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Published in:
Bird Study

DOI:
10.1080/00063650109461213

Publication date:
2001

Bird Study (2001) **48,** 147–158

Why do few Afro-Siberian Knots *Calidris canutus canutus* now visit Britain?

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The nominate (Afro-Siberian) subspecies of the Knot Calidris canutus canutus *breeds on the Taimyr Peninsula in Siberia and occurs commonly in the westernmost Wadden Sea during migration to West and South Africa. The recoveries and controls of 2045 Knots ringed in Britain and Ireland provide no evidence for* canutus *wintering there nor for their regular passage during autumn and spring migration. Five juveniles ringed in the first week of September 1963 were recovered in Africa between eight and 37 days later, and another two birds ringed at the same time (one as an adult) showed up in subsequent years in Spain and Germany at times typical for Afro-Siberian Knots. There have been no comparable bursts of southern recoveries since. The period in 1963 during which the Afro-Siberian juveniles were captured on the Wash was characterized by sustained wind patterns conducive to bringing naive juvenile waders from the Siberian tundra to the southwest. Such conditions have been increasingly rare in later years. The paucity of recent records may additionally reflect a decline in this population. Juveniles leaving Siberia would probably fly a constant compass course to western Europe, a flight of more than 5000 km logically ending in southeastern England. The scarcity of Afro-Siberian type recoveries based on Knots ringed a mere 350 km (five to six hours of flight) west of the Wadden Sea is therefore remarkable.*

A study of the geographical origins of Knots *Calidris canutus* wintering in Europe and Africa (Dick *et al.* 1976) showed that those wintering in Europe originate in north Greenland and the Queen Elizabeth Islands of northern Canada, while longer-billed birds, breeding in poorly defined parts of Siberia, pass through western Europe in autumn and spring while travelling to and from winter quarters in West and South Africa. Roselaar (1983) separated the Nearctic breeders as the subspecies *C. c. islandica*, leaving the Siberian-breeding population as the nominate form *C. c. canutus*, to which Piersma *et al.* (1992) gave the name Afro-Siberian Knots used here. The migration system of *C. c. islandica* was reviewed in detail by Davidson & Wilson (1992) and that of the Afro-Siberian *C. c. canutus* by Piersma *et al.* (1992). Although there are differences in the mean lengths of the wings and bills of the two subspecies, their frequency distributions overlap extensively, so that it is not possible to assign captured individuals unambiguously to one form or the other on the basis of morphological features (Roselaar 1983, Piersma *et al.* 1987, Tomkovich 1992, Tomkovich & Soloviev 1996, Engelmoer & Roselaar 1998).

When summarizing the findings of Dick *et al.* (1976), Dick (1986) noted that populations of Knots breeding in Siberia and wintering in Africa 'do not reach Britain in significant numbers, although on migration they are

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found in the same European estuaries (notably in Germany) which are also used by the Greenland and Canadian populations.' Discussing retraps on the Wash of Knots ringed in Poland and Sweden, Mead *et al.* (1995) noted that it was not clear 'whether these birds were from the Siberian or Greenland population', thereby conveying the continuing uncertainty about the extent to which the *C. c. canutus* subspecies uses British shores during (mainly southward) migration (e.g. Dick *et al.* 1987). Large numbers of *C. c. canutus* spend several weeks in the westernmost parts of the Wadden Sea during southward migration (Piersma *et al.* 1993, Gils & Piersma 1999). By analogy with long-distance migrant ducks such as Wigeon *Anas penelope* and Pintail *A. acuta* which also travel from Siberia and do not see the southern North Sea as a barrier (Scott & Rose 1996), it would be expected that each year some Afro-Siberian Knots would 'overflow' into eastern England.

We use recoveries of Knots ringed in Britain and Ireland between 1960 and 1995 to explore the extent to which Afro-Siberian Knots routinely occur in Britain and Ireland on passage or in winter. We also examine the possible influence of weather systems over Britain and the effects of changes in population size and catching effort on the probability of detection.

