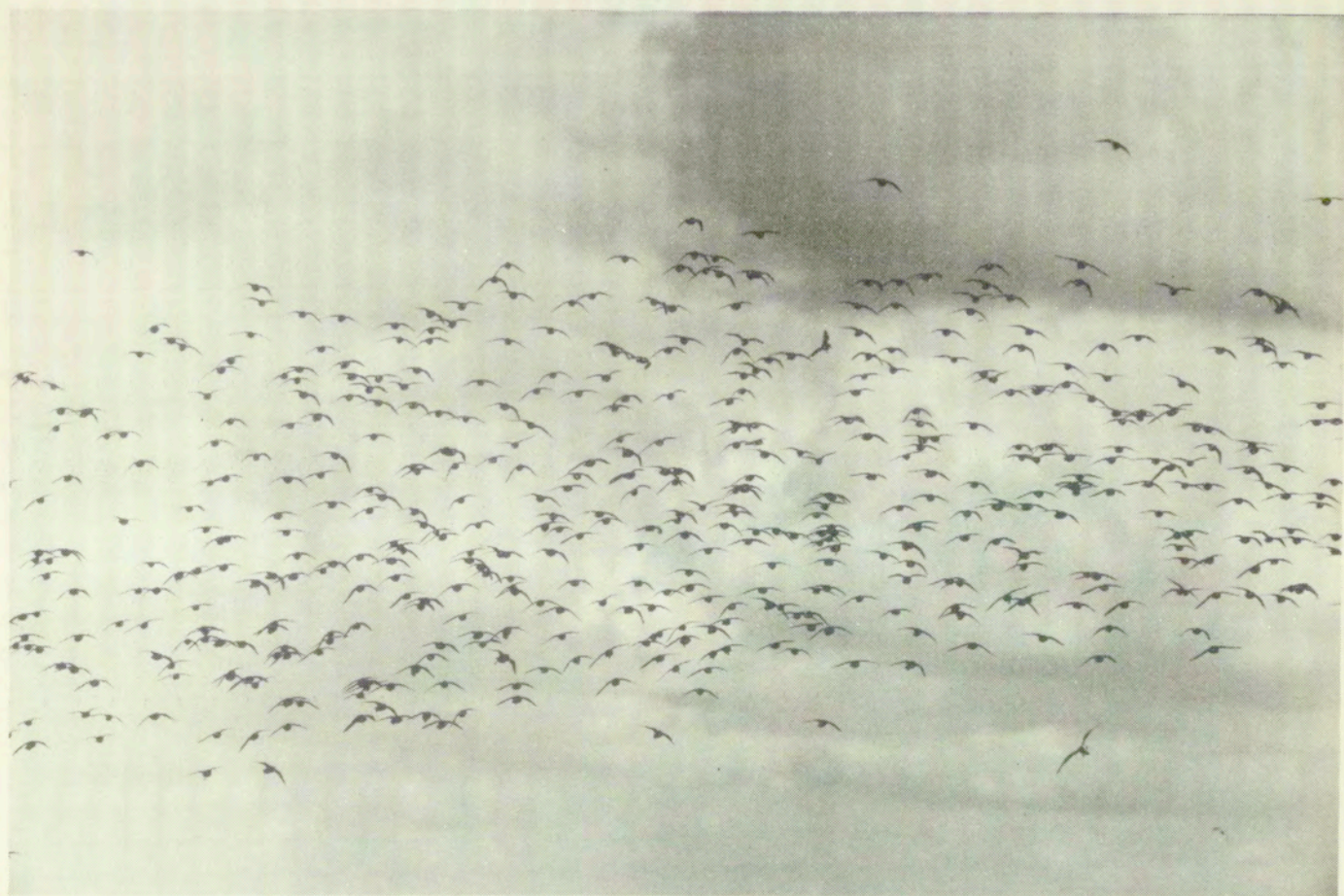

Migration systems reviews



The migration system of European-wintering Knots *Calidris canutus islandica*

N.C. Davidson & J.R. Wilson

Davidson, N.C. & Wilson, J.R. 1992. The migration system of the European-wintering Knot *Calidris canutus islandica*. *Wader Study Group Bull.* 64, *Suppl.*: 39-51.

The *islandica* subspecies of Knot is the most extensively studied. They breed in high arctic Greenland and Canadian arctic islands, as far west as Prince Patrick Island and largely north of 75°N. The population has declined from 609,000 birds in the early 1970s to 345,000 in the mid 1980s, perhaps because of severe summer weather in the Arctic in the early 1970s. Probably all of the population reaches its moulting and wintering grounds in Britain, France and the Wadden Sea in autumn via staging areas in western Iceland (in late July-early August), where they pause to refuel for one or two weeks. At least 50% moult in the Wadden Sea and many then move to Britain and France to join others that have moulted there. Over 60% of the midwinter population is concentrated on relatively few estuaries in Britain. In March 60-75% of *islandica* Knots return to accumulate nutrient reserves on the Wadden Sea; others do so on the western British estuaries. During the first week of May birds fly to a few late spring staging areas in northern Norway and western Iceland, with fewer in north-east Iceland. There they store large fat and protein reserves, leaving in late May weighing 205 - 210 g (fat 30-35% of body mass). After at least a 3,000 km non-stop flight they arrive on arctic breeding grounds in early June with substantial reserves remaining to aid survival before snow melts. Despite the relatively extensive knowledge of *islandica* Knots, several major and unexpected discoveries about the migration and distribution of this subspecies have been made recently. Further research is crucial to understanding how to conserve Knots throughout their range.

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INTRODUCTION

Godfrey (1953) proposed on taxonomic grounds that Knots breeding in Greenland and Ellesmere Island in the Canadian Arctic wintered in the Old World, although even as early as 1927 Bent commented that Knots breeding in north-east Greenland may be the European form (Bent 1927). The European wintering origin of north Canadian Knots was confirmed from ringing recoveries by Morrison (1975). The range of west European wintering grounds of the Nearctic Knots was established by Prater (1974) and Dick *et al.* (1976). On the basis of morphometrics, Roselaar (1983) has separated these Nearctic birds as *Calidris canutus islandica* from the nominate *C. c. canutus* that breeds in Siberia and overwinters in western and southern Africa (Dick *et al.* 1976, 1987; Piersma *et al.* 1992).

Many studies have since documented the distribution and migration of *islandica* Knots. A fairly simple migration system (compared to many waders) emerged, in which Knots make a few very long-distance migratory flights, use only a few staging sites, chiefly in Iceland, and occur on a small number of main wintering sites. Despite being so apparently well-known, major discoveries are, however, still being made. In 1985 Knots staging in late spring in Balsfjord, northern Norway, were discovered to belong to the Nearctic breeding population (Davidson *et al.* 1986; Uttley *et al.* 1987). Similar confirmation for birds further north in Porsangerfjord was obtained in 1987 (Wood *et al.* 1988).

