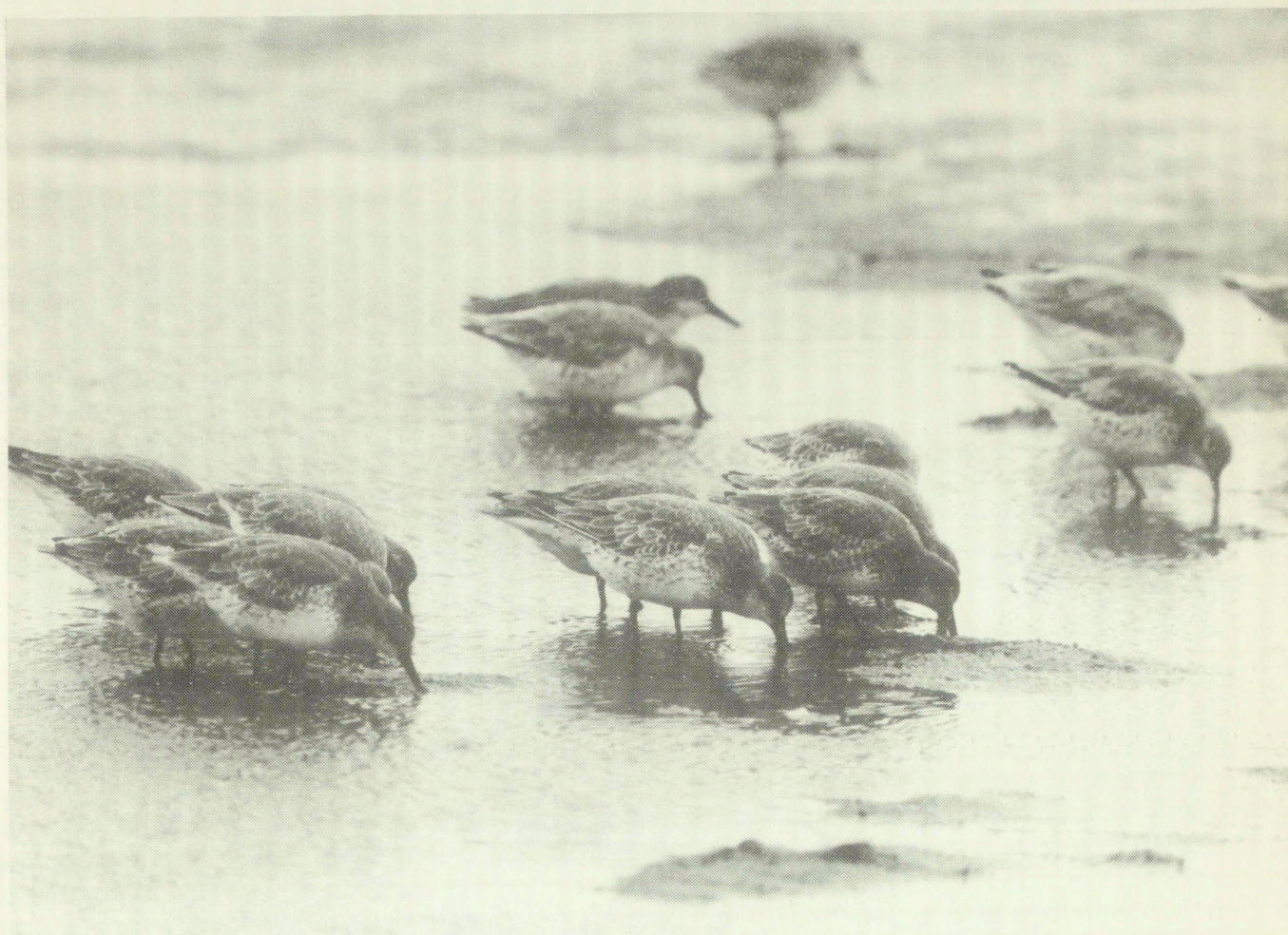


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## Origins and distributions of subspecies



# An analysis of the geographic variability in Knots *Calidris canutus* based on museum skins

Pavel S. Tomkovich

Tomkovich, P.S. 1992. An analysis of the geographical variability in Knots *Calidris canutus* based on museum skins. *Wader Study Group Bull.* 64, Suppl.: 17-23.

