

The migration system of Afro-Siberian Knots *Calidris canutus canutus*

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This paper reviews the current knowledge about *canutus* Knots. We have called this subspecies Afro-Siberian Knots since the two certain aspects about their migration are that 1) most winter in Africa, and 2) they breed somewhere in Siberia. The only two available ringing recoveries do not give proof that *canutus* Knots breed in northernmost Taymyr Peninsula as has been assumed, but rather more to the east, in the Yakutsk area. Breeding Knots have not yet been found there but neither do they appear to have been searched for. During southward migration most Knots stage in the Wadden Sea (the adults in late July - August, the juveniles in late August - September), with some light birds staging briefly earlier along the Baltic coast. All birds moult after arrival on their wintering areas. 98% of the 516,000 Knots wintering in Africa do so on the Banc d'Arguin in Mauritania and in the Archipelago dos Bijagos in Guinea-Bissau, the subspecies thereby being extremely concentrated and potentially at risk. On parts of the Banc d'Arguin and at Langebaan Lagoon, South Africa, wintering populations seem to have been stable for the last 10-15 years, but no comprehensive counts have been carried out in the last 12 years in the most important area, the Banc d'Arguin. In spring, Knots departing from the Banc d'Arguin take a long time to deposit a relatively small load of fuel. Daily mass gains are a factor 3 and 5 higher in South Africa in and the German Wadden Sea respectively. Six major gaps in knowledge about the migration of this supposedly well-known subspecies of Knots are identified.

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INTRODUCTION

In their classic study on the migration of Knots *Calidris canutus* in Europe and Africa, Dick *et al.* (1976) stated that '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' (p. 40). For the last 10 years or so this sounded almost like a funny remark since, once the key staging areas were identified and stocked with research workers, the Knot habit of flying long distances and using few sites has been regarded as an advantage for the

furthering of understanding, rather than a disadvantage (Dick *et al.* 1987, Piersma *et al.* 1987, Piersma 1987). In retrospect, however, the statement may hold more truth than we realized, since even the accumulated knowledge about the supposedly well known migration system of the Afro-Siberian Knots *Calidris canutus canutus* reviewed here is much less complete than anticipated when we started compiling this review a few years ago. The Knots' characteristic of turning up 'out of the blue' in places, instead of yielding steady streams of sightings which allow the linkage of breeding and non-breeding areas, seems to offer them again a fair

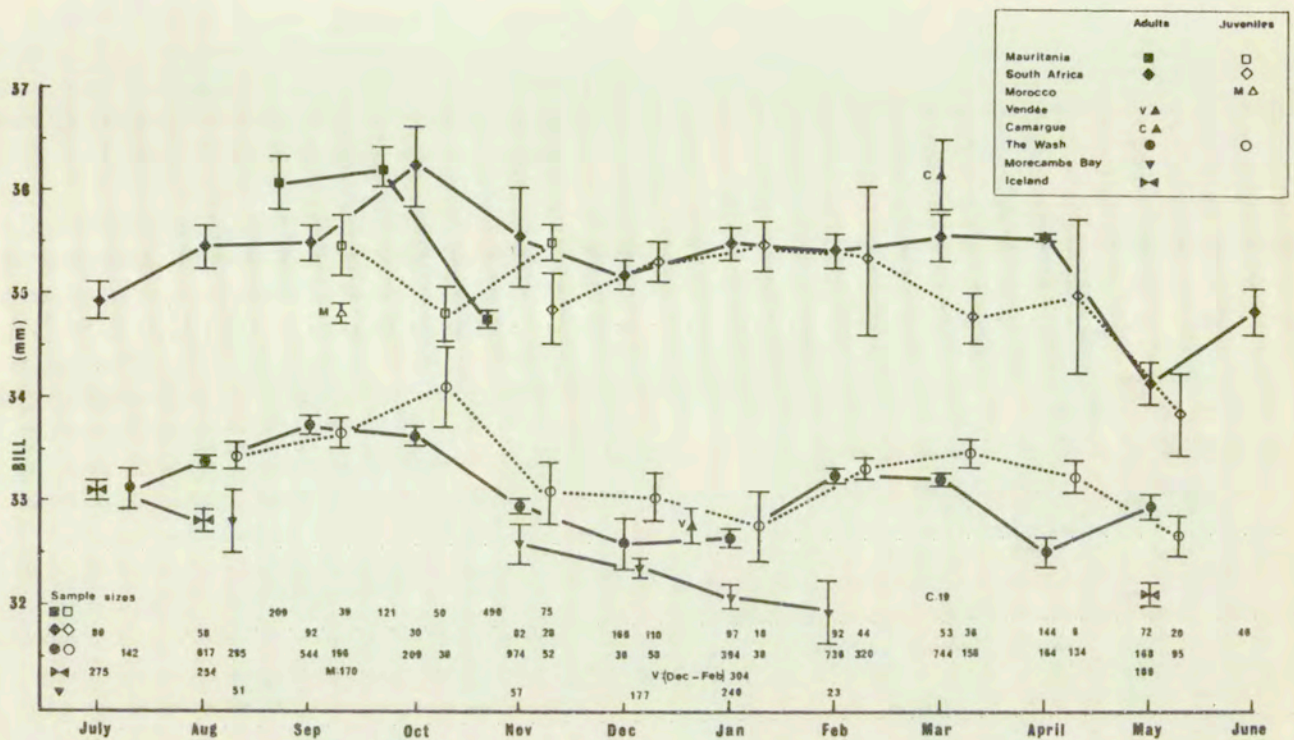


Figure 1. Reprint of the classic illustration in Dick *et al.* (1976: Figure 1) of the seasonally consistent differences in the bill lengths of Knots wintering in Africa

and those wintering in western Europe or staging in Iceland. Reprinted with permission of the Nederlandse Ornithologische Unie (NOU).

amount of secrecy. Indeed, in this review we show that we now know much less about one of our best-known long-distance migrants than we had thought for years, but we feel that this is exciting news for inquisitive and enterprising wader researchers.

