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SUBSPECIES RECOGNITION IN KNOT *CALIDRIS CANUTUS* AND OCCURRENCE OF RACES IN WESTERN EUROPE

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ABSTRACT

Based on migrant and winter specimens, 2 separate populations of Knot *Calidris canutus* are shown to occur in the Netherlands. Both are sufficiently differentiated to deserve recognition on subspecies level. Breeding range, migration routes, and winter areas of both these subspecies are defined. Additional material proves that at least 3 other populations of Knot occur in the Holarctic, at least 2 of these warranting recognition as separate subspecies, but breeding grounds and winter areas are not known for all of these. Morphometrical characters and a map with migration routes for all 5 Knot populations are provided.

INTRODUCTION

When studying taxonomy and plumages of waders for volume 3 of the Handbook of Birds of Europe, the Middle East and North Africa I measured all waders present in the collections of the Rijksmuseum van Natuurlijke Historie in Leiden and the Zoological Museum of Amsterdam, in total about 12,500 skins. These collections contain many waders from western Europe, northern South America and Indonesia, as well as small series of breeding birds from Svalbard and East Greenland, and some birds from Patagonia and West Africa. This wide variation in localities makes these skin collections suitable for research of geographical variation of Holarctic species. A further advantage is, that most birds were obtained quite recently (many within the last 30 years) and that they are usually skinned by experienced staff taxidermists, which are known for trustworthy sexing. Most of the data gathered during the work on the Handbook are published in Roselaar in Cramp & Simmons (1983), but some details are interesting enough to deserve more attention, like those on moults (Roselaar in prep.) and on recognition of races of Purple Sandpiper *Calidris maritima* (Boere *et al.* in press), Knot *Calidris canutus*, Redshank *Tringa totanus*, and others. In this article, attention is paid to races, migrations, and stop-over areas of Knot *Calidris canutus*.

SUBSPECIES OF *CALIDRIS CANUTUS* HITHERTO RECOGNIZED

The number of subspecies of the Knot recognized seems to have been stable for a long time. Hartert mentioned 3 races as long ago as 1920

(though one with a question mark), and these races are still mentioned in recent works like Prater *et al.* (1977): nominate *canutus* breeding in Greenland and the Canadian arctic north of 74°N, and on Taymyr Peninsula, Severnaya Zemlya, and Novosibirskiye Islands in northern Siberia; *rogersi* on Wrangel Island in north-eastern Siberia and in Alaska, and *rufa* in arctic Canada south of 74°N, these races wintering respectively in western Europe and Africa, south-east Asia to New Zealand, and southern USA to Argentina. Some authors doubt the validity of *rogersi* (the question-marked race of Hartert) and this subspecies is then included in nominate *canutus* (e.g. AOU checklist 1957). Much more data on migration are now known than in Hartert's time. A major advance was made when it could be shown that the western population of nominate *canutus*, breeding in high-arctic Canada and Greenland, wintered in western Europe, while the Siberian population of this subspecies migrated through western Europe to winter in West and (partly) South Africa (Dick *et al.* 1976). The occurrence of 2 different populations in western Europe, one as transients the other as winterers, aroused my interest, and I decided to compare all my data on adult specimens from the Dutch collections with those of the British Museum (Natural History) in Tring, where I measured all specimens in adult breeding plumage.

DIFFERENT POPULATIONS OF KNOT OCCURRING IN THE NETHERLANDS

The most simple way to find out if populations with a different timing in migration occur in a country, is to group all birds of a certain age and sex class by month to see if certain measurable characters show monthly variations. Some authors advocate more advanced methods, e.g. Fournier & Spitz (1970), but this does not necessarily lead to a clearer picture. For *C. canutus*, I measured wing, tail, bill, tarsus, and middle toe; for measuring techniques see Cramp & Simmons (1977). I found tail length to be directly correlated with wing length and toe with tarsus; therefore tail and toe are not further considered separately. As the number of specimens was rather poor for some months, I combined some, while in early autumn I treated moulting and non-moulting birds separately, because, according to Dick *et al.* (1976), the population moulting in western Europe stays to winter, while non-moulters are just passing through to moult in Africa. July adults were not available, 2 from June were combined with May. Figure 1 shows 2 groups indeed, a short-billed long-winged population arriving in August to moult and subsequently wintering, and a long-billed short-winged population, occurring August-September (non-moulting and hence apparently migrating) and May. Wing length decreases somewhat from August to April, and one may attribute this to wear. However, *contra* Pienkowski & Minton (1973) I do not think that flight-feather wear normally is an important factor in any wader. So, wing length is a useful parameter for subspecies recognition, save for: (1) juveniles which usually have inferior feather quality and

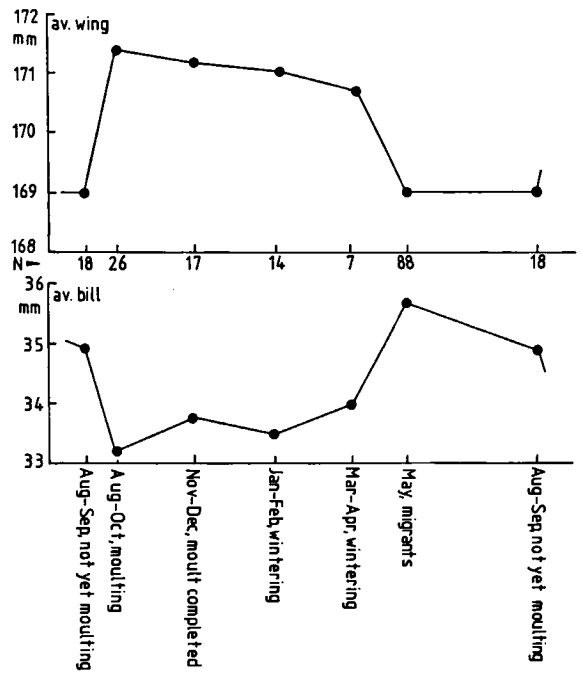


Figure 1. Average wing and bill lengths in certain periods for adult (over 2-year-old) Knot *Calidris canutus* in the Netherlands. Sexes combined; all data refer to study skins.

wear their primaries distinctly in spring and especially summer of the 2nd calendar year, and (2) adults in last stages of primary moult, when only 2-3 outer feathers remain, which abrade quickly within a short period. In fact, if wear had influence on adult wing length, the wing of moulting August-October adults (with old outer primaries) should have been shorter than those of fresh-winged November-December birds instead of longer. Birds with distinctly worn wings, which do of course occur, should not be measured and are not used here.