MATERIAL AND METHODS

Ringing and recovery data

Between 1953 and 1995, 87 786 Knots were ringed in Britain and Ireland, chiefly around the Wash and Morecambe Bay, where the largest numbers of Knots are found. By the end of 1995, this marking had produced 812 useful records of birds found dead and 1233 'controls', here defined as individuals caught and released alive by ringers other than those who had marked them originally, or at more than 30 km from their original catching location (Mead *et al.* 1995). The many other 'repeats' and 'recaptures' by the original ringers are not held in the central British Trust for Ornithology (BTO) files. Few Knots have been marked or recovered in Ireland, although 25–60 000 *C. c. islandica* wintered on the east coast estuaries in the 1970s (Hutchinson 1979), and more than 5000 wintered in Strangford Lough in the northeast in the early 1990s (Sheppard 1993, Cabot 1999).

In addition to the recovery and recapture records supplied by the BTO, we have been able to use daily summaries of the catches of Knots by the Wash Wader Ringing Group. With the exception of several catches in 1969 and 1971, and occasional catches in later years, almost all the newly marked birds were identified as juveniles (hatched in that or the previous calendar year) or adults (more than one year old). Here we use the percentages of young found in large catches (>100 birds) made between 22 August and 30 September in the years 1959–96 as the best available indicators of the age-composition of recent arrivals, splitting the period into two on the supposition that Siberian birds should be more likely to be caught before 11 September.

Weather data and interpretation

Summary descriptions of the weather types and circulation systems over Britain and Ireland for every day from 1861 to 1971 were made by Lamb (1972). Similar summaries for 1972–95 have been published by Hulme & Barrow (1997). Lamb used data from the upper atmosphere and for the sea areas around Britain and Ireland, as well as from land stations. More recently, Mayes (1991, Wheeler & Mayes 1997), who was especially interested in regional differences in rainfall, used Lamb's classification system to provide daily records for four regions of Britain and Ireland (Scotland, Ireland, the southwest of England and Wales, and southeast England), based on surface conditions at land stations only. We have used the synoptic and the southeast England series during the three-week period 22 August to 10 September, the main arrival period for juvenile Knots (Davidson & Wilson 1992, Gromadzka 1992, Piersma *et al.* 1992), for each year from 1960 to 1996.

Lamb (1972) identified seven principal weather types: anticyclones (A), cyclones (C), Westerly (W), Northwesterly (NW), Northerly (N), Easterly (E) and Southerly (S). On many days none of these types is dominant, so that combinations are used (e.g. ANW, CS), 26 in all, with less than 2% unclassified (U). The sizes and timing of Knot catches are too few to be matched against so many weather types. Here we use a secondary grouping of dominant weather types, identifying cyclonic conditions

(C) and winds from the northeast, east and southeast as being most likely to assist movements of Knots into southeast England.

Population classification of recoveries

The published studies of the migration systems of *C. c. islandica* (Davidson & Wilson 1992) and *C. c. canutus* (Piersma *et al.* 1992) were based on morphometric data from, and observations at, breeding, staging and wintering areas, as well as on some of the earlier recoveries of birds ringed in Britain and other countries. These reviews suggested that a very simple classification system might be sufficient to identify the probable breeding and wintering places of most Knots ringed in Britain: birds caught in Britain in winter (October–April) should be *C. c. islandica*, while those taken in May and July–September might be of either race. The second categorization was by recovery location (1) at a time and place appropriate to Nearctic-breeding *C. c. islandica* (northeast Canada, Greenland, Iceland, Britain and Ireland in October–March) or (2) to Afro-Siberian *C. c. canutus* (West Africa, Siberia, Iberia in late April–May, France in May, west Germany in late May; see Dick *et al.* 1987, Prokosch 1988) or (3) to either (Baltic countries, Norway and western Europe at other times). The latter classification system has stood the test of time, and has been used in several migration and feeding ecological studies (Underhill *et al.* 1989, Piersma *et al.* 1991, 1994, Goede 1992, Ntiamoa-Baidu 1993, Gudmundsson 1994).

RESULTS

Origins and destinations

Using the criteria to distinguish between birds of Nearctic and Siberian breeding origin described above, almost all the recoveries of birds ringed in Britain and Ireland in winter were assigned to *C. c. islandica* (Table 1), as were 76.8% of those marked in May–September. Only 20 (0.98%) were in places likely to be used exclusively by *C. c. canutus* and none of these was ringed in the winter period. Of the 140 birds (6.8%) that were recovered in places where, and at times when, either form might be present, the great majority (135) had been ringed in Britain and Ireland in the summer. The five winter-ringed birds were all recovered in the Baltic. They may well represent *C. c. islandica*, as some late summer influx of *C. c. islandica* into this region has been established (Nehls 1987, Dierschke 1995).