Until the publication of Dick, Pienkowski, Waltner & Minton in 1976, general knowledge (e.g. Bannerman 1961; Hollom 1968) dictated that the Knots wintering in Europe originated from a Siberian breeding population, although there was rumour that some of them might have crossed the Atlantic from Nearctic breeding areas (Godfrey 1953; Snyder 1957). Dick *et al.* (1976) argued that there were in fact two populations, distinguishable on the basis of bill length (Figure 1). The Knots wintering in Europe were short-billed, and could be assigned to a Nearctic breeding population. The birds wintering in western and southern Africa were long-billed and were argued to breed in Siberia, presumably on the Taymyr Peninsula (the nearest area in Siberia in which they were known to breed), and to stage only briefly in Europe in spring and autumn. Roselaar (1983) examined the matter again using mainly museum specimens, and added wing length as another discriminating morphological variable between the Nearctic and Siberian breeding populations (wings of the Nearctic birds apparently being slightly longer).

In view of the small overlap between the two groups in his bivariate plots, he decided to give the two populations subspecific status, and named the Nearctic-breeding/European-wintering population *islandica* (see Davidson & Wilson 1992 for review), and the Siberian-breeding/African-wintering population as the nominate *canutus*.

This chapter reviews the current knowledge about *canutus* Knots. We shall see that much is unclear about the migratory linkages between breeding and non-breeding areas of this morphologically most variable (Tomkovich 1992) subspecies of Knots. One thing that is undoubted, however, is that many of the supposedly *canutus* birds winter in Africa, and that they do breed somewhere in Siberia. Hence we have called them Afro-Siberian Knots.

BREEDING GROUNDS

Dick *et al.* (1976, 1987), Roselaar (1983) and all other recent authors writing about Afro-Siberian Knots, have assumed them to breed in the western-most well established breeding area in Siberia, the tundras of the Taymyr Peninsula, and perhaps the New Siberian Islands (Figure 2). Most published distribution maps (e.g. Cramp & Simmons 1983)

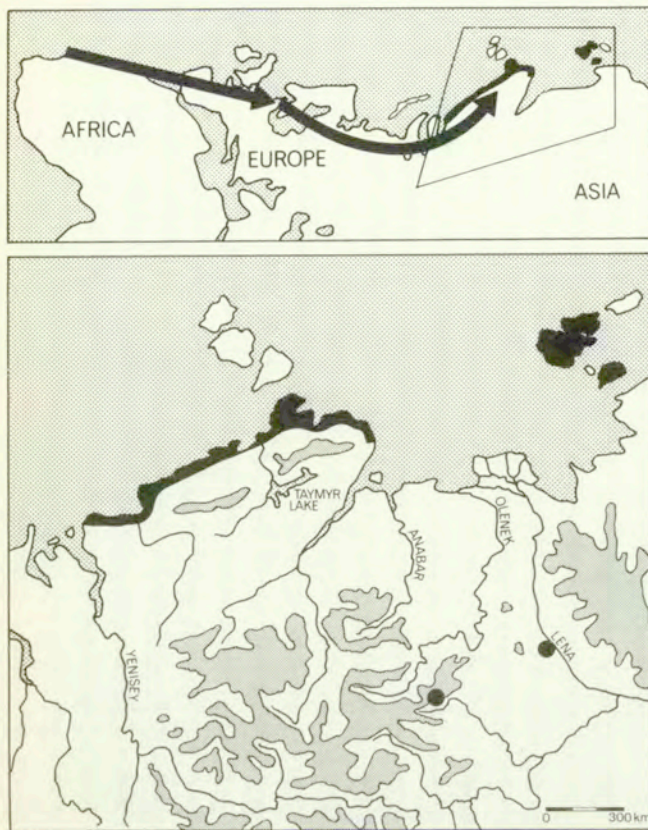


Figure 2. The biogeography of Afro-Siberian Knots *Calidris canutus canutus*. Top: overview of the migration system with the major suggested migration flyway marked by arrow, and the breeding grounds on Taymyr Peninsula and the New Siberian Islands marked in black (breeding areas after Tomkovich 1992, P. Prokosch pers. obs. and L. Lappo & E. Syroechkovsky, Jr pers. comm.). Bottom: map of the Siberian breeding grounds of *canutus*. The known breeding area on the Taymyr Peninsula is shaded black, and the recovery locations mentioned in the text given by two dots. Land higher than 500 m above sea level is light shaded.

denote the entire Taymyr Peninsula as Knot breeding ground. However, during extensive aerial and ground surveys in 1989 - 1991, no Knots have been found more than 50 km from the northern coastline of Taymyr (P. Prokosch pers. obs.), and the classic distribution map is thus incorrect. Figure 2 provides an update.

Moreover, there is only little direct evidence for the conclusion that northern Taymyr provides the main and most important breeding area for African wintering Knots, since:

- 1) the subspecific identity (Nearctic *islandica* vs. Palearctic *canutus*) was based on a difference in the morphology of groups from different non-breeding areas;
- 2) the link with the breeding grounds was derived

from observations on passage dates, localities and departure directions (Dick *et al.* 1987); and 3) Taymyr was identified as the breeding area only because it was the nearest known breeding place in Siberia (e.g. Tomkovich 1987, 1992).