By this method the occurrence of 2 different-sized populations is established for the Netherlands; one may now wonder to what degree these populations overlap in size. As wing and bill show opposite trends, a scatter diagram of wing against bill may reveal the amount of overlap. Figure 2 shows both populations to be well-separated, especially when sex is taken into account: of 165 birds, 27 (16%) are in the overlap area when sex is known, and only 5 (3%) are 'wrong'. When making use of a line drawn by eye (between arrows in figure 2) to separate both populations, only 13% of the birds are assigned to the wrong population even when sex is disregarded. One may wonder if the 5 'wrong' birds are really wrong, viz. abnormally short-billed birds belonging to a long-billed population (2 ♂♂) or *vice versa* (3 ♀♀).

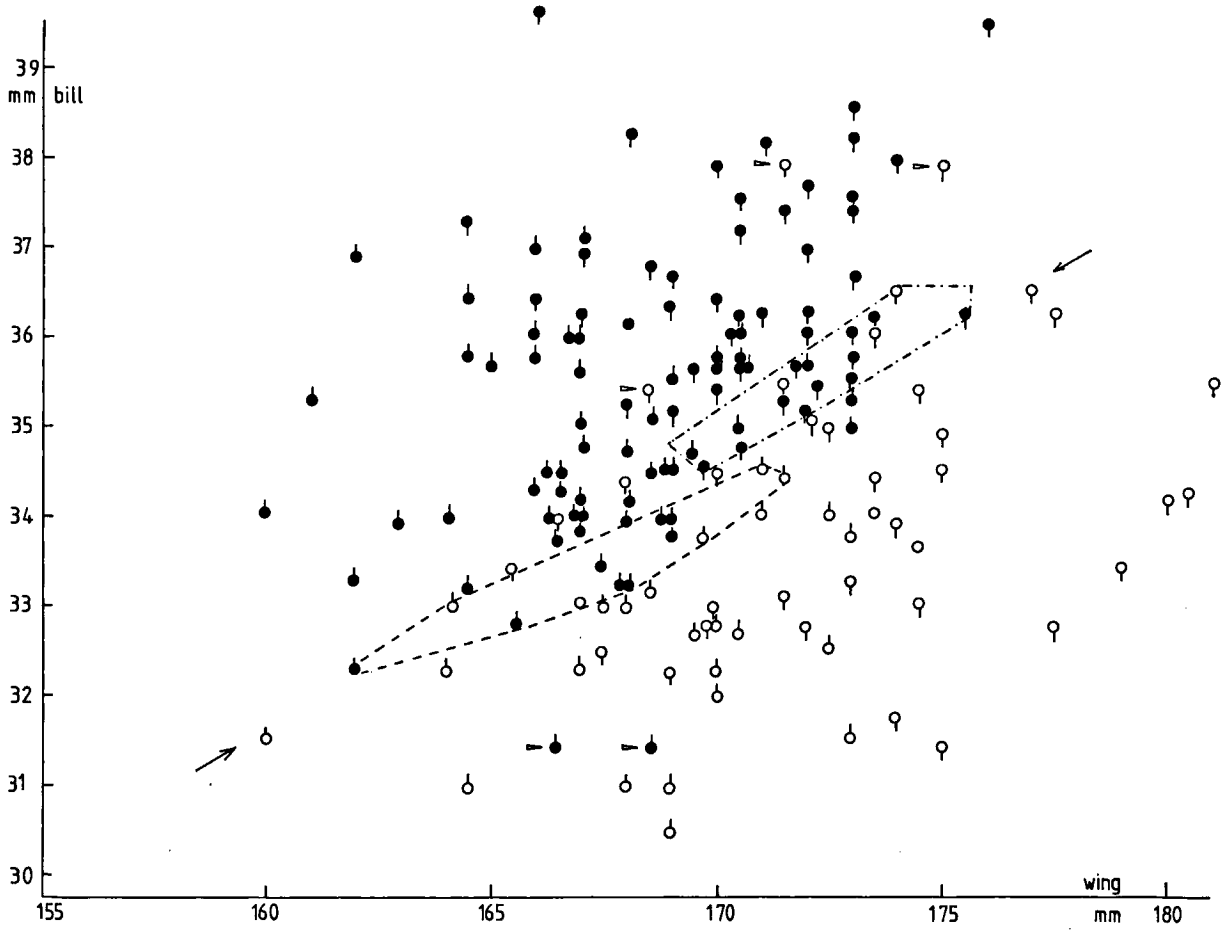


Figure 2. Wing and bill lengths of specimens of adult Knot *Calidris canutus* from the Netherlands. ● non-moulting migrants August-September and May, ○ moulting and wintering birds August-April, ♂ male, ♀ female, ○ sex unknown. ----- overlap area of ♂♂ of both populations (only long-winged short-billed ♂♂ below this, short-winged long-billed ♂♂ above), ····· overlap area for ♀♀. ▷ points to 'wrong' individuals (see text). Line between arrows separates most birds of both populations.

Both ♂♂ are from early August and are probably just-arrived normal short-billed birds which had not yet started primary moult, while the 3 ♀♀ (all December-January) probably are birds from the long-billed population which by exception stayed to winter among the short-bills. With such a small overlap (more than 75% of adults are separable when wing and bill length are known) both populations deserve subspecific recognition, especially as also adult breeding plumages differ (see below). Two problems now arise: (1) what is the breeding range of the Dutch short-billed subspecies and what that of the long-billed race, and (2) what names are available for them.

ORIGIN OF DUTCH SHORT-BILLED, MOULTING AND WINTERING KNOT

As shown by Dick *et al.* (1976), populations from northernmost Canada and Greenland moulth and winter in western Europe and so are probably the short-billed race in the Netherlands. On the other hand, Siberian breeders (excluding *rogersi*) migrate through western Europe to winter in Africa and probably are the long-billed birds. Proof that short-bills are Nearctic breeders is easy to obtain: many measurements of breeders are available and these are completely similar to those of the birds moulting and wintering in the Netherlands (table 1); in a scatter diagram, both show exactly the same distribution. The relation between wintering in western Europe and breeding in high-arctic Canada and Greenland is also proved by many ringing recoveries.