The 20 recoveries assigned to *C. c. canutus* (Fig. 1, and listed in Appendix 1) include seven birds ringed on the Wash on 3 or 6 September 1963, six of which were juvenile. Four of these birds were found dead in Senegal and one in Liberia between 11 and 29 September 1963, eight to 37 days after ringing on the Wash. The other two were found in southern Spain on 15 May 1965 and in Germany on 24 May 1968. The remaining 13 Afro-Siberian recoveries had been ringed between 31 July and 25 September in eight different years from 1969 to 1984; only two were adult when ringed. Eight were recovered in Africa, from Mauritania to South Africa, five (including one adult) in the first autumn or winter, the others within two years. Three of the remaining five of this set of recoveries were in west Germany in May (one adult, two juveniles when ringed; the adult found dead, the juveniles controlled) and one controlled in France in May. The remaining bird, ringed as a juvenile in Norfolk on 11 August 1971, was found dead in Siberia (66.7°N, 112.3°E) on 11 June 1974, quite far to the southeast of the known Taimyr Peninsula breeding range (Fig. 1). The total of 13

Table 1. Composition of the Knot population in Britain and Ireland in winter and in spring/late summer, based on the time and location of the recoveries resulting from ringing at different times of the year.

		Recovered at time and location typical for		
Month of ringing	Recovery details	*C. c. islandica*	either	*C. c. canutus*
October–April	Dead	553	0	0
	Control	817	5	0
May–September	Dead	185	60	14
	Control	330	75	6

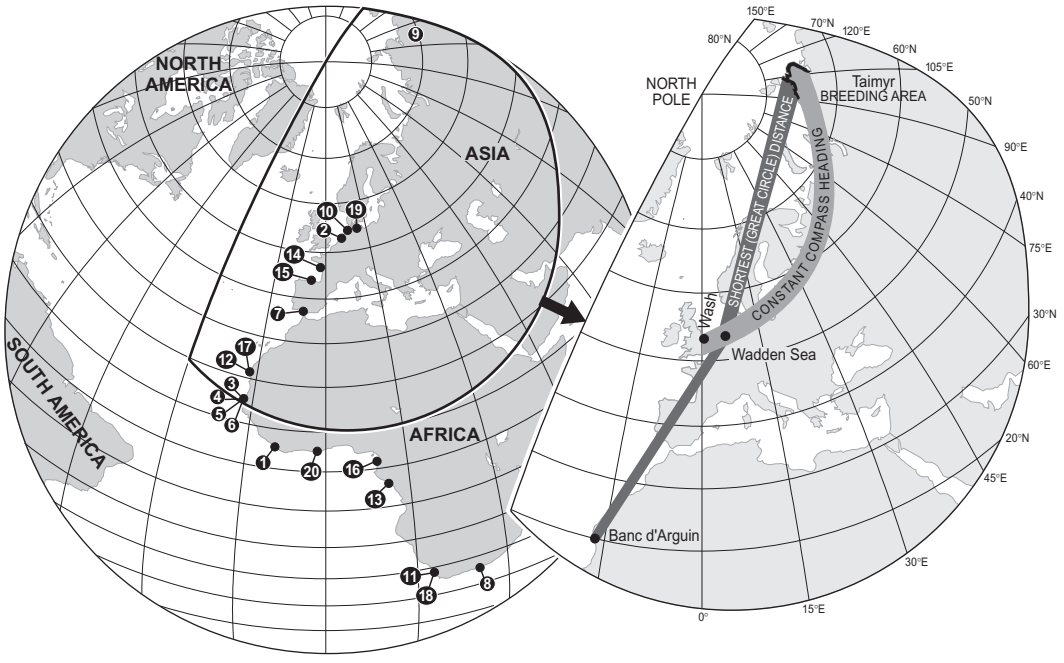

Figure 1. Flyway of Afro-Siberian Knots mapped out on a stereographic projection centred in the Wadden Sea (see Gudmundsson & Alerstam 1998 Fig.4) with all recoveries of British-ringed birds plotted in the left-hand panel; the circled numbers refer to the recoveries listed in Appendix 1. The right-hand panel shows a magnification to illustrate the great circle and rhumbline (constant compass heading) routes between the Wadden Sea and both Taimyr Peninsula and the Banc d'Arguin in Mauritania. It also shows that the Wash is close to the Wadden Sea relative to the distance of both areas from the Taimyr breeding grounds, and that this estuary could form as much a receptacle as does the Wadden Sea during southward migration.

recoveries from African shores, an area sparsely populated by ornithologists, stands in stark contrast to the 127 recoveries of British-ringed birds from Greenland and the Canadian Arctic, areas that would appear to be even less effectively covered.