A comparison of dimensions and plumage characteristics of museum specimens of adult Knots from the northern hemisphere indicated the existence of a fifth and hitherto unrecognized subspecies of Knot, which has been called *C. c. roselaari* ssp. n. by Tomkovich (1990). Birds of this subspecies breed on Wrangel Island and in Alaska, and migrate along the Pacific coast of North America. Apparently they winter in the Gulf of Mexico. They differ from *rogersi* by larger dimensions (especially in bill length) and more intensely coloured belly and undertail coverts. The New Siberian Islands are inhabited by Knots of small dimensions, with a plumage colour similar to that of *canutus* from Taymyr. Birds from the New Siberian Islands are likely to migrate along the eastern coast of Asia. Only slight colour differences were found between *canutus* and *islandica*. The dimensions of birds from Greenland and Taymyr do not differ. The Siberian breeding grounds of long-billed *canutus* from the African wintering areas remain to be located.

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## INTRODUCTION

Scientists hold different opinions with regard to the number of subspecies of Knots *Calidris canutus*. The Soviet literature (Gladkov 1951; Kozlova 1962; Portenko 1972; Stepanyan 1975) takes the view that there are three subspecies: *C. c. canutus* (L.) in the northern part of the Canadian Arctic Archipelago, Greenland, Taymyr and the New Siberian Islands, *C. c. rogersi* Math. on Wrangel Island, the Chukotski Peninsula and Alaska, and *C. c. rufa* (Wils.) in the southern part of the Canadian Arctic. Elsewhere, the subspecies *rogersi* was sometimes unrecognized, with birds from the Far East classified as *canutus* (Bent 1927; Conover 1943; Vaurie 1965; Johnsgard 1981; Godfrey 1986; Harrington 1986). Sometimes, however, Knots from high arctic Canada and Greenland are considered as another independent subspecies (*C. c. islandica* (L.)), so that up to four subspecies are recognized (Cramp & Simmons 1983; Hayman *et al.* 1986). However, contradictions remain since some sources describe the birds of the subspecies *rogersi* as being the largest subspecies (Gladkov 1951; Kozlova 1962; Portenko 1972), whereas others describe them as the smallest (Prater *et al.* 1977; Roselaar 1983; Hayman *et al.* 1986; Barter *et al.*

1988). This discrepancy is a result of 1) difficulty to get comparable museum skins from different parts of the species range and 2) lack of collections from some regions (Tomkovich 1986).

The most thorough examination of the variability in Knots has been carried out by Roselaar (1983), who comes to important conclusions and makes some unexpected speculations. He noted that *C. c. rogersi* (examined by Mathews 1913 in China) distinguishes itself as being small, which means that the bigger birds from Wrangel Island must take another migration route, possibly to the America's. Of course this means that they are not related to *rogersi*, but they may be identical with Knots from Alaska. In Roselaar's (1983) opinion, the breeding areas of *rogersi* lie either in areas for which no breeding records of Knots are known yet, or on Taymyr Peninsula or the New Siberian Islands. In turn, this would imply that the breeding areas of nominate *canutus* are unknown. If this conjecture were true it would change the intraspecific systematics of Knots, especially within the borders of the Palearctic. Roselaar examined little material from the Soviet Union. Further analyses using skins from the Soviet Union are presented here.

## MATERIAL AND METHODS

Skins available in the following collections were examined: Zoological Museum and the Faculty of Biogeography of the Moscow State University, the Zoological Institute, Academy of Sciences of the USSR (Leningrad), the Institute of Biology and Soil Science, Far-eastern branch of the USSR Academy of Sciences (Vladivostok) and the Institute of Biological Problems of the North, Far-eastern branch of the USSR Academy of Sciences (Magadan). I also had at my disposal material of the National Museum of Natural History (Washington, D.C.), of the National Museum of Canada (Ottawa), and of the British Museum of Natural History (Tring).