These discoveries point to a more complex and less well-known migration system than was previously supposed. This brief review summarizes what is now

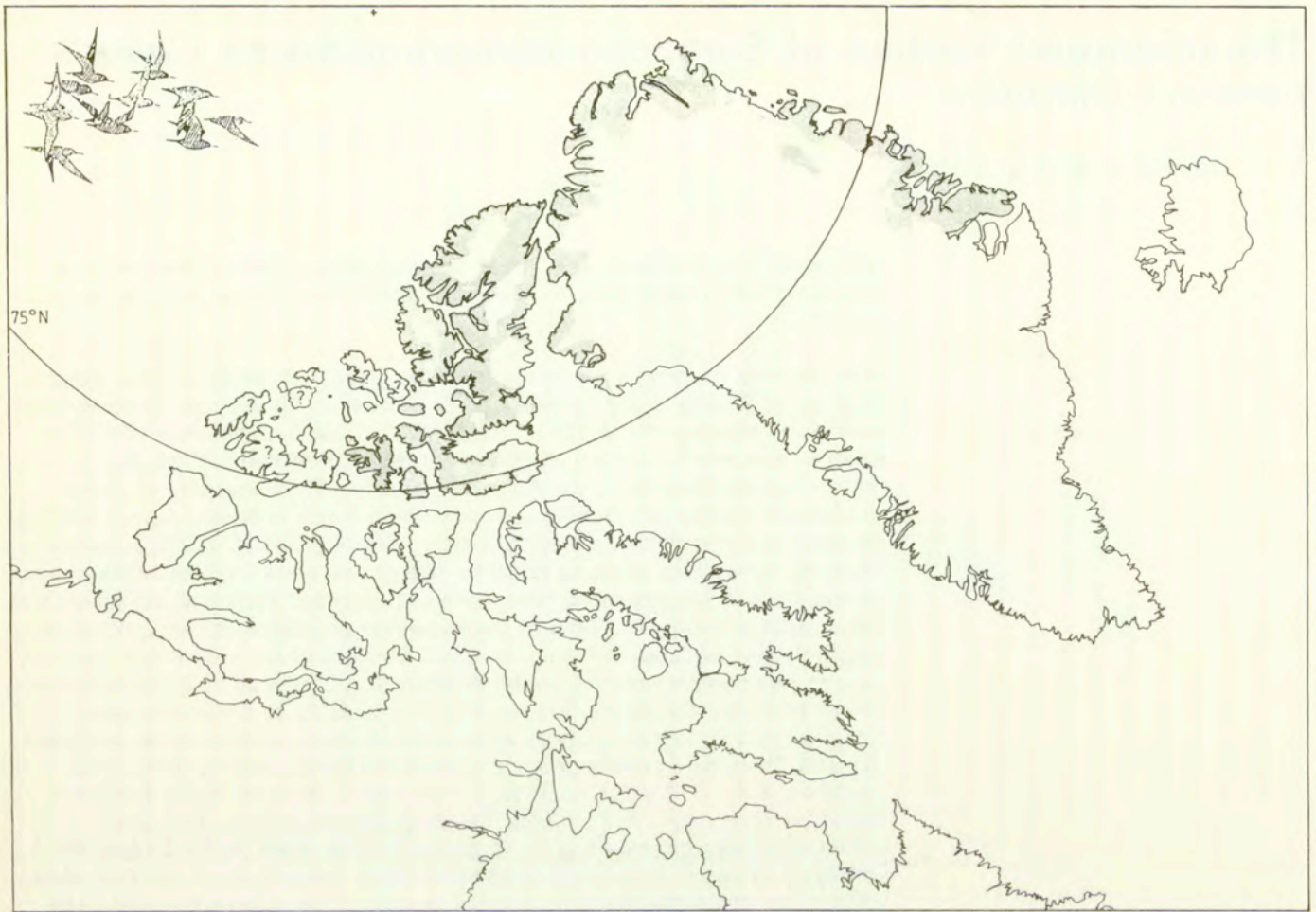


Figure 1. Breeding grounds of *islandica* Knots, derived from Cramp & Simmons (1983) and Meltofte (1985). Most areas shown '?' are now confirmed as *islandica* breeding grounds (Godfrey 1992).

known of the location of breeding grounds, staging areas, migration routes and wintering sites of *islandica* Knots, and points to some of the gaps that still remain in our understanding. Some of these gaps will be filled by the reports of recent research elsewhere in this volume.

BREEDING GROUNDS

Breeding grounds are shown in Figure 1. *Islandica* Knots breed in Greenland north of Scoresby Sund in the east and north of Kap York in the west (Cramp & Simmons 1983; Meltofte 1985). In the Canadian Arctic Knots breeding south of 75°N are considered to be *rufa* (Cramp & Simmons 1983). Further north in the Canadian Arctic *islandica* Knots are known to breed on Ellesmere Island, Devon Island and Axel Heiberg Island, and as far west as Bathurst Island (100°W) (Cramp & Simmons 1983). Presumably Knots breeding on the smaller islands such as Ellef

Ringnes Island (see Savile 1961), north of Bathurst Island are also *islandica*. How much further west *islandica* breed than this has been unclear, but Godfrey (1992) has now confirmed that *islandica* Knots breed as far west as Prince Patrick Island. The precise boundaries between *islandica* and *rufa* in the western and central Canadian Arctic need to be defined.

Islandica Knots generally breed at very low density: 1 pair/km² at most. Most of the population are believed to breed in the Canadian Arctic: Meltofte (1985) estimated 10,000 pairs to be breeding in Greenland and another 10,000 pairs on Ellesmere Island and eastern Axel Heiberg Island, although he believed these to be underestimates. If they are accurate this means that at a total population size of 350,000 birds, Meltofte's calculations suggest that some 50,000 pairs must nest on Devon Island and the islands further west. Even with a Greenland and Ellesmere Island population double that estimated by

Meltofte there may still be 30,000 pairs breeding elsewhere. Much more needs to be known of the breeding distribution and densities.

The affinities of Knots breeding on Spitsbergen and Franz Joseph Land are unclear, but these birds may be *islandica*. The populations are in any case very small (Kålås & Byrkjedal 1981; Meltofte *et al.* 1983; H. Meltofte pers. comm.).

AUTUMN MIGRATION

Although a few adults leave their breeding grounds in early July most adults depart between mid-July and the first week of August (Meltofte 1985). Less is known of autumn migration routes than those in spring. Known routes from the breeding grounds are summarized by Meltofte (1985). Alerstam *et al.* (1986) suggest that birds leaving north-east Canada and west Greenland may cross the Greenland inland-ice on a broader front than in spring because of more favourable weather conditions. Knots leaving north-east Ellesmere Island may, however, fly east via north Greenland. Migration around Peary Land in north-east Greenland is towards the east or south-east.

The only known major early autumn staging area is west Iceland (Wilson 1981; Morrison & Wilson 1992). First adult arrivals are in mid July, with peak numbers in late July. Most adults have left by mid August. Juveniles migrate later: they are first seen in early August with peak numbers at the end of August and the first week of September. Only a very few Knots occur in north-east Iceland in autumn, during late July (Wilson 1981; Whitfield & Magnusson 1987).

Knots use Iceland in autumn to replenish their nutrient reserves for a flight on to west Europe to moult. Numbers appear lower in autumn than in spring, but this may be largely because turnover of birds is rapid in autumn. Evidence from rates of mass gain suggest that individuals pause in Iceland in autumn for 1-2 weeks (Wilson & Morrison 1992).