About 70% of the entries in the 'either' column of Table 1 were birds controlled or found dead in Britain in later years (Table 2; note that the difference in the distribution over Britain and Ireland versus the rest of western Europe between birds recovered dead and as controls is highly statistically significant, $\chi^2 = 21.49$, $P < 0.0001$). They do not help to clarify how many or how often Afro-Siberian birds occur in Britain. The relative abundance of Afro-Siberian birds suggested by the occurrence of 13 recoveries in France and Iberia in May–September is biased upwards by the fact that Knots are shot in France in spring, though they

Table 2. Place of recovery of Knots of uncertain subspecific status, i.e. birds that were ringed in Britain and Ireland in the period May–September, and recovered at the same time of the year in western Europe.

		Area of recovery				
Quantity	Recovery status	Britain & Ireland	Wadden Sea	France & Iberia	Norway	Baltic
Numbers	Dead	30	16	13	1	0
	Control	65	5	1	1	3
Percentages	Dead	50.0	26.7	21.7	1.6	0.0
	Control	86.7	6.7	1.3	1.3	4.0

are not in the other four areas shown in Table 2 (see Dierschke 1995). The two birds found in Norway were probably *C. c. islandica* following the route from north Norway to Canada first identified by Davidson *et al.* (1986). As we have seen, even birds controlled in the Baltic are not necessarily Afro-Siberian.

Davidson & Wilson (1992) note that most juveniles have left Iceland by mid-September, though Nearctic juveniles are still arriving in Ireland in October (Hutchinson 1979). Afro-Siberian juveniles move on from the Wadden Sea in September (Piersma *et al.* 1992), so that the arrivals of the two groups overlap in time. Though there are no detailed records that would enable us to estimate the relative numbers of the two stocks in southeast England in most years, the autumn of 1963 was exceptional. In that year perhaps as many as one-third of the juveniles could have come from Siberia; in most other years it is unlikely that more than 10% did so (Table 3).

A juvenile phenomenon?

There is a striking difference in the proportions that were juvenile when caught and ringed in Britain between the recoveries of birds likely to have been bred in the Nearctic and those from Siberia (Table 4): about one-fifth of the *C. c. islandica* compared with five-sixths of *C. c. canutus*.

The proportions of young in large ringing catches on the Wash were usually much less than those in small catches (Table 5), many of which were probably incidental catches when other species were the main targets. Very few young Knots have been caught before

Table 3. Affinities and recovery history of Knots ringed as juveniles in Britain and Ireland in the autumn of 1963 and in all other years.

		Recovered at time and location typical for		
Year(s) of ringing	Recovery details	*C. c. islandica*	either	*C. c. canutus*
1963	Dead	14	6	6
	Control	39	16	0
	Total	53	22	6
	Percentage of total	65.4	27.2	7.4
Before or after 1963	Dead	135	19	6
	Control	241	17	5
	Total	376	36	11
	Percentage of total	88.9	8.5	2.6

Table 4. Age at ringing in Britain and Ireland of Knots belonging to different populations as shown by the time and place of their recovery.

		Recovered at time and location typical for		
Age	Recovery details	*C. c. islandica*	either	*C. c. canutus*
Juveniles	Dead	149	25	12
	Control	280	33	5
	Total	429	58	17
Adults	Dead	589	35	2
	Control	867	47	1
	Total	1456	82	3
% juveniles	Dead	20.2	41.7	85.7
	Control	24.2	41.2	83.3
	Total	22.8	41.4	85.0

21 August. There were fewer than 3% juveniles in large catches on the Wash before 11 September in seven of the 15 years, in contrast to 80.7% in 1963 and 98.2% in 1973. Fewer samples were obtained in the period 11–30 September. The very high proportion of juveniles in the recovery sample (mostly from the 1963 ringing) assigned to the Afro-Siberian stock cannot just reflect high breeding success and must be attributable to young birds being more likely than adults to overshoot the main autumn staging area in the Wadden Sea. The presence in the 'either' category of 41% of juveniles (Table 4) suggests that some Afro-Siberian birds are included, but that they are probably a minority.