ORIGIN OF DUTCH LONG-BILLED TRANSIENT KNOT

To prove that long-billed migrants from the Netherlands are Siberian birds is more difficult, as no breeders from the USSR were available. Only 2 birds from the Yenisey River were examined (BMNH); though these agreed in size and colour with Dutch migrants, this seems to be too small a sample. More profitably, we may look to timing and distribution of the Knot in Europe and to the numerous Dutch May birds in particular. These May birds were not collected or found dead on roosts or on feeding areas as were other Knot from the Netherlands, but were mainly killed during migration against light-houses: of 89 adult May birds, 74 were light-house victims, and 69 of these were from the south-west of the Netherlands (11 from the Isle of Walcheren, 51 from Schouwen, and 7 from Goeree, originating from 17 different nights, May 1/2 to 17/18, and from 10 different years, spanning 1912 to 1967), and only 5 from the Friesian Islands; of the remaining 15, 10 were collected along the coast of Groningen in the extreme east of the Dutch Waddenzee, 4 were from Vlieland in the western Waddenzee, and 1 was hit by traffic on migration inland in Flevoland. The light-house victims form part of a marked May migration along the coasts of North- and South-Holland which is well-documented by field-observations in recent years (van Dijk & Wassink 1980; figure 3). Especially during eastern or north-eastern winds large flocks pass along at low-level during a short period in May, on days which are remarkably constant throughout the years: a first peak occurs on May 3-6, followed by a

Table 1. Measurements of (A) adult Knot *Calidris canutus* from Ellesmere Island (Canada) and Greenland, and (B) of adults moulting and wintering in the Netherlands.

		WING				BILL				TARSUS			
		mean	Sd	N	range	mean	Sd	N	range	mean	Sd	N	range
(A)	♂	169.2	3.59	21	164-174	31.8	1.15	22	29.8-34.0	31.2	1.04	22	29.4-32.7
(B)	♂	168.8	3.18	25	160-173	32.6	1.11	26	30.5-34.6	30.5	1.19	26	28.4-32.2
(A)	♀	172.7	3.97	9	167-180	33.8	1.29	9	31.9-36.4	31.6	1.10	9	29.7-33.4
(B)	♀	173.3	3.69	36	168-181	34.4	1.54	38	31.4-36.7	31.4	1.33	38	29.3-34.1

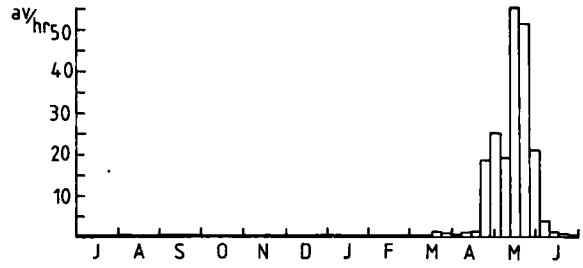


Figure 3. Average number per hour of Knot seen migrating along coast of provinces North- and South-Holland, Netherlands. Southward migration (July-December) based on nearly 12.000 hours counting 1973-1980, northward migration (January-June) on almost 8000 hours 1974-1978 and 1980-1981; numbers of hours counted per week well-spread over year. In total, *c.* 5000 Knot were seen to migrate south in 8 autumns and *c.* 100.000 flew north in 7 springs. Derived from Verslagen Club van Zeetrekwaarnemers, nrs 5-21, 1974-1982.

more important one on May 16-19, with smaller numbers passing until about May 26. Because data are combined per week per year and a particular day like May 16 is not always in the same week, the peaks are not as sharply in the figure a they are in reality. An average of slightly over 50 birds per hour may seem small, but actual counts in years with favourable winds (for man, apparently not for birds) amounted up to 25,000 birds within a few days. As counts are not made during all day-light hours and apparently part of the migration is nocturnal, the real numbers in such a period may be considerably higher. When winds blow from other directions birds probably migrate too, but fly too high to be noticed or even migrate overland rather than following the coastline. As no migration is observed on the North Sea coasts of the Waddenzee Islands, Knot apparently do not proceed further north but fly east over the Waddenzee. Counts on tidal flats in the western Dutch Waddenzee are low in May (probably involving summering immatures only), so these eastbound birds do not make a landfall here (figure 4D); some may stop in the eastern part of the Dutch Waddenzee as shown by skins and counts (figure 4C), and many more stop in the German Waddenzee in Niedersachsen (figure 4B) and Schleswig-Holstein (figure 4A). The timing of visible

