and 10,400 km. respectively, and from the

Taimyr Peninsula to these two areas 8,500 km. and 10,700 km. respectively.

The evidence of the migration routes of Knots wintering in South Africa is very slender, based on a few ringing recoveries and some field observations. Fig. 3 shows the great circle route from South Africa to the Taimyr Peninsula. The few scattered observations of Knot away from previously recognised migration routes occur principally around this band. Bearing in mind the relatively small number of birds wintering in South Africa, we tentatively suggest that this route may be followed by some of the birds involved. There is stronger evidence from observations and ringing that other wader species, e.g. Little Stint *Calidris minuta,* Curlew Sandpiper *C. ferruginea* and Ruff *Philomachus pugnax* - which are common in eastern and southern Africa and more likely to stop on migration - use this route (e.g. Pearson *et al* 1970, Elliott *et al* in prep.).

Further justification for basing our tentative conclusion on few records can be found in British observations. Ringing recoveries and count data show winter movement of Knot from the east coast to the west coast of Great Britain (see above) and Evans (1968) has presented strong evidence from radar studies that waders in Britain normally migrate overland taking the shortest route. However, in an analysis of inland observations of passage waders in Britain, Mason (1969) found that, although the density of observers is probably higher than anywhere else in the world, records of Knot were very few, both in absolute terms and in comparison with the occurrences of other wader species. Even in a later survey, involving regular organised counts at many inland wetlands, the numbers of Knot seen remained low (Mason 1972). Although the distance across Great Britain is short, we note elsewhere in this paper the ability and tendency of the Knot to make long, continuous flights, so that large numbers of Knots passing over an area may result in only few birds visible on the ground.

Overland migration of the Knot *C.c. rufa* is known in North America (Bent 1928, Snyder 1957). Dupuy (1968) and Smith (1968) have recorded two flocks of several hundred Knots flying over Daiet-Tiour, Algeria (30°05' N, 2°25' W) in April 1966, indicating that Knot, at least sometimes, migrate across the desert. A group of six Knots were observed inland at Barberspan, South Africa (26°33' S, 25°56' E) on 12 September 1968 (Milstein 1975). Lack of observations from East Africa may be because of a rapid migration of the relatively small numbers of South African Knots through an area where there are few observers. The low density of literate human population may account for the lack of recoveries in East Africa, the Middle East, and Siberia. It is perhaps significant that more than one third of the ringing recoveries (6 of 16) in Africa were reported by ornithologists studying waders.

A passage over West Africa is also suggested by direct observation and particularly by the ringing recoveries described above. In particular birds have been ringed on autumn migration in Europe and recovered in the same

year in Africa south of Mauritania.

A migration route from the New Siberian Islands via the West African coastline to South Africa involves a flight of at least 15,700 km., compared with 13,700 km. by the direct route. Differences in the timing of primary moult make it clear that postjuvenile Knots moulting in Mauritania do not subsequently winter in South Africa (pers. obs.) although this does not apply to juveniles, and there are some indications that South African Knots include a high proportion of immature birds. If there are intermediate areas on the migration to South Africa they are most likely to be on the west coast of Africa between Senegal and South-west Africa. Our evidence is inadequate to decide which of the routes is used most frequently of whether there is any difference between autumn and spring passage.

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7. SUMMARY

Recent information on winter distribution and numbers of the Knot in Europe and Africa is summarised. Data on the bill lengths, ringing recoveries and visible migration are used to identify the breeding populations of Siberia and Greenland/N. Canada, and to describe their migrations and wintering areas, correcting earlier reports.

Short-billed birds from the Nearctic winter in Western Europe and longer-billed birds, probably from Siberia, move to north-west and southern Africa. There appears to be little overlap in the winter quarters although populations from both breeding areas may occur together in Western Europe during migration periods, particularly in autumn.

Some effects of weather on the migration of Siberian birds are briefly considered, and attention is drawn to the possibility that Knots follow great circle routes, these being the shortest distances between any two points on the earth's surface.

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9. SAMENVATTING

In dit artikel worden de recente gegevens over voorkomen en aantal van Kanoetstrandlopers in de winter in Europa en Afrika samengevat. Snavellengte (Fig. 1), plaats van terugmelding van geringde vogels (Fig. 2, Tabel 2) en waargenomen trekbewegingen worden te hulp geroepen om de broedpopulaties uit Siberië enerzijds en uit Groenland en Noord-Canada anderzijds van elkaar te onderscheiden en om hun trekroutes en wintergebieden te beschrijven, waarbij gelijktijdig verbeteringen op vorige verslagen hierover worden aangebracht.

De conclusie is, dat kort-snavelige vogels, afkomstig uit de Nearctis (Groenland, Amerika), in West-Europa overwinteren, terwijl vogels met een langere snavel, waarschijnlijk afkomstig uit

Siberië, naar noordwest en zuidelijk Afrika trekken. Hun wintergebieden blijken elkaar slechts in zeer geringe mate te overlappen, ofschoon gedurende de trektijden, en dan voornamelijk in de herfst, vogels uit de verschillende broedgebieden samen in West-Europa kunnen voorkomen.

Mogelijke weersinvloeden op de trek van de Siberische Kanoeten worden in het kort genoemd. De aandacht wordt gevestigd op de mogelijkheid dat Kanoetstrandlopers op hun trek, die dan met doelgerichte oriëntatie zou plaatsvinden, een grootcirkel (kortste afstand tussen twee punten op het aardoppervlak) en niet uitsluitend de kustlijnen zouden volgen. (K.H.V.)

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