There has been only one year with large catches in both late August and early September (when *C. c. canutus* is most likely to occur) and later in September (which should be mostly *C. c. islandica*): in 1969 the percentage of young was 7.5% before 11 September and 2.9% later. In 1973 the birds caught in both periods were nearly all juveniles. In five more years, comparisons are possible between peak-period and October catches; in four there were far fewer juveniles in October than earlier, but in 1978 there were as many young (25.8%) in October as in the period 22 August to 10 September (25.7%).

An analysis of data from so few years is further complicated by known (or suspected) variations in the breeding success of the two stocks. There is on-site evidence that few young Knots were reared in northeastern Canada in 1972, 1974 and 1979 (Boyd 1992), or in 1992 and 1996 (R.I.G. Morrison, pers. comm.). The proportion of juveniles in the peak arrival period was 45.0% in 1972, and 91.6% (small sample) in 1979 (Table 5), suggesting that most juveniles were Afro-Siberian. In 1974, the only large catches were made before mid-August and in October, so are useless in this context. In 1996 very few young were taken in the peak period and production was poor in Taimyr as well as in northeast Canada.

Wind and weather factors

Figure 2 summarizes annual variations in favourable winds over Britain and Ireland (Fig. 2a) and over southeast England only (Fig. 2b). Over the entire period there was no trend in the frequencies of suitable winds over the whole of Britain and Ireland (Fig. 2a), but favourable surface winds became less frequent over southeast England (Fig. 2b). In the first half of the period (1960–77), 98 out of 378 of the days were favourable, i.e. a mean of 5.44 days per year. In the second half of the period (1978–95) only 56 days of a total of 378 (i.e. a mean of 3.11 days per year) were favourable ($\chi^2 = 12.82$, $P < 0.001$).

There were two years when there were 11 days with favourable winds over Britain and Ireland during the 21-day period, the year 1963 being one of the two (Fig. 2a). There were seven years in which the number of favourable days in southeast England exceeded the mean ± sd: 1960, 1963, 1968, 1971, 1972, 1976 and 1991 (Fig. 2b). There were no large peak-period catches in 1971 or 1991. The proportions of young in the period 22 August to 10 September in the other years were widely scattered (Table 5).

There were five years when there were no days or one day with favourable winds over southeast England during the 21-day period

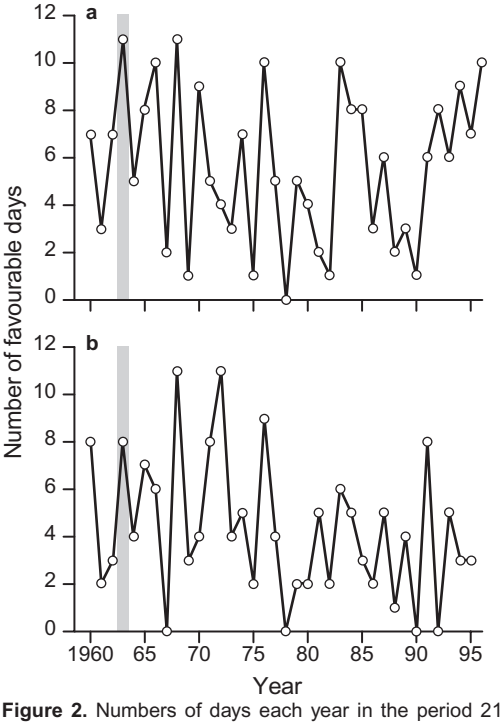

Figure 2. Numbers of days each year in the period 21 August to 10 September on which the winds over Britain and Ireland (a) and over southeast England (b) were likely to have been helpful for the arrival of Knots from Scandinavia and the eastern Baltic states. The year 1963 is indicated by shading.

Table 5. Percentages of juveniles in large (>100 birds) and small (<100 birds) catches of Knots by the Wash Wader Ringing Group in two distinct periods between 22 August and 30 September.