The best proof of a direct connection between a wintering and a breeding area has always been the availability of appropriate ringing recoveries. Ample evidence for such links is present for the other subspecies but no such information is available to link Africa and Taymyr. In contrast, the only two recoveries from the breeding season of supposedly *canutus* Knots are of birds ringed during migration and they are recovered further east than Taymyr (see Figure 2): - a bird ringed on 5 May 1966 in the Vendée, France and recovered at Udachnyy, Yakutsk ($66^{\circ}29'N$, $112^{\circ}15'E$) on 10 June 1974 (Dick *et al.* 1976, Gromadzka 1985); - a juvenile bird ringed in Norfolk, England on 11 August 1971 and recovered near Zhigansk, Yakutsk ($66^{\circ}42'N$, $123^{\circ}00'E$) on 11 June 1974 (J. Clark, BTO, pers. comm.; ringed on 4 August 1971 according to Gromadzka 1985). In addition, there are recoveries of a South African wintering Knot and an early autumn-staging Knot from Poland from the first days of June in supposed staging areas much west of Taymyr (the White Sea and the lower Ob river, respectively; Underhill *et al.* 1989; Gromadzka 1985). Finally, however, a Knot colour-marked on Taymyr as a chick of 50.7 g on 13 July 1990 at a location 50 km west of the outer delta of the Taymyra River (*c.* $76^{\circ}00'N$, $98^{\circ}30'E$), was retrapped at Bottsand on the Baltic coast near Kiel, Germany, on 25 August 1990.

The absence of recovery data from Taymyr Peninsula suggests that it may be unlikely that the majority of the African-wintering *canutus* actually breeds there. Some support for this comes from a comparison of the bill length distributions of Knots from the main wintering site (Banc d'Arguin, Mauritania), two staging sites (France & Germany) and the Taymyr breeding grounds (Figure 3). Birds from Taymyr have shorter bills than those from the other three *canutus*-sites, a difference which was statistically significant for the comparison with the French staging site (ANOVA/Scheffé's test, $p < 0.05$). Although an analysis of variance showed that even the bill length distributions from the three wintering/staging sites in Figure 3 were not uniform (possibly due to site-related differences in sex-ratios), the relatively short bills of some of the nesting birds measured on Taymyr confirm Tomkovich' (1992) findings based on museum specimens that the Taymyr

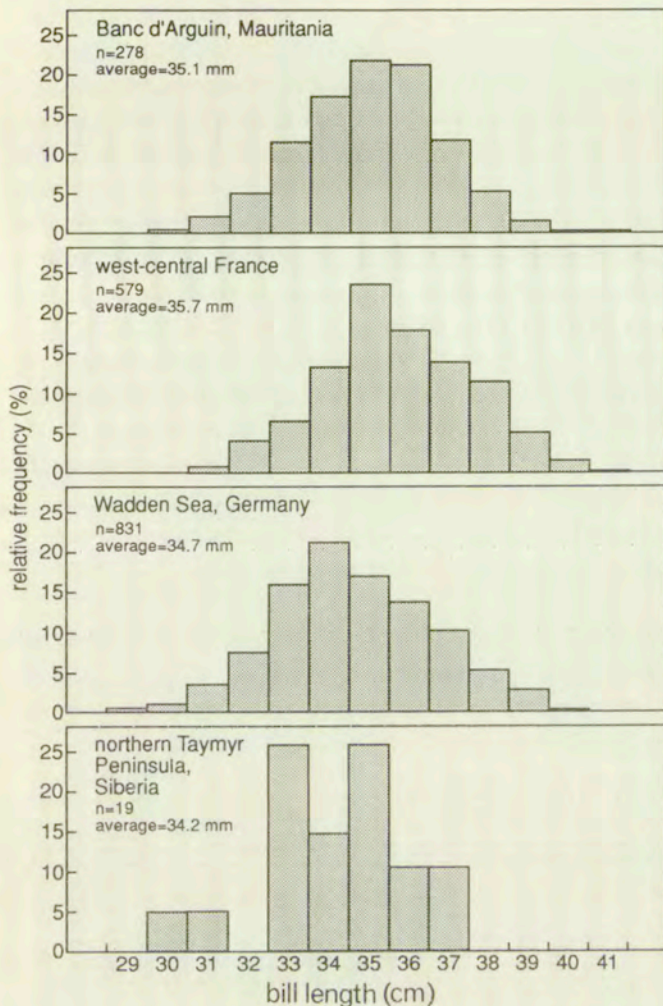


Figure 3. Frequency distributions of the bill length of Knots measured with calipers in the field after capture on the Banc d'Arguin, Mauritania in February-April (see Piersma 1989), the Atlantic coast between Gironde and Loire, France in May (see Bredin & Doumeret (1987), the Wadden Sea coast of Schleswig-Holstein, Germany between 13-29 May (see Prokosch 1988), and the Taymyr Peninsula breeding grounds near Sterlegova, between 26 June and 17 July 1989 - 1991 (P. Prokosch pers. obs.).

Knots do differ in size from *canutus* wintering in Africa, and that they are perhaps more like *islandica*.

The quite large variation in bill lengths of Taymyr breeding Knots (Figure 3) is reminiscent of the results of Goede (1992), who analysed heavy metal concentrations in flight feathers of Knots collected on Taymyr Peninsula. On the basis of the relatively large variation in the arsenic and selenium concentrations found, Goede (1992) suggested that these birds, although breeding in one area, must have wintered in two or more widely separated areas, perhaps western and southern Africa. Therefore, the Taymyr breeding Knots may not be an homogenous stock.

If the Knots wintering in South Africa are part of a homogenous African wintering population of *canutus*, the bill length data (Figure 3) and Tomkovich' findings are at variance with the conclusion of Underhill *et al.* (1989) that Knots from southern Africa breed on the Taymyr Peninsula. This was, however, based on the correspondence between annual average juvenile percentages of Knots found in South Africa and of Dark-bellied Brent Geese *Branta bernicla bernicla* found in Europe (Figure 4), the latter being a population which definitely breeds on Taymyr (Ebbinge 1992). It seems then that, if they are not breeding on Taymyr Peninsula itself, *canutus* Knots must be breeding in an area subject to the same fluctuations in breeding productivity that affect Taymyr Brent Geese, or to common problems during the first migration from the breeding grounds to the wintering areas.