Birds leaving west Iceland fly direct to moulting areas on the coasts of Britain and the North Sea. Arrivals on west British estuaries such as the Ribble and Morecambe Bay begin as early as mid July (Smith & Greenhalgh 1977), as do arrivals in the Wadden Sea (Smit & Wolff 1981). It is therefore possible that some Knots overfly Iceland on their

return from the breeding grounds and fly directly to Europe. It is possibly that these birds sometimes arrive with very low weights and stay for just a few days in places where they occur only occasionally in early autumn. Some Knots appearing in the Western Isles of Scotland (Buxton 1989) and Teesmouth (Davidson & Evans 1988) may have needed to pause briefly to replenish reserves sufficiently to reach moulting areas further south and east: the Teesmouth birds had low fat reserves and very small pectoral muscles (Davidson & Evans 1988). Some Knots (mainly juveniles but also a few adults), pause in south-west Norway and Denmark (Netterstrøm 1970; Andreasson & Råd 1977; Lifjeld 1988). The extent of Knots flying direct from breeding grounds to west Europe needs more investigation. The breeding grounds of any such birds are not known, although the distances involved suggest east and north-east Greenland as the most likely part of their range. Autumn movements are summarized in Figure 2.

MOULTING AREAS

Moult begins on arrival in western Europe, on a few large estuaries in Britain (chiefly the Wash, Dee, Ribble and Morecambe Bay) and the Wadden Sea, and as far south as western France (Cramp & Simmons 1983). On the Wadden Sea primary moult takes 90-100 days and is finished during October. Secondary moult begins at a primary moult score of 20-30 and is completed before primary moult (Boere 1976). In most birds body moult begins in August and is well advanced by September. There is no evidence of arrested post-breeding moult: each individual *islandica* moults at only one site (Boere 1976).

Figure 3 shows the distribution of the about 160,000 Knots occurring in Britain in August and September in the early 1970s (Prater 1981), about 30% of the total *islandica* population of that time. Most of the remainder moult on the Wadden Sea. Their distribution within the Wadden Sea is difficult to determine since the Siberian-breeding *canutus* population also uses the Wadden Sea at this time, as a staging area before flying to West Africa to moult. Most are probably in West Germany and The Netherlands (see Smit & Wolff 1981). In The Netherlands an average of 24,000 occurs in September around the small island of Griend in the middle of the Wadden Sea (Veen & van de Kam 1988). Smit & Wolff (1981) estimated that about 50% of the total *islandica*

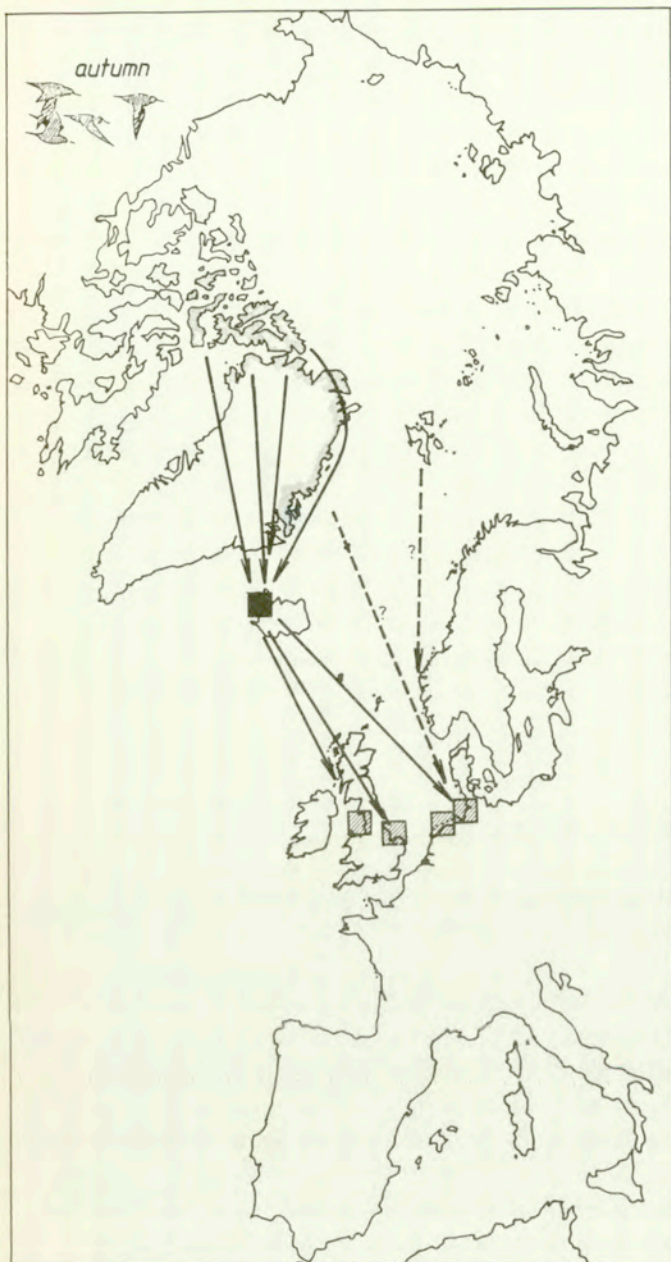


Figure 2. A summary of the autumn migration system of *islandica* Knots. Breeding areas are stippled. The solid symbol indicates the main staging area, and shaded symbols show the main mouling areas.

population moulted in the Wadden Sea. It is only at this time of year in the Wadden Sea that there is any substantial mixing of the two subspecies.

WINTERING AREAS

Islandica Knots overwinter in the British Isles, the Wadden Sea, the Dutch Delta and as far south as western France. The total population is currently estimated as 345,000 birds (Smit & Piersma 1989), a major decrease from Prater's (1976) estimate of 609,000 birds. *Islandica* now has a smaller popu-

lation than the Siberian-breeding *canutus* (512,000 birds according to Smit & Piersma 1989).

Many birds move to Britain from the Wadden Sea after moulting, and movement into Britain continues until at least midwinter. Late winter movements into Britain may also occur during periods of severe weather. Other Knots move westwards in Britain from moulting sites such as the Wash (Cramp & Simmons 1983). There is also a complex pattern of movement during the course of the winter, with some birds moving up the east coast of Britain from the Wash (Dugan 1981).

The winter distribution in the early 1970s is shown in Figure 4. The population was centred in Britain and France. Knots occur in large numbers on only a few estuaries in midwinter: in the early 1970s the main estuaries, with 70,000 - 80,000 wintering birds, were Morecambe Bay and the Wash in England and the Baie d'Aiguillon in Vendée, France. Other major sites were the Wadden Sea (although numbers there are much lower there than in autumn and spring), Baie du Mont St.Michel in France, the