	22 August–10 September				11–30 September			
	Large		Small		Large		Small	
Year	%	*n*	%	*n*	%	*n*	%	*n*
1960	1.1	439						
1963	80.7	2379	46.5	79				
1967	8.6	222	82.7	75				
1968	1.2	1919	(50.0)	14				
1969	7.5	295	67.5	83	2.9	726		
1970					1.7	120		
1972	43.4	458	(75.0)	24				
1973	98.2	113	(78.6)	14			100.0	115
1975	0.6	974	97.6	127				
1976	0.0	320	12.5	232				
1977	11.9	176	21.5	65			41.8	79
1978	23.7	994	68.9	103				
1979			91.6	83				
1982	0.7	294					100.0	54
1983	9.9	314	85.4	89				
1984					25.4	118		
1985							42.0	112
1988							29.6	54
1990			48.0	50				
1992	2.1	290	4.5	67				
1993					69.7	905		
1994			46.5	129				
1995			98.4	62			11.1	45
1996	0.7	444						

During the period 11–30 September one would expect few Afro-Siberian juveniles to remain. During missing intervening years no Knots were caught on the Wash in either period. The figures in parentheses are based on samples smaller than 25 birds.

(Fig. 2b). For these years, the proportions of juveniles in the period 22 August to 10 September were 8.6% in 1967, 23.8% in 1978 and 2.1% in 1992 (when breeding success of nearly all bird species was exceptionally low in the ranges of both *C. c. canutus* and *C. c. islandica*, Ganter & Boyd 2000). There are no adequate catch records from 1988 and 1990 (Table 5).

An exceptional number of southern recoveries resulted from the very large catches at Holbeach on 3 and 6 September 1963 which showed a very large proportion of juveniles (Table 5). Conditions for arrivals from the east or northeast had been quite favourable in the preceding ten days, 1963 being the only year with 11 cyclonic and no anticyclonic days over Britain and Ireland in the critical period. In complete contrast, in 1973, when almost all the Knots caught in the main arrival period were juveniles as well (two of which, captured rather later in September, yielded *C. c. canutus*-type recoveries; Appendix 1), there were no cyclonic and 13 anticyclonic days in the 21-day period.

DISCUSSION

Was 1963 special?

Dick *et al.* (1976) noted that there were exceptionally large numbers of juveniles on the Wash in August–September 1963, attributing their presence, along with heavy autumn passages of Curlew Sandpipers *Calidris ferruginea* and Little Stints *C. minuta*, to persistent northeasterly winds due to low pressure systems centred over southern Scandinavia. Thus they supposed the Knots to have come from the east, not the northwest. The lack of any recent equivalent to the influx in 1963 suggests that the conditions that brought it about may be infrequent. Dick *et al.* (1976) noted that there were similar heavy passages of other waders breeding in northern Eurasia in 1969 and 1970. More than 10 000 Knots were ringed in Britain in those years, but they have yielded only one southern recovery.

In fact, the ringing of Knots has continued unabated in Britain since 1985, and it is possible to predict the number of Afro-Siberian-type recoveries expected on the basis of the numbers ringed recently. If the 43 526 Knots ringed between 1963 and 1974 resulted in 13 Afro-Siberian recoveries (a likelihood of 0.030), and the 19 320 Knots ringed between 1975 and 1984 in seven Afro-Siberian recoveries (a likelihood of 0.036), then we would expect seven to nine Afro-Siberian recoveries over the period 1985–95 during which 23 901 Knots were ringed.

Discrepancy in population size estimates of *C. c. islandica* remains unexplained

There is no evidence from ringing in Britain that any Knot of Siberian breeding origin ever spends the winter in Britain and Ireland or, indeed, in the rest of western Europe. Therefore, the suggestion that almost half of the Knots wintering in Europe might originate from Siberian breeding grounds, put forward by Whitfield *et al.* (1996) to reconcile their population estimates based on a review of Nearctic breeding densities with the numbers counted in Europe in winter, is questionable. In occasional years, some young of the year from Siberia may have reached Britain in late summer, but their numbers have been rather low. During northward migration in May, Afro-Siberian Knots are virtually absent (Dick *et al.* 1987).

Population decreases in *C. c. canutus*?