Morphological variability in Knots was always assessed on the basis of their size and their plumage colour in adults, but sometimes also in juveniles. I only examined the skins of full-grown birds. Conover (1943) pointed out that the breeding plumage in May - early July is best suited for geographical comparisons. Bill length (exposed culmen), and tarsus were measured with an accuracy of 0.1 mm. Wing length was measured with a ruler with an accuracy of 0.5 mm. To avoid breaking the wings, I measured wing length by pressing the wing against the ruler without stretching it. This complicates the research in that my measurements will differ from those in the recent literature (Prater *et al.* 1977; Cramp & Simmons 1983; Roselaar 1983). My measurements of wing shortening due to preparation and drying of skins are close to those published by Engelmoer *et al.* (1983). Within the first three years wing length decreased with 1.5 - 2.7% of the original measurement. Most of the birds from the Chukotski Peninsula were collected in 1986 - 1988 and were measured in late 1988. Consequently, it is to be expected that the measured wing length values are somewhat larger than those of the remaining completely dry specimens which were collected earlier. This has to be kept in mind when making comparisons between birds from Chukotski and elsewhere. Within the examined birds from north Chukotski, there were three that were shot on the Spit of Beljaka which differed from all the others in bill length and the rufous colour of belly and undertail. I therefore assigned them to the Wrangel Island migrant birds and excluded them from further analyses.

Knots are sexually dimorphic in body size as well as plumage colour, and sex was therefore always taken into account. Since females appeared to geographically vary less than males, the description of plum-

age variation is mainly based on males.

## GEOGRAPHIC VARIATION

### Biometric data

A preliminary analysis of the morphological variation of Knots from Siberia and the Far East led to the conclusion that there are four distinct populations (Tomkovich 1986). These breed on Taymyr, the New Siberian Islands, Wrangel Island and in the mountain regions of the Chukotski Peninsula, respectively. Table 1 gives the biometric data of these four breeding populations and in addition those of migrants from the Far East and from some other areas of the northern hemisphere. It is evident from Table 1 that the Knots from the New Siberian Islands, which were always considered con-specific with birds from the nominate subspecies *canutus* from Taymyr, are smaller in all measurements.

Even more important were the size differences between Knots from Wrangel Island and those from Chukotski Peninsula: the birds from Wrangel Island were largest. All the differences are statistically significant (Student's *t*-tests; parameter values not presented for brevity).

Although birds from the New Siberian Islands tended to be even smaller than those from the Chukotski Peninsula, the small differences were not significant except for wing length in females and bill length in males. A comparison of the large Knots from north Asia shows that the birds from Wrangel Island were bigger than the birds from Taymyr, but these differences are only significant for males. For the females only the difference in bill length was significant.

I had only two males and one female from Alaska at my disposal with which to test the supposed similarity between the Knots from Wrangel Island and those from Alaska (Portenko 1972; Roselaar 1983). All three were big birds of which wing length and tarsus length (and in males also bill length) corresponded to the values of Wrangel birds. The bill of the single female was slightly longer than of Wrangel females (Table 1).

Roselaar (1983) suggested that the Knots from Wrangel Island do not move south along the Pacific coast of Asia but more likely cross the Bering Strait and go down the Pacific coast of North America. To test this, I compared migrant Knots from the Far

Table 1. Biometric characteristics (in mm) of adult Knots from different areas of the breeding range and migration routes. Some of the material from Chukotski

Peninsula was not dried out completely (see text). Eastern North America does not include the High Arctic.