The problem posed by the Taymyr Peninsula birds and their undetermined wintering grounds could be dismissed as relatively unimportant if the local breeding populations were small. However, with reported breeding densities of 0.01-0.1 pair/ha (P. Prokosch pers. obs.) on a coastal strip of 50 km wide and 500 km long (i.e. 25,000 km² or 2.5 million ha) we would estimate totals of 50,000 to 500,000 breeding adults only. Whatever the precise figures are, the Taymyr Peninsula breeding population is likely to be larger than 100,000 birds and would weigh heavily in any wintering population (see next page).

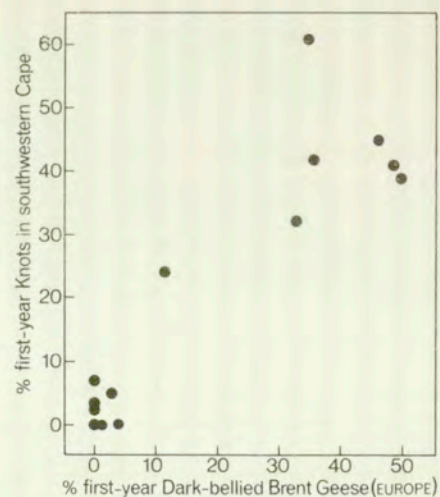


Figure 4. Correlative evidence for a Taymyr-breeding origin of Knots wintering in South Africa: the Dark-bellied Brent Geese wintering in Europe are certain Taymyr-breeders and their productivity is nicely correlated with relative juvenile Knot abundance in the southwestern Cape (from Underhill *et al.* 1989: Table 3; $r = 0.91$, $n = 14$).

According to Vaughan (1992, p. 236) large areas in Yakutia such as the Upper Olenek region have been particularly little researched ornithologically, and breeding areas of Knots may thus have been overlooked in this part of Siberia so far. With Tomkovich (1992) we therefore conclude that somewhere in Siberia, perhaps in the Yakutsk region (probably in the highlands west and east of the lower Lena River), important breeding populations of Afro-Siberian Knots remain to be discovered.

SOUTHWARD MIGRATION

The best direct observations of Knots leaving their Siberian breeding grounds are now 90 years old! To quote Birula (1907, translated by Pleske, taken from Dick *et al.* 1976): 'during the night of 27-28 August 1900 in Middendorff Bay, west Taymyr... 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 in from the

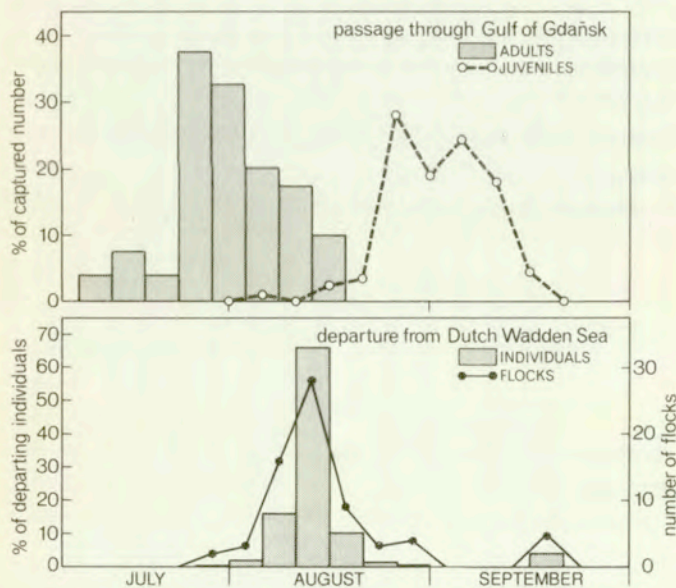


Figure 5. Timing of southward passage through western Europe of probable Afro-Siberian Knots. In the top panel relative numbers of Knots captured in walk-in traps on the shore of the Gulf of Gdańsk, Poland are given (only the earliest wave of long-billed adults ($n = c. 200$) and all juveniles ($n = 516$), from Gromadzka 1992). In the lower panel the timing of visible departures towards the SW from the Dutch Wadden Sea is summarized (based on 4920 individuals; part of the data presented in Piersma *et al.* 1990, and rest from observations on Griend by T. Piersma, P. Wolf, J. van Gils and P. Battley unpubl.). All birds except those from September were in partial or complete summer dress.

south...'. This is a month later than the main period of rapid passage of adults through the Baltic (late July-early August; see Figure 5 and Gromadzka 1992) and later than the main departure of supposedly Afro-Siberian Knots from the Wadden Sea to Africa (Figure 5). Could this indicate that adult Knots passing the Taymyr coast in a westward direction in late August are from another population, or should we explain it away by assuming that Birula's observation was exceptional? From 16-20 July 1989, a very poor breeding season due to harsh summer weather, large flocks of up to 1000 Knots and Bar-tailed Godwits *Limosa lapponica* were encountered on the north coast of Taymyr Peninsula ($c. 97^{\circ}\text{E}$) during their westward migration (P. Prokosch pers. obs.). These observations fit more easily in the known timing of migration.

The observations in the Gulf of Gdańsk (Figure 5) are in line with those of Nehls (1987) at a more westward site in the southern Baltic: an early (August) passage of adult birds and a later (September) passage of juveniles. There is some evidence for a departure of Knots on long-distance flights from the Wadden Sea in September (Figure 5), and indeed, the last 166 Knots which were observed during departure from the Wadden Sea were all in juvenile or winter plumage. There is evidence for a passage by small numbers of Knots along the Moroccan coast in August and September (Pienkowski & Knight 1977), but no firm data on the period of arrival on the Banc d'Arguin (probably August-September; Dick 1975). On the Banc d'Arguin, Mauritania, emaciated juveniles with body masses of 65-80 g were captured until late October 1973 (Dick & Pienkowski 1979). If these low weight birds are indicative of recently arrived individuals, as suggested by Dick & Pienkowski, then juveniles keep arriving on the wintering areas until October/early November.