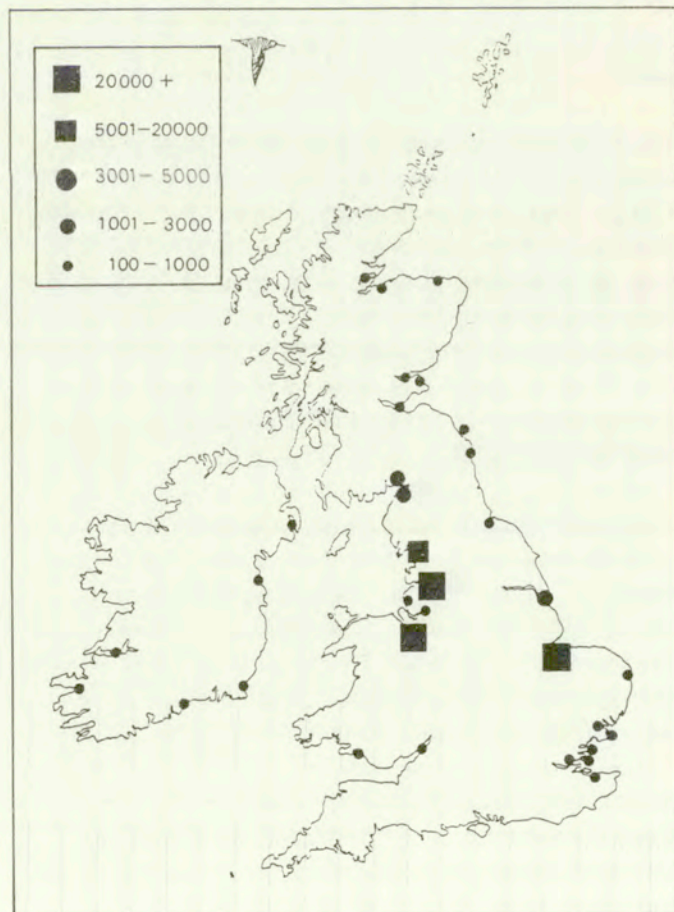


Figure 3. Autumn (August-September) distribution of *islandica* Knots in the British Isles during 1969-75 (redrawn from Prater 1981).

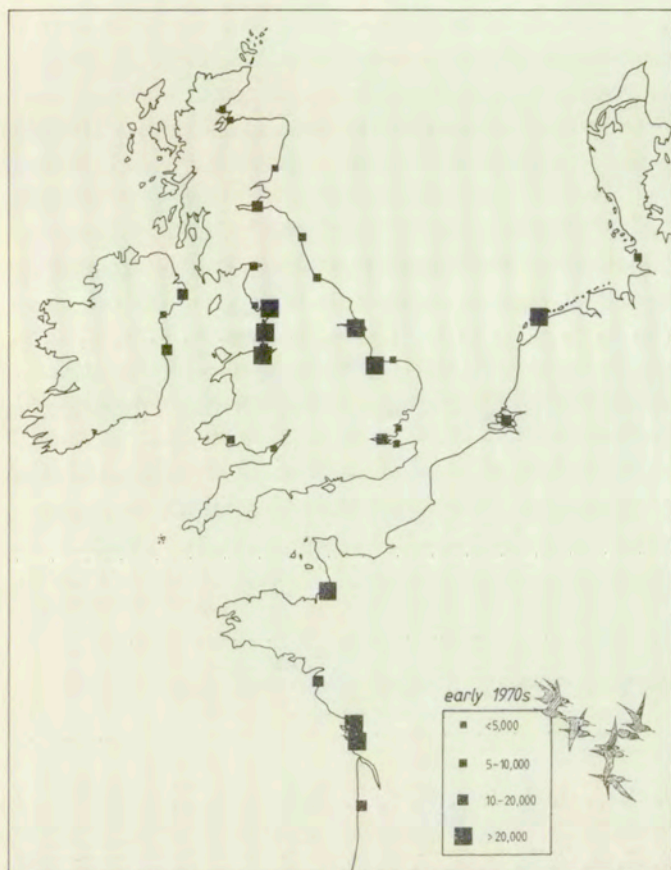


Figure 4. Winter distribution of *islandica* Knots during the early 1970s (derived from Prater 1974, 1981; Smit & Wolff 1981).

Dutch Delta, and the Solway Firth, Ribble, Dee and Humber estuaries in England (Prater 1974).

The most southerly confirmed wintering grounds for *islandica* Knots are in western France. Some Knots, possibly of this subspecies, overwinter on the Iberian peninsula. Numbers are small and even in the early 1970s there were only 10,000 in Spain and 5,000 in Portugal (Prater 1976). The few thousand Knots in Morocco are thought to be *canutus* (Cramp & Simmons 1983). The extent and location of any overlap between the two subspecies in southern Europe and North Africa is not known. There is also some very circumstantial evidence from birds ringed at the same time as known *islandica* birds that some may overwinter further south in western and southern Africa (Davidson & Evans 1986). This possibility would repay further investigation.

Table 1 shows that the decline in the total population since the early 1970s has been most marked in France, Great Britain and Ireland, and less so in the Wadden Sea and the Delta (Smit & Piersma 1989). The population remains centred, however, around the North Sea and in Britain, and major

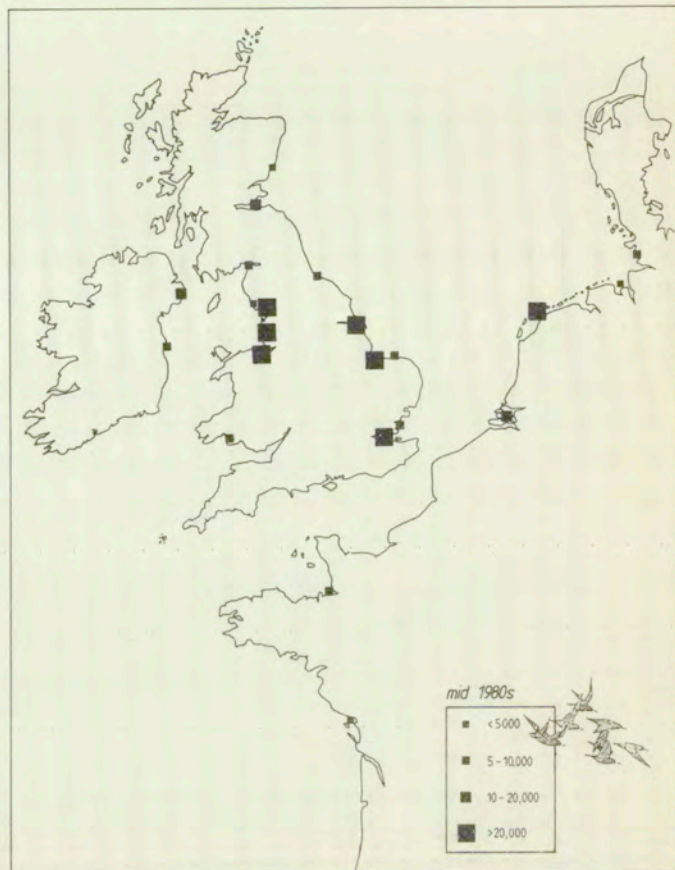


Figure 5. Winter distribution of *islandica* Knots during the mid-1980s (from Smit & Piersma 1989).

decreases in the population have been on the fringes of the wintering area (Figure 5). In Britain the population has decreased most on west coast estuaries such as Morecambe Bay, Dee and Ribble. Now just 22 estuaries support the great majority of the wintering population. The single most important is the Wash with 88,000 birds (25% of the population).

Table 1. Changes in the numbers of wintering *islandica* Knots.