Nevertheless, it is remarkable that no recoveries of British-ringed Knots of certain Afro-Siberian origin were obtained from individuals ringed between 1985 and 1995, given that ringing in the previous 22 years had yielded 20 such recoveries (Appendix 1). Based on counts in the late 1970s and early 1980s, Smit & Piersma (1989) concluded that the total Afro-Siberian population counted 516 000 birds, compared with 345 000 *C. c. islandica*. The population of *C. c. islandica* is believed to have since increased to about 400 000 birds (Davidson 1998). In January/February 1997, the first count since 1980 of *C. c. canutus* on their main wintering area (Banc d'Arguin in Mauritania) suggested a decrease in the local population from 364 000 to 230 000 birds, a 37% decline (Zwarts *et al.* 1998). The estimated numbers of birds wintering in the other main wintering area (Archipélago dos Bijagos, Guinea-Bisssau) showed an even steeper decline over the ten-year period between 1983 and 1993 (from 90 000 to 31 300 birds, a 65% decrease; Salvig *et al.* 1994). It is therefore likely that the Afro-Siberian Knot population decreased by about 40% sometime between 1980 and 1997, most likely in the late 1980s. Thus, the lack of evidence for Afro-Siberian Knots in recent British catches may reflect a population decline in addition to a lack of favourable winds in summers with peak chick production.

Navigational considerations

The shortest way to return from the Siberian breeding grounds to the intertidal areas of western Europe and Africa would be to follow the great circle route (Fig. 1). However, a migratory flight along a great circle between locations at diverging longitude, as here, necessitates constant adjustments to the compass course (Alerstam 1990). Even though there is evidence that birds fly great-circle-type trajectories in high-arctic regions (Alerstam 1996), confirmed by observations of adult Knots departing from Taimyr Peninsula in appropriate great circle directions to the Wadden Sea (P.S. Tomkovich & T. Piersma, unpubl. data), in the case of naive juveniles the use of a route based on constant compass headings (Fig. 1) provides a more likely

scenario. There is a wealth of experimental evidence (based on passerines) of genetically fixed clock-and-compass mechanisms steering inexperienced juvenile birds in the direction of their wintering areas (e.g. Berthold 1996, Helbig 1996). With a clock and a constant compass heading of about 238°, freshly fledged Knots could certainly find their way from the Taimyr Peninsula to western Europe, but what would prevent them from overshooting the relatively small gap between the Wadden Sea and southeastern England?

It might perhaps be argued that juveniles only succeed in making the trip if the flock in which they migrate contains an experienced adult, for example a late male (female Knots leave the breeding area immediately upon hatching, the males remain to escort the chicks; Whitfield & Brade 1991, Tulp *et al.* 1998). Such adult males, with experience of the Wadden Sea from previous spring passages, could, perhaps inadvertently, prevent their young flock-mates overshooting the southern North Sea. The highly skewed distribution of the annual percentages of young (Table 5) suggests that, even in years when few Afro-Siberian birds are present, there may be considerable differences in the distribution of adults and juveniles within the wintering range of *C. c. islandica*. Recoveries of Knots ringed in Greenland offer some support: most have been in Britain and Ireland, but all three shot in France in autumn were juveniles (P. Lyngs, pers. comm.). This suggests that young Nearctic Knots are also liable to overshoot their usual arrival areas.

Why have Afro-Siberian Knots not evolved to use eastern English estuaries regularly during southward migration? Is it an example of 'ideal-free distributional principles' in action? Does the Wadden Sea provide ample high quality habitat, so that the Wash, perhaps being slightly off the direct route to West Africa (arguably so if birds follow great circle trajectories, see Fig. 1), does not need to be exploited? Or is there a clear quality difference, or an effect of differential competition from Nearctic-breeding Knots between the two areas?

ACKNOWLEDGEMENTS

We thank Petra de Goeij for pleasant company during the work sessions on Texel. Funding from the Netherlands Organisation for Scientific Research (NWO), through a PIONIER-grant to T.P., enabled us to buy the recovery data from the British Trust for Ornithology (BTO). We are indebted to the BTO for permission to use those data. Note that part of the BTO Ringing Scheme is funded by a partnership of the BTO and the Joint Nature Conservation Committee (on behalf of English Nature, Scottish Natural Heritage and the Countryside Council for Wales, and also on behalf of the Environment and Heritage Service in Northern Ireland). The Scheme also receives support from Duchas The Heritage Service – National Parks and Wildlife (Ireland). The volunteer ringers give freely of their time and expertise and also provide a substantial part of the Scheme's funding. We thank the Wash Wader Ringing Group (WWRG), and especially Phil Ireland, for supplying us with, and allowing us to use, free of charge, their records of Knot catches. The catches in September 1963 that produced the anomalous African recoveries were made by H.B. with a team from the WWRG, using rocket-nets belonging to the, then, Wildfowl Trust, to which we remain grateful. We are indebted to Peter Lyngs who, on behalf of the Danish ringing scheme, provided us with recovery details of Knots ringed in Greenland. We thank Dr Julian Mayes of the Department of Environmental and Geographical Studies, Roehampton Institute London, for providing us with his series of daily airflow patterns over different regions of Britain and Ireland for 1950–95. H.B. acknowledges financial assistance from the Canadian Wildlife Service. We thank Gudmundur A. Gudmundsson for help with the map, which was drawn in final form by Dick Visser. This is NIOZ publication 3332.