In southern Africa, adult and juvenile Knots start arriving in late October (Pringle & Cooper 1975). There is one recapture indicating a direct southward link between Mauritania and South Africa: a juvenile Knot ringed on the Banc d'Arguin on 28 September 1972 was recaptured at Langebaan Lagoon, South Africa on 8 June 1975 according to Dick *et al.* (1976). It is possible that between late August/early September and half October Knots eventually spending the winter in southernmost Africa pause somewhere in equatorial West Africa (perhaps the coast of Gabon), and accumulate energy reserves for the flight to the southern tip of the continent.

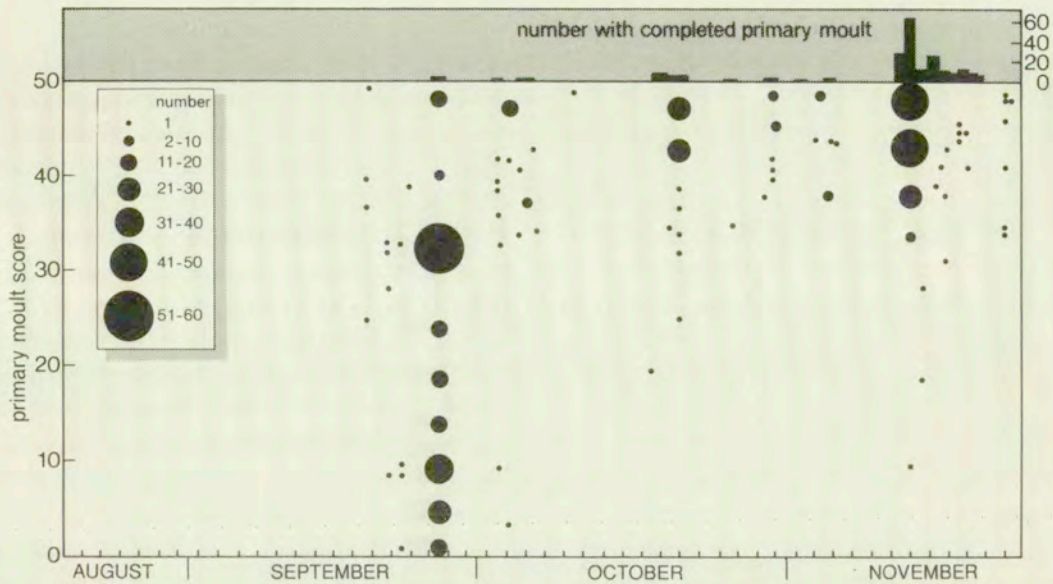


Figure 6. Time course of the completion of primary moult by adult Afro-Siberian Knots on the Banc d'Arguin,

Mauritania, in autumn 1973. This figure is adapted from Figure 17 in Dick (1975, p. 34).

MOULTING AREAS

There are no indications that Afro-Siberian Knots start their post-breeding wing and body moult on the breeding grounds, nor do they appear to start this on the autumnal staging areas in the Wadden Sea (Cramp & Simmons 1983; pers. obs.). Adult Knots wintering on the Banc d'Arguin in Mauritania are likely to start soon after their arrival in August or September (Dick 1975), most birds completing primary moult in the course of November (Figure 6). There is evidence that females are a few weeks ahead of males, having arrived earlier on the wintering grounds (Dick 1975). In southern Africa adult Knots undergo primary moult somewhat later, in the period November-January (L.G. Underhill pers. comm.). Since primary moult is closely correlated in time with the secondary moult and the body moult (Boere 1976), Afro-Siberian Knots replace their entire plumage soon after arrival on the respective wintering areas in Mauritania, Guinea-Bissau and southern Africa. In the case of Afro-Siberian Knots, the (wing) moulting areas are thus the wintering areas.

In spring, Afro-Siberian Knots have already started their moult into the breeding plumage two months before the northward departure from the wintering sites (Piersma 1989; Zwarts *et al.* 1990). Although most birds develop a full summer plumage in Africa, many resume body moult whilst on the spring staging areas in the Wadden Sea (pers. obs.). They arrest this moult before the departure to Siberia in early June.

WINTERING AREAS

Of the half million (516,000) Afro-Siberian Knots counted in coastal areas along the Atlantic shores of Africa, c. 362,000 are found on the Banc d'Arguin in Mauritania, c. 144,000 in the Archipelago dos Bijagos in Guinea-Bissau and almost 10,000 in southern Africa (Figure 7; Smit & Piersma 1989). The two West African areas contain no less than 98% of the entire population. At 520,000, Afro-Siberian Knots are

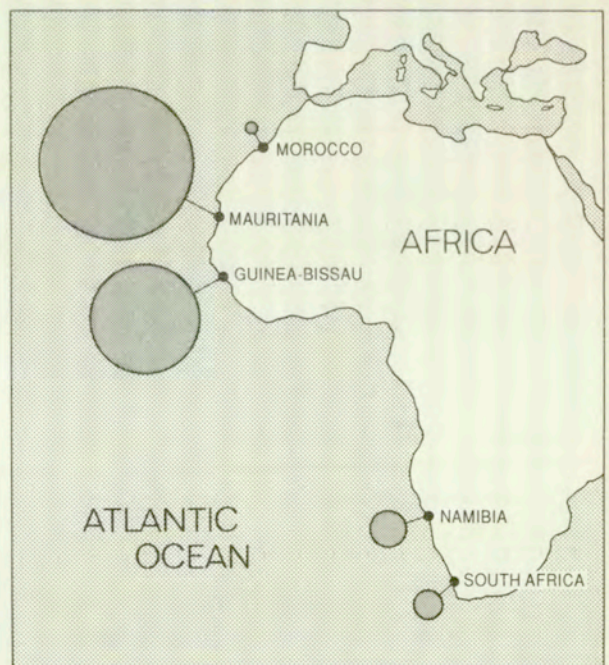


Figure 7. Midwinter distribution of Afro-Siberian Knots along the coasts of Africa (after Summers *et al.* 1987; Smit & Piersma 1989).

the most numerous subspecies, yet they may also be the subspecies potentially most at risk in view of their extremely concentrated wintering distribution.