Region	Wing		Bill		Tarsus	
	Male	Female	Male	Female	Male	Female
Taymyr						
mean $\pm$ SD	162.3 $\pm$ 2.2	168.6 $\pm$ 4.2	32.5 $\pm$ 1.8	34.9 $\pm$ 1.8	31.0 $\pm$ 1.8	32.3 $\pm$ 1.5
range (n)	158.5-166 (18)	163.5-173 (6)	29-35.2 (15)	33.2-37.3 (7)	28.7-35.8 (18)	30.5-33.9 (7)
New Siberian Islands						
mean $\pm$ SD	155.1 $\pm$ 3.5	160.1 $\pm$ 2.7	30.0 $\pm$ 0.9	33.4 $\pm$ 0.6	29.5 $\pm$ 1.7	31.4 $\pm$ 1.2
range (n)	150.5-160.0 (5)	158.0-164.0 (4)	29.0-31.0 (7)	32.8-34.4 (6)	26.0-30.9 (7)	30.0-33.4 (6)
Wrangel Island						
mean $\pm$ SD	166.8 $\pm$ 3.6	170.4 $\pm$ 3.5	36.1 $\pm$ 1.8	36.6 $\pm$ 1.4	32.5 $\pm$ 1.1	32.9 $\pm$ 1.3
range (n)	159.5-172.5 (17)	166.0-175.5 (12)	33.3-38.9 (18)	34.7-38.3 (11)	30.6-35.5 (19)	30.7-35.5 (12)
Chukotski/Anadyrland						
mean $\pm$ SD	159.3 $\pm$ 5.7	166.1 $\pm$ 3.1	31.7 $\pm$ 1.5	33.6 $\pm$ 1.1	30.4 $\pm$ 1.3	30.9 $\pm$ 1.3
range (n)	150.0-166.0 (10)	162.0-170.5 (10)	28.9-33.5 (10)	31.5-35.3 (10)	28.6-32.7 (10)	29.5-32.8 (10)
Soviet Far East						
mean $\pm$ SD	164.4 $\pm$ 3.4	168.5 $\pm$ 2.3	30.8 $\pm$ 1.8	32.2 $\pm$ 0.8	30.7 $\pm$ 0.4	30.5 $\pm$ 1.0
range (n)	160.0-169.5 (8)	166.5-171.0 (3)	27.0-32.5 (8)	31.4-33.0 (3)	28.3-31.4 (8)	29.6-31.6 (3)
Alaska						
range (n)	164.0-170.0 (2)	168.0 (1)	34.2-34.8 (2)	38.9 (1)	31.0 (1)	33.1 (1)
Washington State						
mean $\pm$ SD	165.8 $\pm$ 3.6	170.3 $\pm$ 8.5	35.6 $\pm$ 1.8	38.4 $\pm$ 1.4	32.9 $\pm$ 1.0	32.3 $\pm$ 0.9
range (n)	159.5-169.0 (6)	162.0-179.0 (3)	33.4-38.0 (6)	36.9-39.6 (3)	31.9-34.4 (6)	31.7-33.4 (3)
eastern N. America						
mean $\pm$ SD	162.8 $\pm$ 5.9	167.8 $\pm$ 4.1	35.6 $\pm$ 1.2	36.9 $\pm$ 1.6	31.6 $\pm$ 0.9	32.1 $\pm$ 0.9
range (n)	153.5-176.0 (13)	161.5-173.0 (12)	33.8-37.5 (13)	34.2-39.0 (10)	30.6-33.2 (13)	30.7-33.9 (11)
Greenland & Bathurst Isl.						
mean $\pm$ SD	163.0 $\pm$ 3.1	165.8 $\pm$ 6.2	32.8 $\pm$ 1.7	33.9 $\pm$ 0.1	30.8 $\pm$ 1.1	30.3 $\pm$ 0.6
range (n)	161.5-166.5 (4)	157.5-168.5 (4)	30.7-34.8 (4)	33.8-33.9 (3)	30.7-31.9 (4)	29.8-31.1 (4)

East and from Washington State with Knots from Wrangel Island (Table 1). The dimensions of migrants from the Far East tended to correspond well with those of Chukotski breeders. Only wing length was larger in male Far East migrants, and bill length shorter in females. Knots from Wrangel Island and Alaska did not differ in size from the spring migrants from Washington State, except for bill length in females. This was longer in birds from Washington State than in those from Wrangel Island. The close correspondence in biometrics of birds from Wrangel, Alaska and Washington State corroborates the view that the breeding population from Wrangel Island migrates along the East Pacific coast, while those from Chukotski follow the Asian (West) Pacific coast.

Another possibility is that the Knots breeding on Wrangel and in Alaska belong to the subspecies *rufa* which breeds in the eastern Low Arctic of Canada (Morrison & Harrington 1992). Comparison of migrants from both the west and east coasts of North America (Table 1) indicate that only tarsus lengths of males differed significantly. Furthermore, the wing length of male *rufa* was shorter than that of male birds from Wrangel Island.