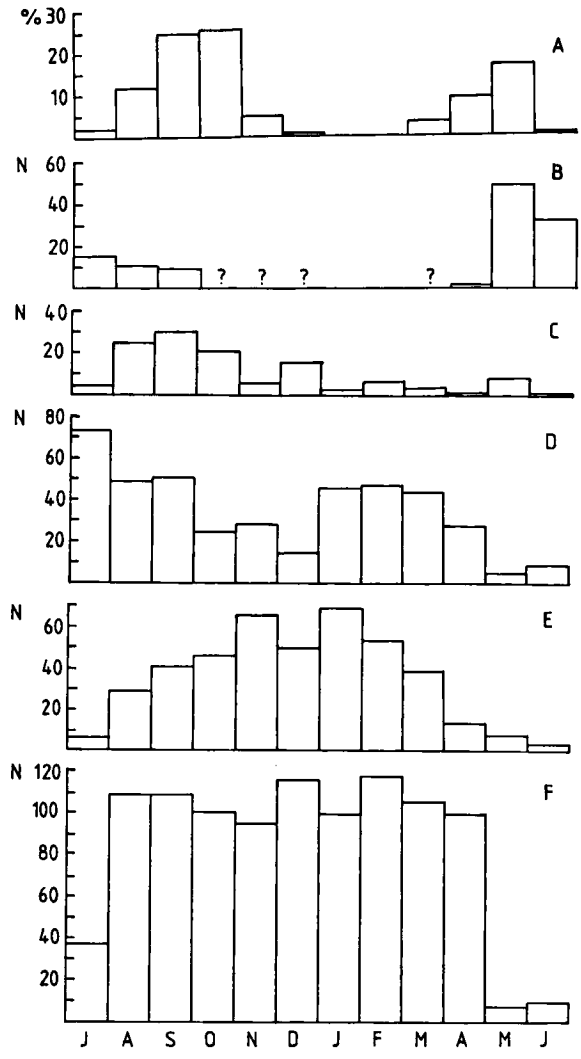


Figure 4. Averages of monthly maxima for (A) Schleswig-Holstein (northern German Waddenzee), (B) Niedersachsen (western German Waddenzee), (C) eastern Dutch Waddenzee, (D) western Dutch Waddenzee, (E) the Wash (eastern England), (F) Morecambe Bay, Dee, and Ribble estuaries (Irish Sea). N in 1000's; in A, number in % of average year total. A to D after Smit & Wolff (1981), E and F from Prater (1981).

migration in the Netherlands coincides well with the departure from the Vendée (France) roosting locality and with arrival in the German staging areas (Dick 1979). It may be concluded that one population is involved. Also, weights of Dutch lighthouse victims are rather low—123 (99-155) in 9 birds—and point to a distant origin. As the next stops of the German birds

are known to be either in the Porsanger area in northern Norway (Håland & Kålås 1980) or in the White Sea after crossing Finland (Bianki *et al.* in Glutz *et al.* 1977), undoubtedly Siberian birds are involved.

Prater (1981) suggested that the sharp decline in spring numbers in the estuaries of the Irish Sea (figure 4F) was caused by a departure to the Waddenzee to accumulate fat. This cannot be true: (1) the numbers in the western Dutch Waddenzee (figure 4D) and in the Wash (figure 4E) show a steady decline after a slight February-March peak; (2) the observed migration in May in the Netherlands does not coincide with departure from the Irish Sea and is directed north-east; (3) lighthouse victims are mainly from the south-west of the Netherlands, which is outside a possible Irish Sea-Wash-Waddenzee route, and (4) Irish Sea birds *do* accumulate fat, at least in Morecambe Bay, and departure there coincides with arrival on Iceland in early to mid-May (Prater and Wilson 1972, Morrison 1971, Morrison 1975). Siberian Knots migrate along the coast of the European continent when adult Nearctic birds are concentrated around the Irish Sea and on Iceland, and hence both populations are largely segregated then.

NAMING OF PALEARCTIC AND NEARCTIC KNOT, FORMERLY UNITED IN NOMINATE *CANUTUS*.

The restricted type locality of Linnaeus' name *canutus* is Sweden (cf. Hartert 1920). Unfortunately, only 1 Swedish adult was available, but this was undoubtedly a Siberian bird by its plumage and measurements. Also, 2 adult birds from nearby Copenhagen and 1 from Rügen (East Germany) were Siberian. One may wonder whether adult Nearctic birds may ever come farther east than western Norway and western Jutland in autumn, though some juveniles occasionally do (Andreassen & Råd 1977). Without evidence that Nearctic birds ever reach Sweden, and, should they do so, probably in very small numbers compared with Siberian birds, the Siberian race migrating through western Europe has to be named *canutus*. The oldest available name for Greenland and north Canadian birds is *islandica* Linnaeus, 1767; high-arctic Canadian and Greenland birds are common on migration on Iceland and we do not have reasons to believe that Siberian nominate *canutus* ever reaches Iceland in any substantial numbers. One may not like to describe geographical variation from migrant or wintering birds, but it is a fact that all names to be used for recognizable subspecies of the Knot—*canutus*, *islandica*, *rufa*, and *rogersi*—were based on migrants; hence, we first have to define these migrants in a more appropriate way than was done in the past before we can apply any of these names to birds from breeding areas.

CHARACTERS AND RANGE OF THE SUBSPECIES OF KNOT

Based on breeders, migrants, and wintering birds, we may distinguish 5 populations, from which at least 4 are separable as a subspecies. These subspecies differ in measurements or in adult breeding plumage; 2 of them, *rufa* and *islandica*, are linked to certain breeding areas, as shown by measurements and plumage of known breeding birds, the breeding ranges of the others are not yet fully established and require further study. Table 2 shows the measurements of the at least 4 races to be recognized: short-billed short-winged *rogersi* (migrating through eastern Asia, wintering Australia and New Zealand), long-billed medium-winged nominate *canutus* (migrating through western Europe, wintering in Africa), short-billed long-winged *islandica* (breeding northern arctic of Canada and Greenland, wintering western Europe), and long-billed medium-winged *rufa* (breeding southern part of high-arctic Canada). From west to east, bill length alternates, which is most fortunate to identify specimens from areas where distributional ranges meet. Nominate *canutus* and *rufa* at one side and *rogersi* and *islandica* on the other overlap widely in size

Table 2. Measurements of adult Knot *Calidris canutus*. (A) Nominate *canutus*. Sweden, eastern Denmark, East Germany, Netherlands (migrants May and non-moulters August-September), and Yenisey River (USSR). (B) *C.c. islandica*. Ellesmere Island (Canada), Greenland, and Netherlands (combined from table 1). (C). *C.c. rufa*. Melville Peninsula and Victoria and Southampton Islands (Canada), Great lakes and Atlantic coast of eastern North America, Surinam, and Patagonia. (D) *C.c. rogersi*. Amur Bay (USSR), Japan, eastern China, Indonesia, southern New Guinea, and New Zealand.

		WING				BILL				TARSUS			
		mean	Sd	N	range	mean	Sd	N	range	mean	Sd	N	range
(A)	♂	167.3	2.86	59	161-173	34.6	1.34	60	32.3-37.2	31.4	1.24	60	28.6-33.9
	♀	170.5	2.69	53	165-176	36.5	1.33	53	33.9-40.4	31.8	1.26	53	29.6-34.9
(B)	♂	169.0	3.34	46	160-174	32.2	1.19	48	29.8-34.6	30.8	1.16	48	28.4-32.7
	♀	173.2	3.71	45	167-181	34.3	1.50	47	31.4-36.7	31.4	1.28	47	29.3-34.1
(C)	♂	165.8	2.66	14	159-169	34.8	1.08	14	33.3-36.4	32.2	0.68	14	30.9-33.0
	♀	171.6	2.73	17	167-175	36.7	1.38	17	35.0-40.2	32.2	1.02	17	31.0-34.5
(D)	♂	164.4	4.31	17	157-172	31.7	1.20	17	29.3-33.3	30.3	1.04	17	28.4-31.5
	♀	168.4	3.58	15	164-174	33.7	1.36	15	30.9-36.2	31.3	1.26	15	29.0-33.5

(figure 5), but these pairs differ distinctly in colour of fresh adult breeding plumage.