We know that European-wintering Knots have greatly declined in numbers in the 1970s (Smit & Piersma 1989), possibly as a result of reduced survival and reproduction on the breeding grounds in 1972 and 1974 due to bad weather (Boyd 1992; Davidson & Wilson 1992). Numbers of Knots wintering at the major West African wintering areas are only known since the 1980s, the first complete count of the Banc d'Arguin being made in 1979 (Trotignon *et al.* 1980), and the first reliable extrapolation of sample counts for the Archipelago dos Bijagos only in 1987 (Zwarts 1988). We will therefore never know whether a population change comparable to the one of European-wintering Knots has recently taken place. It is possible, however, to look for changes in the numbers of Knots counted on two restricted areas, one in Mauritania and one in South Africa (Figure 8). At neither site is there evidence for dramatic increases or decreases in numbers since the late 1970s, although the series of counts from the region of Iouik (Banc d'Arguin) is far from perfect in view of the absence of midwinter figures since 1980. No review of the late summer or spring numbers of Afro-Siberian Knots is available, and this potentially fragile Knot-population is thus basically unmonitored.

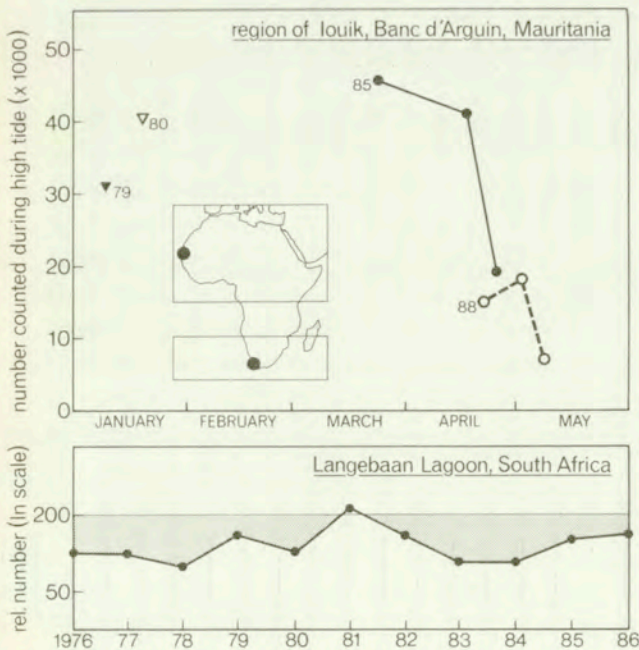


Figure 8. There is no evidence for dramatic changes in the numbers of non-breeding Afro-Siberian Knots according to counts of an area on the Banc d'Arguin, Mauritania (top; from Trotignon *et al.* 1980, Piersma 1982, Piersma *et al.* 1989 & unpubl.) and Langebaan Lagoon, South Africa (lower panel; from Underhill 1987: Figure 2).

NORTHWARD MIGRATION

The northward departure from Africa and the late spring passage through Europe is the best studied aspect of the biology of this subspecies (Dick *et al.* 1987; Bredin & Doumeret 1987; Piersma *et al.* 1987; Prokosch 1988; Piersma 1989; Piersma *et al.* 1990; Zwarts *et al.* 1990). Knots in southern Africa leave in late April to unknown staging sites, birds ringed in South Africa showing up in west central France and Schleswig-Holstein, Germany, in May (Dick *et al.* 1987). Knots wintering on the Banc d'Arguin leave northwards in early May (Piersma *et al.* 1990). The fact that numbers of Knots in the Baie d'Aouatif drop from mid April onwards (Figure 8) is difficult to account for but suggests a certain redistribution on the Banc d'Arguin in late April, or a limited movement to more northerly staging sites along the West African coastline (Baie d'Arguin, Lagoons of Dakhla and Khnifiss; for the latter area see Baouab *et al.* 1987). There is evidence for turnover in the Knot population of the Banc d'Arguin in April, suggesting that at least some Knots from Guinea-Bissau or even South Africa use the Banc d'Arguin as a spring staging post (Zwarts & Piersma 1990).

The timing of departure from West Africa and the passage through Europe is summarized in Figure 9. From 5-10 May onwards, Afro-Siberian Knots arrive on their European staging sites. Most birds immediately fly to the German Wadden Sea (>200,000; Prokosch 1988), but large numbers (up to 30,000) may stay for a fortnight on the Atlantic coast of France (Bredin & Doumeret 1987), and lesser numbers (up to 10,000) may use the Tejo Estuary in Portugal (Dick *et al.* 1987) and the Westerschelde in the Dutch Delta (Schekkerman *et al.* 1992). Four sightings in May-June 1985 of Knots colour-marked on the Banc d'Arguin in April 1985 (Ens *et al.* 1989) confirm the direct link between the West African wintering and one of the European staging sites. The 'lesser' staging sites in Portugal, France and The Netherlands are used only briefly, with most birds presumably carrying on to the German Wadden Sea at the earliest opportunity (Dick *et al.* 1987). In west central France the high turnover rate and short staging period of 1-2 weeks were confirmed by colour-marking/resighting studies (Bredin & Doumeret 1987). The Knots leave Germany in the last days of May and early June, passing southernmost Sweden (Blomqvist & Lindström 1992) and the Gulf of Finland (Dick *et al.* 1987) around 10 June, the departure and passage dates thus apparently fitting reasonably well (Figure 9). From 7 to 11 June