	Prater (1976)		Smit & Piersma (1989)	
		%		%
France	110,000	18	19,000	6
Great Britain	350,000	57	218,000	63
Ireland	55,000	9	30,000	9
Wadden Sea	65,000	11	58,000	17
Delta	14,000	2	15,000	4
Elsewhere	15,000	3	5,000	1
Total	609,000		345,000	

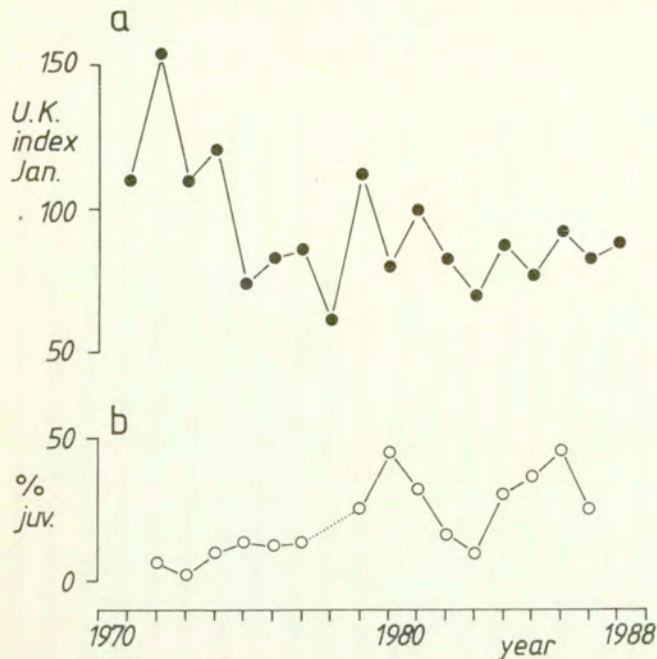


Figure 6. A: The January population index for Knots in the United Kingdom, from Salmon *et al.* (1987, 1988). B: The percentage of juvenile Knots in cannon-net samples from some British estuaries, from Underhill *et al.* (1989).

The population, at least in Britain, seems to have declined mostly before 1979 and to have been at its lowest in the winter of 1977/78 (Figure 6A). Thereafter numbers in Britain have increased very little. The reasons for the population decline are not clear, but probably involve a series of poor breeding seasons during the early 1970s (see review in Boyd 1992). This is supported by the consistently very low proportions of juvenile Knots caught on some British estuaries (Figure 6B). In at least one of these years (1974) there is evidence that not only were few young reared but also there was high adult mortality on the breeding grounds during a period of severe weather in late June (Morrison 1975). The proportions of juveniles in the population have been variable but generally higher in the 1980s but this has not resulted in a substantial increase in the overall population size.

Underhill *et al.* (1989) showed that there was no link between the annual breeding productivities of *islandica* and *canutus* Knots, but that the breeding productivity of *canutus* Knots was linked to those of other species of waders and Dark-bellied Brent Geese *Branta b. bernicla* known to breed in northern Siberia. Similarly, in some years during the early 1970s when breeding success of Nearctic waders was poor, breeding productivity of the Light-bellied Brent Geese *B. b. hrota* breeding in the same areas

of Greenland and high arctic Canada was also very low (Prater 1979). Interestingly, however, there is no overall long-term link between the breeding productivity of *islandica* Knots and this Brent Goose population (Figure 7A). Nor is there a link between the breeding performance of *islandica* Knots and the Barnacle Goose population breeding in east Greenland (Figure 7B), although the breeding productivity of the two goose species are linked (Figure 7C, see also de Boer & Drent 1989). Why there should not be a similar link between the breeding of *islandica* Knots and geese to that for the Siberian breeding populations is not clear but could be due to differences in breeding distribution. Figure 7 indicates that in years during the late 1970s and 1980s of good breeding productivity of *islandica* Knots, goose breeding productivity remained low.

SPRING MIGRATION

Early spring

Many Knots return eastwards to use the Wadden Sea, particularly the Schleswig-Holstein part, as their early spring staging area. Prokosch (1988) estimates that 250,000 - 400,000 *islandica* Knots use the Schleswig-Holstein Wadden Sea in early spring. This is 60-75% of the total population. Birds move to the

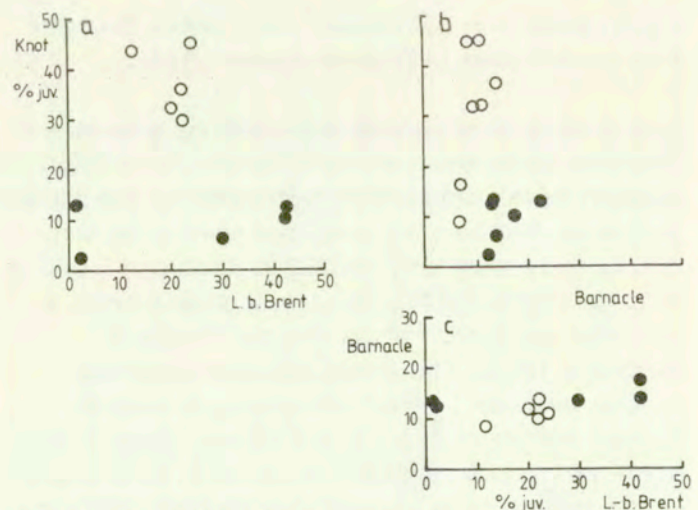


Figure 7. The relationships between the breeding productivity of *islandica* Knots (% juveniles in caught on some British estuaries, from Underhill *et al.* 1989) and (A) Light-bellied Brent Geese *Branta bernicla hrota* breeding in Greenland and high arctic Canada, (B) Barnacle Geese *Branta leucopsis* breeding in east Greenland (B), as well as (C) the relationship between juvenile percentages of the two geese species (geese data from de Boer & Drent 1989, and F. de Boer pers. comm.). Each symbol is for a different year, solid symbols for early 1970s and open symbols for late 1970s and early 1980s.

Wadden Sea in spring from a very wide range of their wintering areas to the south, west and north, including west France, the Delta, the Wash, Teesmouth, Firth of Forth, Moray Firth and even the west coast of England (Prokosch 1988). Not all birds use the same area for autumn moulting and spring staging: for example some that moult in autumn on the Wash move to the Wadden Sea in spring (Prokosch 1988). Most movement to the Wadden Sea occurs during mid to late March (Figure 8).

Some *islandica* Knots remain on their wintering grounds such as the Wadden Sea, western France, western Britain and the Wash through until early May. In the early 1970s western British birds congregated particularly in Morecambe Bay, where at least 80,000 occurred during April (Prater & Wilson 1972; Prater 1981), but numbers in recent years have been much lower.

Late spring

Knots leave their early spring staging areas mostly in the first two weeks of May (Figure 8). The precise date probably depends on when weather conditions become favourable. Most leave the Wadden Sea before the arrival there in mid May of most *canutus* from West Africa. Furthermore most *canutus* use different parts of the area so there is little overlap. In some places such as Trischen, however, counts suggest that both subspecies occur at the same time in early May (Figure 8). Similar early May departure times occur from other early spring sites such as Morecambe Bay (Prater & Wilson 1981) and the Wash.

Birds fly direct to two main late spring staging areas: western Iceland (Prater & Wilson 1972; Wilson 1981; Morrison & Wilson 1992) and northern Norway (Davidson *et al.* 1986; Uttley *et al.* 1987), a distance of 1,500 - 2,000 km. Until the mid 1980s it was thought that only Iceland was used at this time of year. In addition to the main areas in west Iceland, an estimated 8,000 Knots use north-east Iceland as a late spring staging site (Whitfield & Magnusson 1987). Choice of late spring staging site is not dependent on which early spring site is used. For example birds from the Wadden Sea go to both Norway and both parts of Iceland in late spring (Davidson *et al.* 1986, Prokosch 1988).