Nominate *canutus* (*s.s.*) is the darkest subspecies, entirely deep rufous below including vent and under tail-coverts; black marks on upperparts heavy, rufous marks deeply coloured but rather small, rounded on tips of scapulars. *C. c. rufa* is the palest subspecies, showing mainly white vent, lower flanks, and under tail-coverts, and hardly any rufous to upperparts: black marks above are restricted and narrow, upperparts appearing silvery-grey, rufous restricted to some on scapulars in ♂, hardly any in ♀; deep rufous forehead, cheeks, foreneck, and chest contrast markedly with silvery crown, hindneck, and mantle. *C. c. islandica* is close to nominate *canutus*, but rufous on upperparts is slightly less deep, more yellowish on hindneck, and the black marks above are distinctly narrower, rufous on scapular-tips showing as large paired squarish dots. *C. c. rogersi* has slightly more rufous above than *rufa*, but appears less greyish, as black marks on upperparts are much more prominent, especially on mantle and scapulars; vent and under tail-covert are white as in *rufa*, but marked with black, not nearly uniform. Juveniles, immatures, adults in non-breeding plumage, and often adults in worn breeding dress (July to September) are usually indistinguishable to race by plumage, though juvenile *rufa* averages paler above than other subspecies (Conover 1943) and some *rogersi* show much broader dark marks to upperparts and upper wing-coverts than usual. An attempt to identify juveniles and non-breeders can be made with help of measurements (figure 5). Full bill length is attained from 1-2 months after fledging and does not appreciably change after death. For wing, 2% of live or freshly dead birds has to be subtracted to make them comparable with the skins used in figure 5; for juvenile wing 7 mm has to be added to make them comparable with adult, for 1-years olds 3½ mm. When adults show a heavily worn wing-tip, measuring to tip is not advocated; when not too worn, one may find full wing length by adding 5 mm to length of p9 or, when p9 is frayed too, by adding 13 mm to p8 or to the shadow of p8 on p9.

Based on museum specimens (data in brackets) and on literature, distribution of the 5 populations is as follows (most references on migration of *islandica* and nominate *canutus* were already given in previous paragraphs and are not repeated here):

Calidris canutus islandica (type locality: Iceland).

Breeds eastern and northern Greenland and Canadian high arctic from Ellesmere and Devon Islands west to Bathurst and Melville Islands (breeding specimens examined from