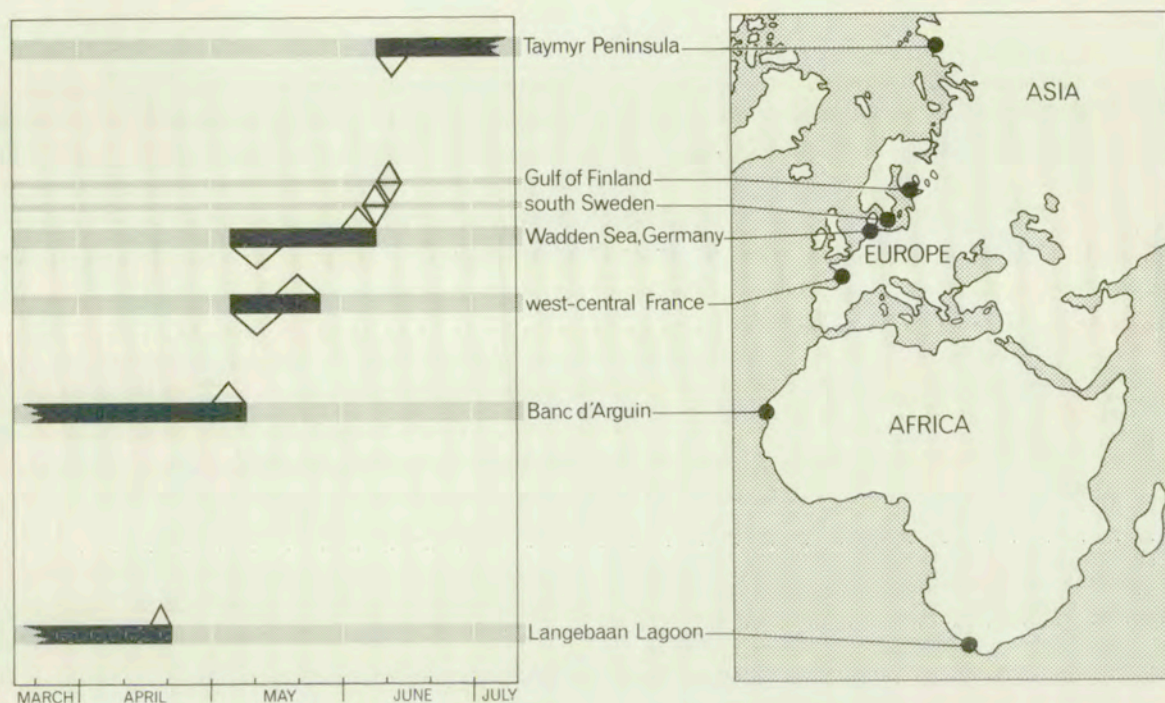


Figure 9. Timing of spring migration of Afro-Siberian Knots along the coasts of Africa, Europe and northern Asia. Black blocks indicate periods of staging, upward pointing triangles periods of departure and downward pointing triangles periods of arrival. No block indicates the occurrence of passage birds only. Data for Langebaan Lagoon, South Africa from Dick *et al.*

(1987) and M. Waltner (pers. comm.), for the Banc d'Arguin, Mauritania from Piersma *et al.* (1990), for France, Germany and Finland from Dick *et al.* (1987), for south Sweden from Blomqvist & Lindström (1992), and for Taymyr from Dick *et al.* (1987) and H. Hötter (pers. comm.).

1990, H. Hötter and co-workers (pers. comm.) recorded an eastward passage of Knots in the Pyasina Delta in northern Taymyr.

In addition, there is evidence for a consistent passage of thousands of Knots through the White Sea area (H. Schekkerman & R. Lambeck pers. comm.). Although of unconfirmed subspecific status, a South African ringed bird was recovered there in early June. Part of the *canutus* population may therefore use an extra stopover site en route from Europe to Siberia.

The use of the 'lesser' spring staging areas in Portugal, France and The Netherlands varies widely from year to year. Numbers of Knots staging in May in west central France, the most important area of the three for which also the longest series of observations is available, vary by a factor five. The short staging times and the very low body masses of staging birds suggest that the French coastal wetlands are used as 'emergency sites' (Dick *et al.* 1987; Bredin & Doumeret 1987; Smit & Piersma 1989), by individual Knots which are unable to make it from West Africa to the Wadden Sea in one flight. Work on the Banc d'Arguin in two seasons (1985

and 1986) have shown that it is unlikely that the differences in staging numbers (particularly large numbers in 1985, small numbers in 1986) are due to differences in body mass gains on the wintering area or the birds' masses at departure (Piersma 1989). Rather, it appears that the wind conditions *en route* from Mauritania to Europe vary a lot between years (Piersma & van de Sant 1992), and are associated with the use of the 'lesser' staging sites. In years with strong tailwinds few birds stage in France but in years with weak tailwinds many do so (Piersma, Bredin & Prokosch in prep.). Staging on an extra site in spring may delay the average spring migrant Knot by a week or so in terms of fattening. Whether this has repercussions on the population's breeding performance is unclear, and an area of interesting exploration for the future.