A comparison between Knots from Greenland and Taymyr is also of interest since their identity as separate subspecies is sometimes doubted. The *islandica* birds from Greenland and Canada have slightly longer wings and tails and shorter bills and tarsi

(Dick *et al.* 1976; Cramp & Simmons 1983; Roselaar 1983; Prokosch 1988). According to the material that was available to me all measured values were identical, with the exception of tarsus length of females, which was relatively short for three birds from Greenland and one from northeast Canada.

#### Plumage colour

It is usually assumed that the east Asian breeding Knots are of an intermediate plumage colour between the dark birds with bright rufous colour from northeast Canada, Greenland, Taymyr and New Siberian Islands, and the lighter coloured *rufa* with a 'silvery' back and pale rufous below from the south Canadian Arctic (Mathews 1913; Conover 1943; Kozlova 1962; Portenko 1972). The differences in plumage colour between the 'dark' subspecies *islandica* and *canutus* are small and were clearly characterised by Roselaar (1983). Samples available from Greenland and Taymyr do have much in common. I was able to recognize only a lesser intensity of the rufous and less black on the upper-parts in *islandica*.

The plumage of Knots from Taymyr and the New Siberian Islands is similar. The upper-parts of birds from Wrangel Island and Chukotski Peninsula are also similar to each other. Portenko (1972) correctly noticed that Knots from Wrangel in comparison with birds from Taymyr and the New Siberian Islands are more variegated, whitish-grey, with black and buff spots. The edges of feathers and markings are wider. In contrast to *rufa* they have darker upper-parts with light narrow edges of feathers on a black background, rather than the grey back plumage with black spots characteristic of *rufa*. The redness in the back-plumage of New Siberian Island birds is more intense, and the rufous spots on the scapulars are of a deeper colour and less yellow. Compared with birds from Taymyr, Portenko (1972) noted a lighter yellow-brown colouring of the ventral side in the breeding birds from Wrangel. This difference may not be a characteristic feature, however, since in the course of the breeding season a fading in colour from rufous to yellowish takes place. Nevertheless, the rufous under-parts of the Wrangel Island birds is of a deeper colour than in *rufa* specimens.

Considerable plumage differences exist between birds from Wrangel Island and relatively nearby Chukotski Peninsula. The latter birds can be described as 'white-bellies'. In only 5 of 18 specimens did a rufous colour cover a considerable part of belly and undertail. In contrast few (2 out of 32) Wrangel

specimens had only little rufous on their belly and undertail, a significant difference in plumage distribution (Chi<sup>2</sup>-test,  $p < 0.01$ ).

The extent of white on the underparts in birds from Chukotski Peninsula was similar to the plumage of *rufa*. Among the birds from Taymyr and the New Siberian Islands light bellies were rare. The difference in relative frequency of light bellied birds from the New Siberian Islands and Chukotski Peninsula is significant (among 16 New Siberian birds only 3 were without and 2 with few rufous feathers; Chi<sup>2</sup>-test,  $p < 0.01$ ). These plumage differences corroborate the presence of different populations indicated by biometric data.

Plumage colours of birds from Wrangel Island and Alaska were similar. It is interesting to note that the large and medium upper wing coverts of Knots from Wrangel, Alaska and Washington State are more worn than in *rufa* birds. This may indicate differences in moult schedules between these two supposed populations. Among all neighbouring breeding populations of Knots, plumage colour differed most between birds from northeast (*islandica*) and more southerly parts of the Canadian Arctic (*rufa*).

#### MIGRATION AND SUBSPECIFIC RECOGNITION

Roselaar's (1983) analysis has made clear that discussions about subspecific identity should include details of their migratory behaviour. My research has shown the birds from the assumed *islandica* and *canutus* (Taymyr) populations to be identical in size and having small differences in plumage colour. Therefore these subspecies are only slightly differentiated. Recent findings about the spring migration through north Norway (Davidson *et al.* 1986; Uttley *et al.* 1987; Wood 1988) cast other doubts as to which breeding populations the name *canutus* is applicable.