In west Iceland birds start arriving in late April with large numbers arriving during the first week of May and peak numbers occurring in the second and third weeks of May (Wilson 1981, Morrison & Wilson

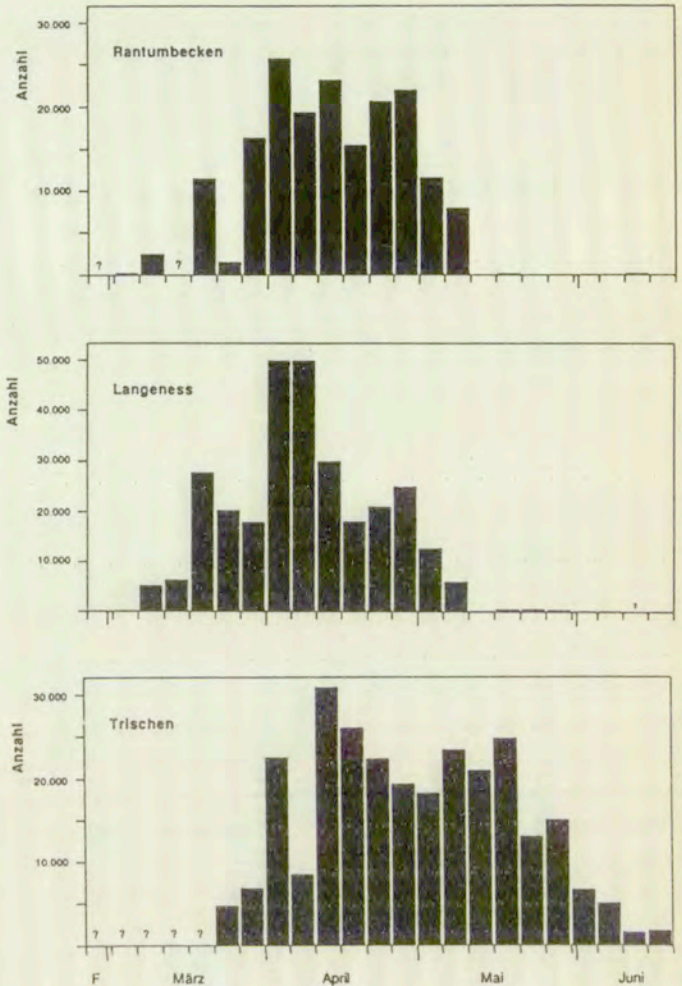


Figure 8. Occurrence of Knots during spring in the 1980s in three parts of the Schleswig-Holstein Wadden Sea, from Prokosch (1988). Only *islandica* occur in the Rantumbecken and Langeness; both *islandica* and *canutus* occur on Trischen.

1992). Very large numbers of Knots use this area: in the early 1970s 200,000 were estimated for south-west Iceland alone (Wilson 1981), about 60% of the total population. Knots arrive in Balsfjord in north Norway slightly later: first arrivals are 5-8 May, with most arrivals between 12-18 May (Uttley *et al.* 1987; Strann 1992). Numbers using Balsfjord varied between 12,000 - 28,000 in three successive years (1984-86).

At least 30,000 Knots occur in Porsangerfjord in northern Norway (Håland & Kålås 1980). These were confirmed in 1987 as being almost certainly part of the *islandica* population (Wood *et al.* 1988). As in Balsfjord birds are present from the first week of May, with largest numbers present in the third week of May.

Colour-marking and ringing at Balsfjord in 1985 and 1986 showed that there was very little population turnover there after 12 May (Davidson & Evans 1986). The recurrence at Balsfjord in subsequent years of many Knots marked there in 1985 and 1986 indicates that most individuals are faithful to a particular late spring staging site.

However not all individuals are so faithful. Some Balsfjord Knots had moved to Porsangerfjord as early as 16 May in the year following their marking (Wood *et al.* 1988), but it is not clear whether individuals use both fjords in one year. Interchange between the two may account for the between-year variation in numbers in Balsfjord (Strann 1992).

More surprising are the links between Balsfjord and Iceland established from observations of colour-marked birds. One observation is of a within-year movement: a Knot marked on 11-13 May 1986 had moved to west Iceland by 26 May. It probably remained there for at least 5 days. It is not clear whether this use of both late spring staging areas (with a migration route lengthened by 1,500 km) in one year is abnormal. Some Balsfjord Knots have also been seen in west and north-east Iceland in subsequent Mays. At least some of these arrived in Iceland during the normal arrival period for Knots, strongly suggesting that individuals are using different late spring migration routes and sites in different years. This must involve departure from the early spring staging area in markedly different directions in different years, a migration pattern that appears to be unique amongst birds following such a precise long-distance migration. One Balsfjord bird was reported from west Greenland in early June of the following year, strongly suggesting that this bird had passed through Iceland and followed the usual migration route from there (see below). Use of different routes in different years is surprising since many Knots return to the same breeding grounds in subsequent years (e.g. Morrison & Davidson 1990, unpubl.). Perhaps others are more peripatetic? Much still needs to be established about these patterns of late spring migration.

Knots stay 2-3 weeks on their late spring sites, departing mostly during the last week of May. Most Knots left west Iceland between 26-30 May during the early 1970s and almost all had left by 1 June (Wilson 1981; Morrison & Wilson 1992). Similar timings for departure (25 May - 2 June) were reported by north-east Iceland (Whitfield & Magnusson 1987). In northern Norway departures

were on similar dates to Iceland. Departures from Balsfjord were between 25-29 May in three successive years (Uttley *et al.* 1987). Departures from Porsangerfjord are less precisely known, but are broadly similar to elsewhere: most departures in the last week of May (Davidson *et al.* 1986; Strann 1992).

Alerstam *et al.* (1986) established that Knots leaving west Iceland flew west across the southern part of the Greenland inlandice to the west coast of Greenland, before flying up the west coast to the breeding grounds. Departure directions from north-east Iceland are similar (Whitfield & Magnusson 1987). Although this is longer than the direct great circle route (e.g. 2,700 km compared to 2,300 km for a flight to northernmost Ellesmere Island), weather conditions are generally more favourable. Alerstam *et al.* (1986) suggest a migratory divide in which this route is used by birds breeding in north-west Greenland and most of northern Canada, whilst those breeding in north Greenland and north-east Ellesmere Island migrate across northern Greenland, perhaps from north Norway staging sites. This is consistent with observed arrival directions from the east of Knots in northern Ellesmere Island. For birds flying to westernmost breeding grounds such as Bathurst Island, the flight distance from either Iceland or Norway will be considerably in excess of 3,000 km. There is a suggestion that some Knots fly direct to east Greenland from Britain and the Wadden Sea, so missing out the more northerly late spring staging areas in Iceland (Cramp & Simmons 1983), but this is unsubstantiated.

Breeding ground arrivals

Arrival timings indicate a direct flight from Iceland and Norway to breeding grounds, although in some years birds crossing the inlandice from Iceland pause in west Greenland if they encounter bad weather (Alerstam *et al.* 1986). First arrivals are from 26 May in north-east Greenland and a few days later in northern Canada, with main arrivals during the last few days of May and early June (Meltofte 1985). At Alert in northernmost Ellesmere Island first arrivals are 29-31 May with largest numbers present during the first week of June (Davidson & Morrison 1989, 1992; Morrison & Davidson 1990). Similarly in west Ellesmere Island first arrivals are 27 May - 1 June (Parmalee & MacDonald 1960; Nettleship 1984). In years when snow melt is late birds congregate for a few days on snow-free areas before dispersing to their breeding grounds on surrounding areas (Meltofte 1985; Morrison & Davidson 1990).