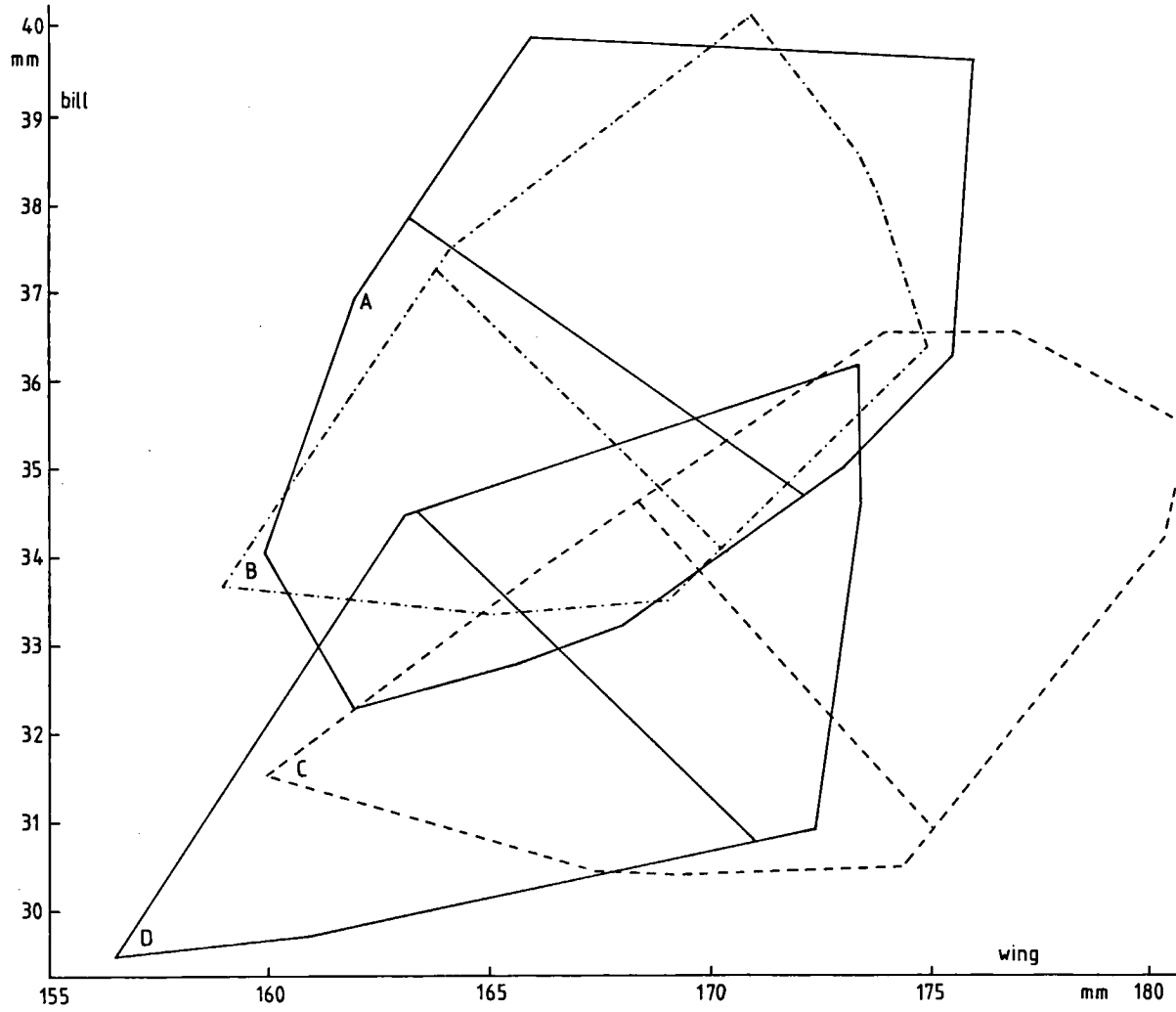


Figure 5. Outlines of individual plots of 4 races of Knot, based on adult skins. (A) 97 birds of nominate *canutus*, (B) 31 of *rufa*, (C) 83 of *islandica*, (D) 32 of *rogersi*. Oblique lines within each outline seperate most sexed specimens (♀ right-above line, ♂ left-below): in A, 12% mis-sexed by this line, in B 6%, in C 24%, in D 19%. In live and freshly dead adult birds, wing averages 2% more; in skins of juveniles, wing is 7 mm shorter than adult, in 1-year-old, 3½ mm shorter.

Greenland and Ellesmere, May 31 to July 15). Has bred Svalbard (Løvenskiold 1964). Leaves breeding area July and migrates along northern Greenland across Jan Mayen (Aug. 12) and over western Greenland (adults July 1-26, juveniles up to Sep. 16) and south-eastern Greenland (juveniles Aug. 30) across Iceland to coastal Norway, Denmark, Waddenzee, and Britain; some migration occurs previous to moult from Norway south- and south-westward and from Waddenzee westward to Britain (Dick *et al.* 1976). 4 not-yet moulting adults were examined from the German Waddenzee, Aug. 15-28. Many birds moult Waddenzee (mainly western) and Britain. During winter, numbers of Knot leave the Waddenzee: smaller estuaries with sub-marginal habitat are then occupied in Britain and Ireland (Prater 1981) and in south-western Europe. In spring, moulting areas are reoccupied, but adults in particular show a tendency to move westward and by late April these are mainly concentrated in estuaries around the Irish Sea. This area is left by late April and early May for Iceland, and from here

adults move across southern and along western Greenland to reach breeding areas mid- or late May. No spring specimens were seen from southern Greenland and this area is perhaps largely overflown. Migration in spring is more southerly than in autumn and Norway is hardly touched. For time-table of Dutch specimens, see figure 6.

June to late July. On autumn migration, main stop-over areas are James Bay in late July and the Atlantic coasts of North America in August, mainly Massachusetts and New Jersey, sometimes Bay of Fundy, Virginia, or elsewhere. The birds cross the western Atlantic to Guyana and Surinam (reached mid-August and early September) and from there migrate

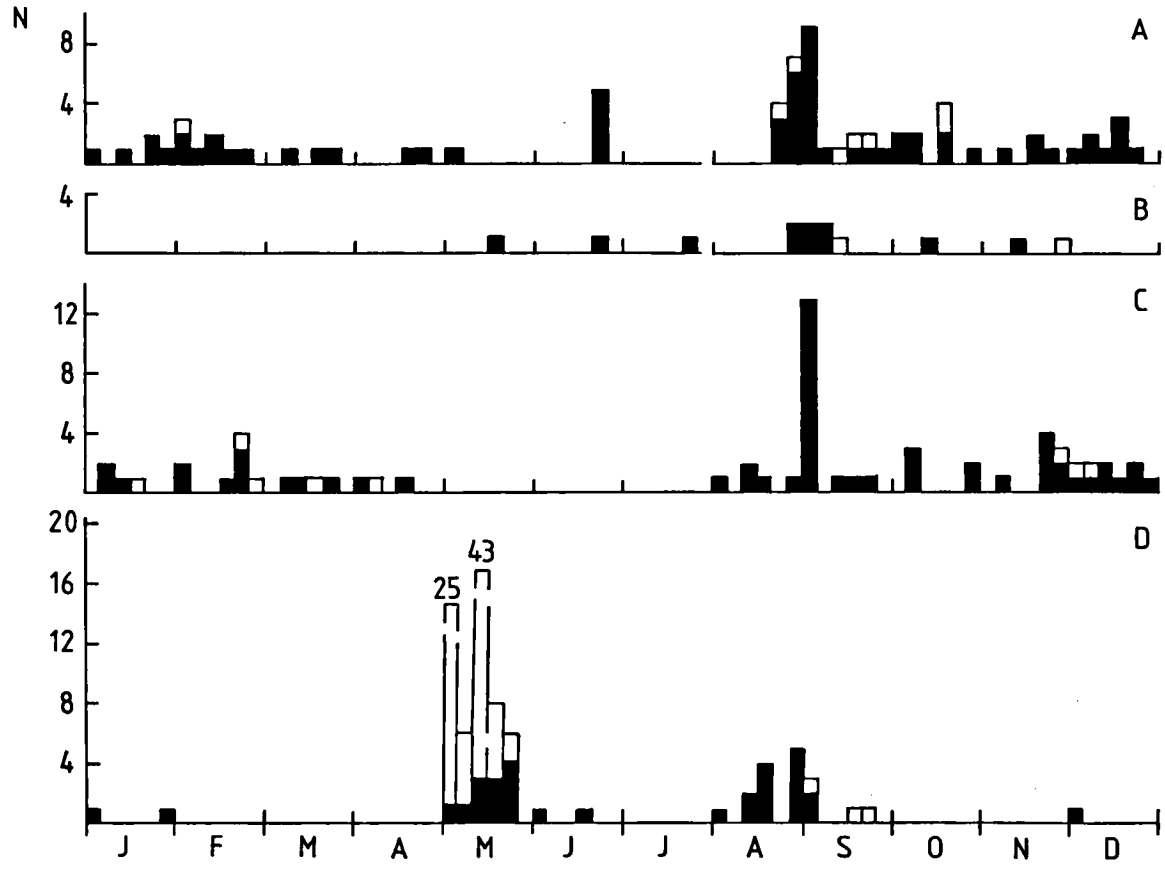


Figure 6. Occurrence of Greenland and north-arctic Canadian Knot *C.c. islandica* (A juvenile and 1st half of 2nd calendar year, C adult) and of Siberian Knot *C.c. canutus* (B juvenile and 1st half of 2nd calendar year, D adult) in the Netherlands, based on skins identified by means of figure 2 (7 mm added to juvenile wing). □ light-house victims, ■ others.