Siberian-breeding *canutus* are thought to winter in Africa and only stage in Europe during their migrations. On their way to the breeding grounds they follow a route over the Wadden Sea, the Baltic and the White Sea (Dick *et al.* 1976, 1987; Piersma *et al.* 1987; Prokosch 1988). The *islandica* birds from Greenland and north-east Canada winter in western Europe, and pass through Iceland and northernmost Norway during their migrations between wintering and breeding grounds (Dick *et al.* 1976; Davidson *et al.* 1986; Davidson & Wilson 1992). Some *canutus*

birds may, however, winter in Europe (Dick *et al.* 1976; Gromadzka 1985). Adding to the puzzle are the observations of Kokhanov & Skokova (1967) and Tatarinkova (1982) of a spring passage of good numbers of eastward flying Knots along the Murmansk coastline, possibly from north Norway. The most serious objection to connecting the African winterers passing Europe in late spring and early autumn with the nominate *canutus* from Taymyr, is that Taymyr breeders have rather short bills, and not long bills as found in African wintering birds. It appears that the tradition of inferring subspecific identity of Knots in Europe from bill dimensions alone is now obsolete.

Since their small bill is not proof of a Nearctic breeding origin, and because of the existence of spring migration observations to the east near Murmansk, close to north Norway, it is possible that part of the Norwegian spring migrants are in fact breeding on the Taymyr Peninsula as previously supposed by Håland & Kålås (1980). It remains possible that birds from breeding populations in Greenland and northeast Canada and Taymyr may all winter in western Europe. This hypothesis could

explain the rather large discrepancy between the numbers found wintering and the estimated number of breeding pairs (Meltofte 1985; but see Godfrey 1992 for another explanation).

It is clear that a large-billed population wintering in west and south Africa migrates through Europe (Dick *et al.* 1976, 1987; Piersma *et al.* 1987, 1992; Prokosch 1988). Their breeding area remains to be identified. Judging from the recoveries of birds ringed in South Africa (one recovered in Narjan Mar, Archangelsk Region) and others in western Europe (Gromadzka 1985), it is possible that long-billed birds do indeed fly to Siberia. The two existing ringing recoveries from England and France are in fact from Yakutia near the Arctic circle, more to the southeast than Taymyr (see Figure 1). This indicates that the long-billed birds from Africa and Europe fly to central Siberia. Breeding birds from the nearby New Siberian Islands are short-billed and this could mean that the breeding range of the long-billed African winterers must be situated somewhere in the mountain tundras of Yakutia. Since they differ only by average bill length from birds of Taymyr which also migrate westwards (in 1990 the first direct