If snow cover conditions are favourable Knots start to breed soon after their arrival on the breeding grounds, and often earlier than other waders in the same areas. At Lake Hazen in northern Ellesmere Island egg-laying began in the period 15-23 June (Nettleship 1974), i.e. about two weeks after arrival. First-egg dates were earlier in west Ellesmere Island: 5-14 June (derived from Parmalee & MacDonald 1960). This implies that egg-laying here begins within about 7-10 days of arrival. In north-west Greenland Prokosch (1987) estimated that egg-laying was mostly during the first week of June. This is

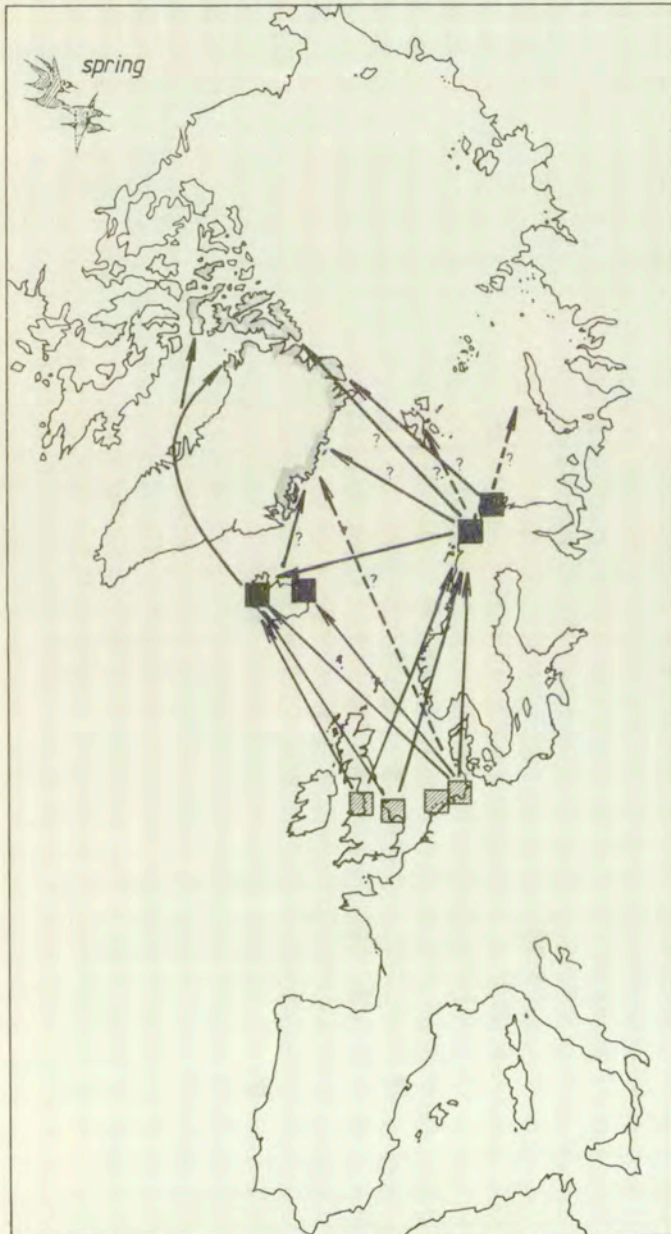


Figure 9. A summary of the spring migration system of *islandica* Knots. Early spring staging areas are shaded symbols, late spring staging areas are solid symbols and breeding grounds are stippled. Question-marks indicate presumed routes for which there is no firm evidence, and the broken line indicates a possible route.

typical of elsewhere in Greenland, where most clutches are started during the first two weeks of June (Melfoite 1985). Spring migration routes are summarized in Figure 9.

MASS CHANGES DURING MIGRATION

Autumn

Less detail is known of mass patterns during autumn than spring migration. The mass of birds departing from their breeding grounds is not known. Arrivals in Iceland in late July average about 110 g (Wilson & Morrison 1992). Average mass remains similar at about 140 g during July and August as a consequence of the continual arrival of light birds and the departure of heavy ones. Individual birds may increase mass rapidly, at c. 3 g/d and leave averaging 135 - 155 g (Wilson & Morrison 1992). The fat loads of departing birds are not known, but seem unlikely to exceed 15-20% of body mass. Those arriving in Britain at the same time have slightly lower average masses (about 120-130 g, Wilson & Morrison 1992). This may then increase slightly since a mass of c. 135 g is maintained during post-breeding moult (Boere 1976; Branson 1981). This mass pattern implies that *islandica* Knots, at least once they have reached their autumn staging area, do not need to store such a large fat reserve as in spring when it is needed for both breeding and survival on the breeding grounds.

Spring

To make the very long-distance flights between their breeding grounds and wintering and staging areas, *islandica* Knots accumulate large reserves of fat as fuel. They also increase the size of their pectoral muscles and protein reserves. The dynamics and functions of these reserves in spring have been recently described by Davidson & Evans (1986, 1988). Figure 10 summarizes the spring pattern of accumulation of total mass by *islandica* Knots at their various staging sites. Much of this mass gain is fat, but muscle protein mass also increases. There are several interesting features of this spring pattern. At early spring sites there is considerable variation between sites and years in the timing of mass accumulation and possibly also in departure timing. Birds depart, however, with similar average mass, of 185 - 195 g. Late spring staging area arrival mass is c. 135 - 145 g so Knots lose about 50 g of mass during the flight. This is only a partial depletion of fat reserves as birds arrive in northern Norway with 11-15% of their body mass as fat.