Calidris canutus rufa (restricted type locality: New Jersey, fide Ridgway 1919 and Peters 1934).

This race breeds Victoria, Jenny Lind, and Southampton Islands and Melville Peninsula, as well as on islands in the northern Hudson Bay. Present in breeding area from 1st week of

along an unknown route to Argentina, mainly Bahia Bustamente and eastern Tierra del Fuego (Devillers & Terschuren 1976), and other winter areas yet to be discovered. Hence, mainly occurs on the Atlantic coasts of North and South America, though one juvenile appeared to have reached California and some may winter on the Pacific coasts of Central and

South America (Conover 1943). In spring, migrant Knot are seen Rio Grande do Sul (Brazil, April) and Surinam (early May); they again cross the western Atlantic to the east coast of the USA (more widespread than in autumn, Florida to Massachusetts, early to late May). The next stop is in the Great Lake area and from there the breeding areas are reached via Hudson Bay (late May). This outline is mainly based on Morrison *et al.* (1980) and Harrington Morrison (1980). Specimens were examined from breeding area (June 25 to July 30), Rawson (Chubut, Argentina, 5 birds, Nov. 27), Viamonte (Tierra del Fuego, Mar. 6), Surinam (2nd calendar year, Apr. 24, June 17), South Carolina (May 5-15), Virginia (May 25), Wisconsin (May 24), New York ('May'), and from inland Point Pelee (Ontario, May 25) and Toronto (May 26-28).

Calidris canutus canutus (restricted type locality: Sweden, fide Hartert 1920).

The nominate subspecies migrates across Finland and around northern Norway in autumn (examined Varanger area, Aug 22), originating from breeding areas somewhere in Siberia. Knot are known to breed on Taymyr Peninsula, Severnaya Zemlya, and Novosibirskiye Islands, but actually no breeding birds were examined to proof that these were really similar to nominate *canutus* or belonged to *rogersi*. Russian authors usually assign Siberian breeders to nominate *canutus*, except for Wrangel Islands breeders (e.g. Dementiev & Gladkov 1951). Recapture of a Vendée bird as far east as Udachnyy in Yakutskaya ASSR (*c.* 66° 20′ N, 113° E) (Dick *et al.* 1975) and a bird from the Wash (England) in inland USSR on River Lena (*c.* 67° N, 123° 25′ E) (*Wader Study Group Bull.* 25: 17, 1979) show that some nominate *canutus* migrate far east into Siberia. Specimens from Sweden (Aug 9), Copenhagen (Sep 4), Rügen in East Germany ('Aug'), and several from the Netherlands (figure 6) were examined. Probably Britain is usually only reached by juveniles, especially in periods with easterly winds. Adults probably migrate quickly via Vendée and Morocco to moult and winter in Mauritania, Sénégal, or Bijagos Archipelago in Guinea Bissao; part of the population reaches South Africa. In spring, reverse migration is via Morocco, Vendée, German Waddenzee, and Porsanger area (northern Norway) or White Sea to breeding area. Specimens referable to nominate *canutus* were examined from Morocco (Sep 8), Cota Doñana (May 14), north-western France (May 15, June 4), Netherlands (figure 6), and Yenisey River (June 14). Skins from Gabon ('Sep'), Walvis Bay (Oct 26), Nepal ('Sep'), and Rangoon (Apr 12) all had measurements in the overlap area between nominate *canutus* and *rogersi*, and could not be identified; a bird from Quetta (Pakistan, Aug 12) was typical nominate *canutus*: Knot seem to be stragglers only in the whole area from north-east Africa, Arabia, and the Indian Subcontinent east to western Malaya and Sumatra.

Calidris canutus rogersi (restricted type locality: Shanghai, China, fide Vaurie 1965).

A good subspecies, differing from others in its adult breeding plumage and by a short bill (the latter character is shared by *islandica*). Occurs in eastern Asia and south to Australia and New Zealand as a migrant and wintering bird. Populations breeding Wrangel Island (USSR) and Alaska are usually assigned to this subspecies, but this is not correct, as will be shown below.

C. c. rogersi undoubtedly breeds somewhere in Siberia, but the breeding area is either situated in an area for which no breeding records of Knot are known yet (perhaps somewhere in the coastal mountain ranges of eastern Siberia), or this race breeds Taymyr Peninsula, Severnaya Zemlya, and Novosibirskiye Islands, in which case the breeding area of nominate *canutus* is unknown, or the known breeding range of the Knot in Siberia is in part occupied by nominate *canutus* and in part by *rogersi*. Birds similar to topotypical *rogersi* are known from stop-over areas in Amur Bay (USSR), Japan, and again from eastern Java, southern New Guinea

(Hoogerwerf 1964) and northern Australia, but the species is hardly known from areas in between, as it is rare or unrecorded in e.g. Sumatra, Malaya, Borneo, Celebes, Moluccan Islands, Micronesia, and Hawaii. Thailand and Tonkin Bays and Taiwan are cited by Glutz *et al.* (1975), but it is not known whether Knot occur here in any strength. The main winter areas are southern Australia, Tasmania, and New Zealand (Ornith. Soc. New Zealand 1970, Condon 1975, Glutz *et al.* 1975). Specimens were examined from Amur Bay (eastern USSR, Aug 14 to Sep 2, May 18), Japan ('May'), Shanghai (May), west Java (2 skins only, although large numbers of other waders were collected: apparently rare; Sep 12-24), east Java (8 birds: apparently not uncommon as a migrant; Sep 20-Oct 6, Nov 24), Ambon (Molucca Islands, Nov 19), southern New Guinea (near Merauke, 4 birds, Nov 9 and Apr 5), and New Zealand (no data). One bird from Shanghai (♀, May) was extremely large (wing 180, bill 38.4, tarsus 34.1) and is excluded from table 2 and figure 5: more probably it either belonged to nominate *canutus* or to the Alaska-Wrangel population (see below) than to the generally small-sized *rogersi*.