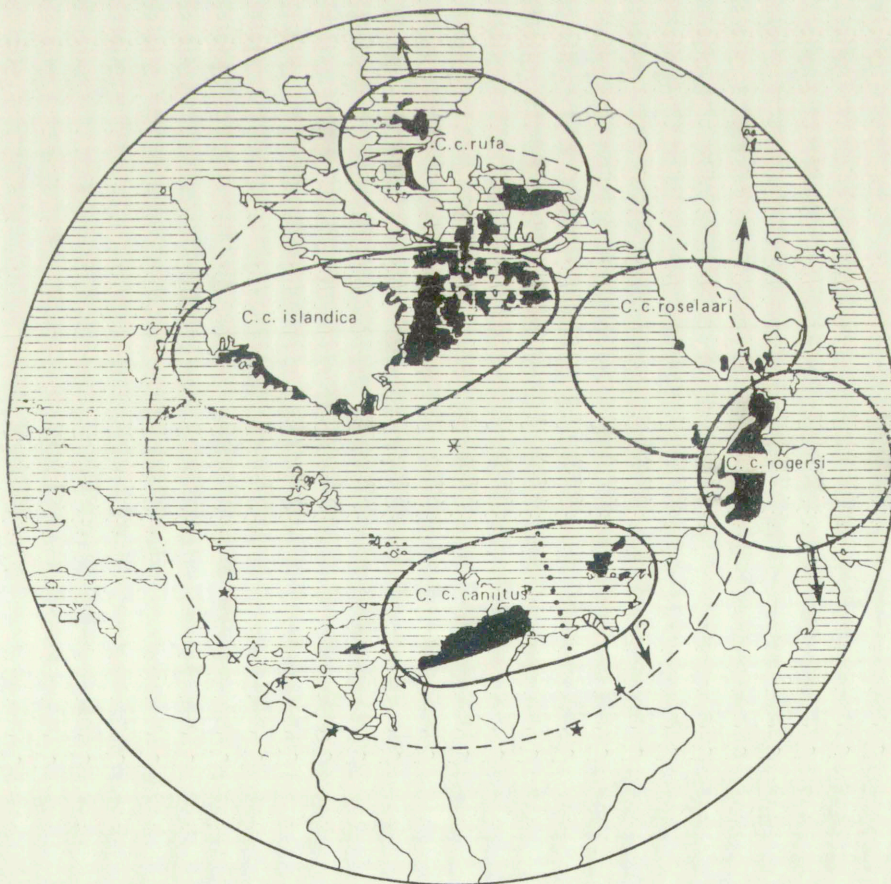


Figure 1. Breeding distribution of Knot subspecies and directions of their departure (arrows) to wintering

grounds. Asterisks indicate locations of recovery of birds marked in South Africa and western Europe.

recovery of a Taymyr-hatched juvenile Knot was received from Kiel, Germany), it is not yet necessary to give them a new subspecific name.

Their small body size indicates that the birds from the New Siberian Islands and Chukotski Peninsula migrate along the east Asian Pacific coast to Australia and New Zealand to winter. Descriptions of migrant *rogersi* from Shanghai by Mathews (1913) agree perfectly with the plumage colour and size of breeding Knots from Chukotski Peninsula that I have examined. *Rogersi* Knots therefore definitely winter in Australasia.

The presence of New Siberian Islands breeding birds along the east coast of Asia is suggested by the presence there of specimens with intensely rufous coloured bellies. It is likely that Portenko (1972) referred to such specimens when he stated that *canutus* is to be found as far east as the Sea of Ochotsk. In inland eastern Siberia migrating Knots are only rarely recorded, but two museum specimens from the middle reaches of the Indigirka river resembled the New Siberian Island birds and suggest an easterly migration route. Although breeding birds from the New Siberian Islands are on average smaller than the birds from Taymyr, their plumages are indistinguishable and there is therefore no need to separate them as a new subspecies. For the Australasian wintering quarters of Knots it seems that not only do *rogersi* occur, but also probably the subspecies *canutus* from the New Siberian Islands. Two recent recoveries of Australian Knots from inland Siberia (see *Wader Study Group Bull.* 58, 1990) give additional support for the idea about the migration of Knots from the New Siberian Islands to Australasia. It is also likely that the nominate subspecies *canutus* consists of two or three (including the large-billed African winterers) populations.

There is a close resemblance between birds from Wrangel Island and Alaska. These differ from *rogersi* and *rufa* specimens. This suggests that Roselaar (1983) is correct in identifying a breeding population which migrates along the Pacific coast of America. It may winter in the Gulf of Mexico. These birds have been generally included in *rufa* but they hardly mix with other known *rufa* wintering in South America (Harrington & Leddy 1982; Harrington 1986; Morrison 1984) and have a little different timing of moult (Harrington in Morrison 1984). The birds from both Wrangel Island and Alaska have been named as a new subspecies *Calidris canutus roselaari* ssp. n. by Tomkovich (1990).

## ACKNOWLEDGEMENTS

This contribution is a revised version of my 1990-paper in the Bulletin of Moscow Society of Naturalists. It was translated from Russian into German into English by Ingrun Schweimler, Mario Hoppema and Theunis Piersma. I wish to thank V.M. Loskot, E.A. Shapoval, A.V. Kondratiev, N.P. Osadchaya, V.A. Nechaev, R.C. Banks, H. Ouellet and P.R. Colston for help with collections, and N.C. Davidson, M. Barter, J. Gromadzka, T. Piersma, C.S. Roselaar, B.A. Harrington, R.I.G. Morrison for reprints and/or valuable discussions.

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