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(MS received 3 February 2000; revised MS accepted 6 October 2000)

APPENDIX 1

Details of the sites of ringing and recovery of Knots that obey the 'prescriptions' of the subspecies *C. c. canutus*. Note that the geographical co-ordinates represent back-calculations to a degree scale from listings on a full-minute scale; this may have introduced small aberrations.

No.	Ring no.	Age	Date	Degrees latitude	Degrees longitude
Ringing details					
1	CX25424	Juv	03.09.63	52.9N	0.0E
2	CX25661	Ad	03.09.63	52.9N	0.1E
3	CX25719	Juv	03.09.63	52.9N	0.0E
4	CX26635	Juv	06.09.63	52.9N	0.1E
5	CX26864	Juv	06.09.63	52.9N	0.1E
6	CX27680	Juv	06.09.63	52.9N	0.1E
7	CX27556	Juv	06.09.63	52.9N	0.1E
8	CR76777	Juv	30.08.69	50.9N	0.9E
9	CC71522	Ad	11.08.71	52.8N	0.4E
10	CC88850	Juv	29.08.72	52.8N	0.4E
11	CC90761	Ad	31.07.73	52.8N	0.4E
12	CV66659	Juv	21.09.73	52.4N	6.4W
13	CE09516	Juv	25.09.73	52.1N	1.4E
14	CE33239	Juv	22.08.78	52.8N	0.4E
15	CJ33445	Juv	02.09.78	51.4N	0.9E
16	CE34540	Juv	10.09.79	52.8N	0.4E
17	CE34536	Juv	10.09.79	52.8N	0.4E
18	XS25388	Juv	23.09.83	54.6N	1.2W
19	XS22736	Juv	08.09.84	57.5N	4.2W
20	CJ33479	Juv	09.09.84	51.4N	0.9E

Ad, adult; Juv, juvenile.

continued

APPENDIX 1 continued

No.	Country	Degrees latitude	Degrees longitude	Date	Recovery status	Distance (km)	Days
Recovery details							
1	Liberia	6.9N	10.8W	11.09.63	Dead	5206	8
2	W. Germany	55.1N	8.4E	24.05.68	Dead	594	1725
3	Senegal	14.8N	17.3W	29.09.63	Dead	4507	26
4	Senegal	14.8N	16.9W	25.09.63	Dead	4488	19
5	Senegal	14.8N	16.9W	25.09.63	Dead	4488	19
6	Senegal	14.9N	17.4W	13.10.63	Dead	4497	37
7	Spain	36.8N	6.4W	15.05.65	Dead	1857	617
8	Mozambique	26.0S	32.6E	10.10.70	Dead	9102	406
9	Russia	66.7N	112.3E	11.06.74	Dead	6346	1035
10	W. Germany	54.4N	8.8E	21.05.86	Control	579	5013
11	S. Africa	33.1S	18.0E	23.12.73	Control	9698	145
12	Mauritania	19.9N	16.3W	24.11.73	Dead	3712	64
13	Congo Braz.	4.8S	11.9E	07.10.79	Dead	6391	2203
14	France	46.4N	1.2W	14.05.80	Control	726	631
15	Spain	43.5N	5.7W	03.05.86	Control	998	2800
16	Gabon	0.5N	9.3E	19.11.79	Dead	5874	70
17	Mauritania	19.4N	16.5W	19.01.80	Dead	4000	131
18	S. Africa	33.1S	18.0E	14.04.85	Control	9921	569
19	W. Germany	54.4N	8.8E	17.05.85	Control	878	251
20	Ghana	5.1N	2.9W	26.10.84	Unknown	5156	47

Dates are given in the form: day.month.year, e.g. 03.09.63 = 3 September 1963.