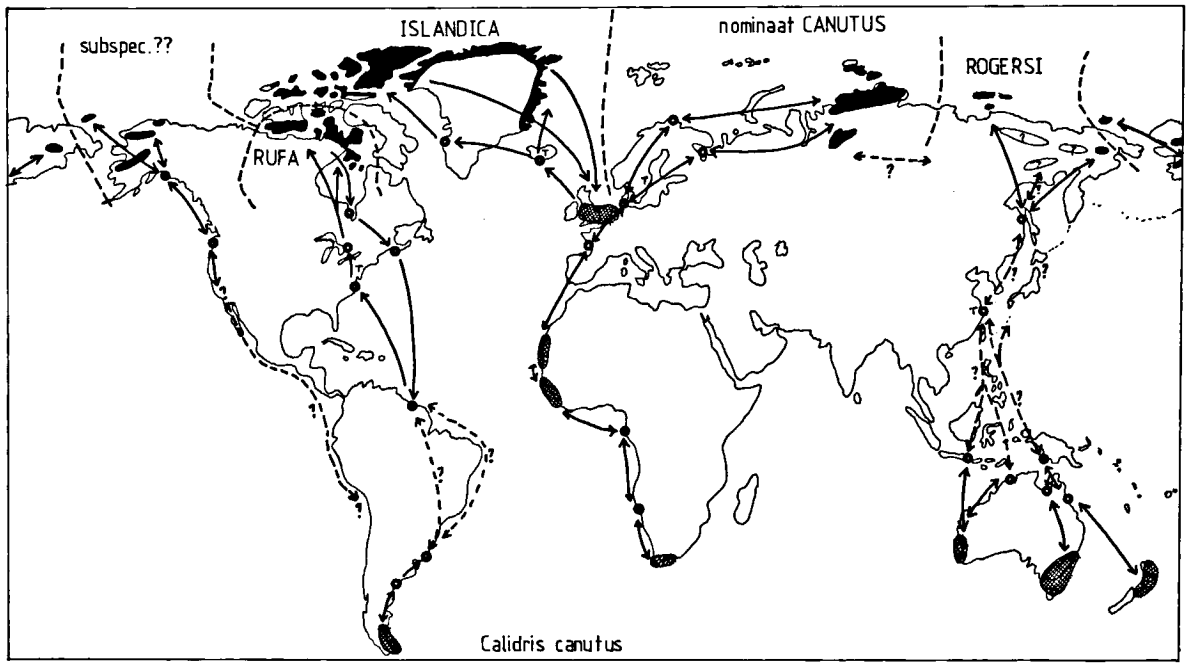
Calidris canutus ssp.

Of a fifth population, breeding in Alaska, no birds were examined. Published data on measurements (e.g. Ridgway 1919) show that wing and bill are large, as in *rufa* and hence also similar to nominate *canutus*; they are not *rufa*, however, as the colour of both adult breeding plumage and juvenile is dark as in nominate *canutus* or *rogersi* (Conover 1943). In the past, Alaska birds were usually assigned to *rogersi*, but this east Asiatic subspecies is small and Alaska breeders do not reach their breeding area from the south-west (as one would expect when *rogersi* was involved), but from the east-south-east, with a last stop-over area at Copper and Bering River Deltas in southern Alaska, where over 40.000 birds have been seen (Kessel & Gibson 1978). Earlier spring stop-over sites of this population are Gray's Harbor (Bent 1927) and Willapa Bay (Gabrielson & Lincoln 1959) on the Washington coast of the USA, where large numbers assemble in May. The other whereabouts of this population are a mystery: they probably winter on the Pacific coast somewhere between southern California and Chile (in latter, perhaps near Puerto Montt, as for Hudsonian Godwit *Limosa haemastica*). Major stop-over areas are apparently still overlooked, as they are for *rufa* and *rogersi*. Wrangel Islands birds are not *rogersi* either, as they are similar to those of Alaska: measurements of 3 Wrangel specimens received by courtesy of Mrs. W. J. van der Plas-Haarsma showed large dimensions and do not fit *rogersi*. With measurements of the Alaska-Wrangel breeders similar to nominate *canutus* and colour probably close to *rogersi*, I refrain from assigning a separate name to this population as long as no more data are available. These are needed to show whether size shows a sufficiently limited overlap with *rogersi* or whether colour of adult breeding plumage is really different from nominate *canutus* to warrant recognition of a fifth subspecies.

SUMMARY

Data from the Netherlands show that the difference between Knot *Calidris canutus* from northern high-arctic Canada and Greenland, moulting and wintering in the Netherlands, and of Siberian breeders, passing through in August-September and May, is sufficient to warrant recognition of 2 races, *islandica* and nominate *canutus* respectively, instead of one as currently accepted, differing in size (bill especially) and adult breeding plumage. A much paler subspecies, *rufa*, with measurements rather similar to nominate *canutus*, breeds in the southern Canadian Arctic and winters on the Atlantic coasts of Argentina. A fourth subspecies, *rogersi*, breeds somewhere in Siberia and migrates mainly along the coasts of south-east Asia and across Philippines and Indonesia to winter-areas in Australia and New Zealand; it is characterized by short bill, rather short wing, and a rather pale ground-colour of adult

breeding plumage, though the latter is more heavily pigmented black on upperparts, upper wing-coverts, vent, and under tail-coverts than still paler *rufa*. Known breeding areas of the Knot in Siberia are Taymir Peninsula, Severnaya Zemlya, and Novosibirskiye Islands, but on which of these nominate *canutus* and on which *rogersi* breeds, or whether other Siberian breeding sites have to be discovered, is unknown. Many stop-over sites and the wintering areas of a fifth population, breeding Wrangel Island (USSR) and Alaska, are also to be discovered on the Pacific side of the Americas; as no specimens were examined, it is not known whether this population can be attributed to nominate *canutus* (with which it seems to agree in size), to *rogersi* (to which it is probably identical in colour), or to a separate, as yet unnamed, subspecies.



Distribution map of *Calidris canutus*. Black: breeding area. Hatched: winter quarters. Dots: known and probable stop-over areas. T: type-localities of each subspecies. Solid arrows: known migration routes. Broken arrows: possible migration routes.

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