SEASONAL CHANGES IN MASS

Like Knots of other subspecies, body masses fluctuate considerably during the annual cycle of *canutus*. Figure 10 summarizes the currently available information on seasonal changes in body mass of adult birds in identified *canutus* populations. During their

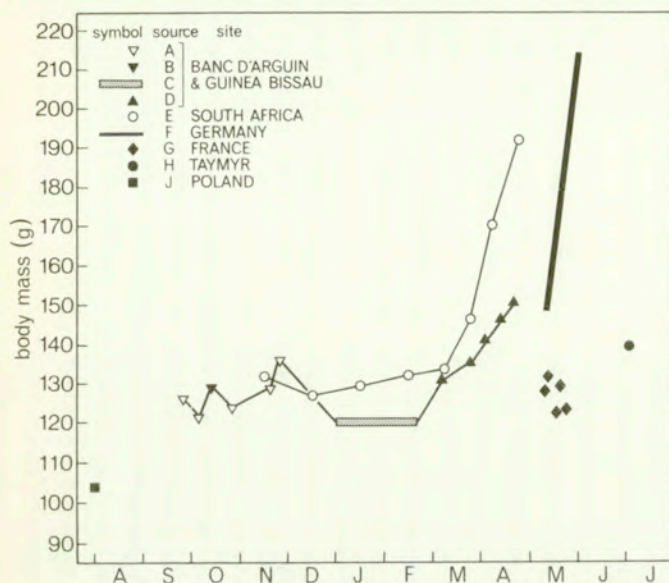


Figure 10. Summary of the seasonal changes in average mass of the migratory cohort of adult Afro-Siberian Knots. Average mass values for large catches (> 5 birds) or series of catches for the major and best known wintering and stopover areas are included. Sources: A: Dick (1975); B: Lensink & Meininger (1990); C: Zwarts *et al.* (1990); D: Piersma (1989); E: Summers & Waltner (1978); F: Prokosch unpubl.; G: Bredin unpubl.; H: Prokosch *et al.* unpubl.; I: Gromadzka (1992).

first winter in the south, juveniles differ from adults by arriving on the Banc d'Arguin 20-30 g lighter (Dick & Pienkowski 1979), and by not showing the spring increase in mass (Piersma 1989): second calendar year birds do not moult into breeding plumage either and remain in Africa for the northern summer.

No information is available on the mass changes at the end of the breeding season in Siberia, when Knots have to prepare their southward departure. The adult Knots staging briefly on the Polish coast in August-September weigh 100 - 110 g (yearly averages: Gromadzka 1992; Meissner 1992), and gain mass at an average rate of 2.54 g/d (computed from Gromadzka 1992: Table 3). Their mass during stop-over in Poland is the lowest reached by adults during their annual cycle (Figure 10), but may pertain only to a relatively unsuccessful segment of the population (as are birds staging in west central France in spring).

We know next to nothing about mass changes during their further southward migration. The body masses of Knots caught in late July/early August in the Dutch Wadden Sea (a period when only *canutus* Knots are supposed to be present) range from 120 to 210 g (M. Engelman pers. comm.), perhaps suggesting that Knots gain a maximum of (210 - 120 g =) 90 g at

their major southward stopover sites in the Wadden Sea. After arrival on the wintering areas in Mauritania and in South Africa, Knots weigh between 120 and 130 g, and stick to this average throughout the northern winter (Figure 10). The birds in southern Africa remain 10 g heavier than those in West Africa. Neither group shows the winter peak in body mass known from so many northerly wintering waders, including *islandica* Knots (Johnson 1985).

Six (South Africa) to eight weeks (Banc d'Arguin, Mauritania) before their northward departure, *canutus* Knots start depositing the nutrient reserves required for the ensuing long-distance flights (Figure 10). At Langebaan Lagoon, South Africa, the population average daily mass gain of 1.7 g/d (Summers & Waltner 1978; M. Waltner pers. comm.) is almost three times the rate achieved by Knots on the Banc d'Arguin (c. 0.6 g/d; Piersma 1989). After their arrival in Europe, Knots staging in Schleswig-Holstein, Germany, gain as much as 3.4 g/d. This population average mass increase is closely mirrored by individual inter-seasonal daily mass changes (Piersma, Prokosch & Bredin in prep.). Average departure mass in South Africa must be close to 200 g. Those leaving the German Wadden Sea for the flight to Siberia (c. 5000 km) weigh on average more than 200 g, which contrasts with the earlier departure from Mauritania for a similarly long flight (4600 km to the Wadden Sea) of c. 165 g (extrapolated to a departure on 2 May from Figure 10). All of this means that the summary model of mass changes in spring presented by Dick *et al.* (1987: Figure 9) is now somewhat outdated, and requires major adjustments. For example, the South African Knots would never make it to Europe in time, if daily mass gains on the Banc d'Arguin are limited to 0.6 g/d. However, in view of the important role of tailwinds in subsidizing long-distance flights (Piersma & Jukema 1990; Piersma *et al.* 1991), an eventual re-evaluation should take into account potential wind-induced savings on mass loss during flights.

During incubation on Taymyr Peninsula, Knots weigh almost 140 g on average (Figure 10). Since they weigh only 120 - 130 g during midwinter in Africa, they therefore carry more nutrient reserves during breeding than during wintering.

A WELL-KNOWN SUBSPECIES REVISITED

Having taken nine pages to summarize the annual cycle of *canutus* Knots, it is perhaps hard to main-

tain that we only know little about this subspecies. However, as alluded to in the introduction, there remain several major gaps in knowledge about this well-known subspecies. In order of presentation, our reappraisal has revealed that we do not know:

- 1) where the majority of *canutus* Knots breed;
- 2) where the Knots breeding on Taymyr overwinter;
- 3) about the mass changes during southward migration;
- 4) how *canutus* Knots make it to southernmost Africa in autumn, nor how they get back in spring (do they use as yet unknown staging sites in the Gulf of Guinea?);
- 5) how and if the data fit together in a closed travel budget, even though we have a large data-base on body mass changes in spring; and
- 6) whether the population of *canutus* Knots has shown any numerical changes in recent years. We are therefore unable to evaluate whether this subspecies, of which 98% winter at only two discrete coastal areas, is currently under pressure.

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