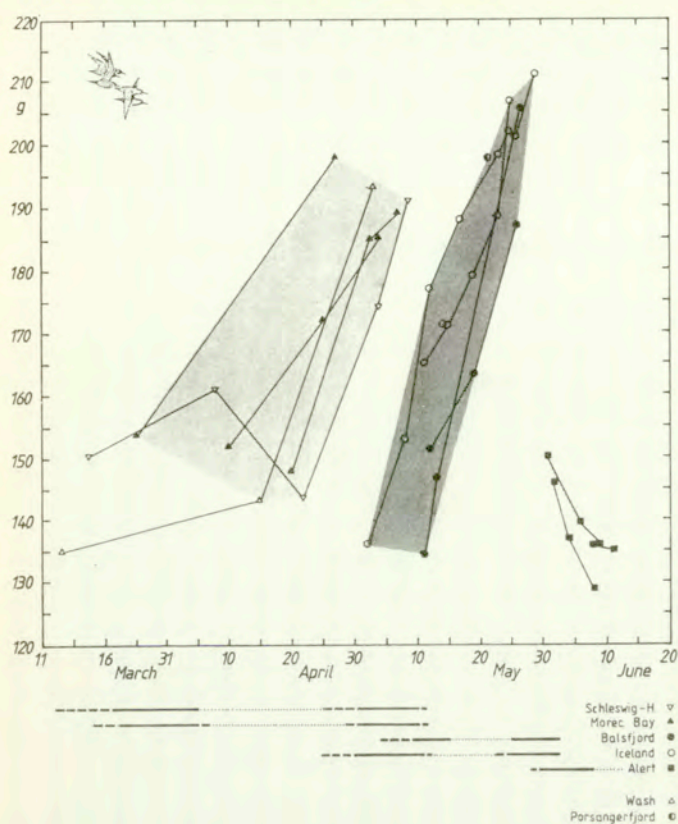


Figure 10. Summary of the patterns of total body mass of *islandica* Knots during spring. Light shading is early spring staging areas, heavy shading is late spring staging areas and vertical hatching is breeding grounds. Data points are mean values. Lines join points for a single year, except for the Wash and Schleswig-Holstein where data from several years is combined. Main arrival and departure periods for each area are shown as solid lines below the main figure, with dotted lines joining the arrival and departure period for an area. Sources are for Schleswig-Holstein: Prokosch (1988); Morecambe Bay: Prater & Wilson (1972); Balsfjord: Davidson & Evans (1986, 1988, unpubl.); Iceland: Prater & Wilson (1972), Wilson & Morrison 1992; Wash: Branson (1981), Davidson & Evans (1986); Porsangerfjord: Wood *et al.* (1988); Alert, Ellesmere Island: Morrison & Davidson (1990).

As for the early spring staging areas, there seems to be some variability between years and sites in arrival timing and mass on late staging sites. Rates of average mass gain (mostly fat) are rapid, in some years up to 3-4 g/d (see Evans 1992). However the variability diminishes as departure time approaches, such that departures at the end of May are mostly at similar mass (205 - 210 g). This implies that the birds are not always increasing mass at the maximum possible rate on their late spring sites, and there is some evidence from Iceland that individuals of lower than average mass early in May gain mass at a faster rate than heavier than average birds (Wilson & Morrison 1992). The departure mass of 205 g from Balsfjord represents 33.5% fat.

Departure mass in Balsfjord in one year (1985) appeared much lower (187 g) - see also Evans (1992). This sample was weighed shortly before most birds departed whilst that of the following year was caught immediately after the bulk of the population has left (pers. obs.). It is possible, therefore, that in Balsfjord the earlier departing birds are lighter than those departing later. Perhaps these birds are flying to nearer breeding areas such as east Greenland, with the later departing fatter birds flying to northern Canada.

Knots arrive on their breeding grounds in northern Ellesmere Island weighing an average of 143 - 150 g (Figure 10; Davidson & Morrison 1989; Morrison & Davidson 1990), a fat load of about 16% of body mass. Hence during a 3,000 km flight Knots use only about half their fat reserves. On the available evidence, total mass loss during the flight from Norway to Ellesmere Island is about 60 g, surprisingly little more than that apparently lost during the shorter flight of only 1,500 - 2,000 km between early and late spring staging areas. Perhaps weather conditions during the early May flight are less favourable than those in late May, so causing the birds to expend more energy during the flight. Alternatively the high mass loss of birds reaching Iceland and Norway may be illusory if the earliest (low mass) arrivals are birds that have left their early spring staging site earlier and lighter than is apparent from the peak masses shown in Figure 10. The reasons for this apparent discrepancy need further investigation, as does the apparent discrepancy in the mass lost during migration between Iceland and Britain and The Netherlands of 50 g in spring (Figure 10) and 25 g in autumn (Wilson & Morrison 1992).

Recent studies at Alert in northernmost Ellesmere Island have confirmed that the fat and protein accumulated at staging areas is only partly used to fuel the migratory flight there (Davidson & Morrison 1989; Morrison & Davidson 1990). Substantial reserves of both fat and protein are carried to the breeding grounds. Mass appears to then decrease rapidly (1.5 - 2.5 g/d) in the two weeks between arrival and breeding (Figure 10). Estimated daily energy expenditure during this period is high (Davidson & Morrison 1992), so it appears that these reserves are needed to aid survival after arrival on the breeding grounds, a time when food is scarce and weather conditions can be harsh. It remains possible, however, that this decline is an artefact of the later arrival of lighter birds (Morrison & Davidson 1990). Further detailed studies of birds arriving on

their breeding grounds are needed to examine this. Nevertheless the maintenance of fat reserves through into the breeding attempt may be vital, since there is evidence that only Knots that were heavier than average at the end of May in Iceland may have survived years in the early 1970s when weather conditions were very severe on the breeding grounds and breeding productivity very low (see Figure 6; Wilson in prep.).

CONCLUSIONS

Islandica is the most studied Knot subspecies, yet despite the great amount of knowledge of their life, it is surprising how many gaps emerge from this review of the migration system. Some have become apparent only recently since the discovery of the Norwegian spring staging areas and the way in which Knots use them. Amongst the most major gaps are the extent of the Canadian breeding grounds and the centre of the breeding population; the departure condition of birds leaving their breeding grounds and the routes they use; how many birds if any move direct between breeding grounds and western Europe, missing out Iceland in autumn and spring; the distribution of moulting birds in the Wadden Sea; whether there is any overlap of wintering grounds with *canutus* with some *islandica* possibly overwintering in Africa in some years; the extent to which individual birds use different late spring staging areas in the same and successive years, and how such a mechanism arises; the breeding grounds of birds staging in Balsfjord and Porsangerfjord; the departure condition of early and late departing birds from spring staging areas, and the relationship between timing, departure condition and distance flown; the extent to which fat and protein reserves are used after arrival on the breeding grounds; the body condition of birds leaving their breeding grounds in autumn and of those passing through Iceland; and the reasons for the apparent discrepancies in flight costs between western Europe and Iceland and Norway in spring and autumn.

Do we, however, really need to fill these gaps, since even with them we still know a great deal more about *islandica* Knots than other subspecies and other waders? The answer must be yes, since Knots are vulnerable birds. They depend on just a few key coastal wetlands for their survival during winter and migrations. Many of these wetlands are under threat of habitat degradation and habitat loss through land-

claim (Davidson *et al.* 1991). Such habitat loss may be a contributor to the continuing low population level of these Knots since the late 1970s (Smit & Piersma 1989). The effective conservation for these birds depends on understanding the role of the various places they use, yet some key sites such as Balsfjord have been identified only in the last six years, and the breeding grounds of most of the population are still unknown. Study of *islandica* Knots has provided the first evidence that arctic-breeding shorebirds take reserves of both fat and protein to their breeding grounds, and that these may be vital for their survival. Much still remains, however, to be understood about the links between spring body condition, migration, survival and breeding productivity of these Knots, let alone other subspecies and species. Such understanding is fundamental.

The evidence is overwhelming that Nearctic-breeding *islandica* use the wintering grounds and staging sites described in the review. Evidence reviewed in Piersma *et al.* (1992) is strong also that the longer-billed *canutus* that overwinter in Africa breed in Siberia. It has been generally supposed that these birds breed on the nearest Siberian breeding grounds, the Taymyr Peninsula (e.g. Underhill *et al.* 1989). Tomkovich (1987, 1992) has, however, recently produced evidence that Knots breeding on the Taymyr Peninsula have shorter bills than *canutus*, but bills of indistinguishable length to *islandica*. This raises the possibility that Taymyr-breeding birds could be overwintering in western Europe amongst *islandica*. Without ringing recoveries linking breeding and wintering grounds this may be very difficult to establish, but the information on Knots in western Europe and Africa warrants further appraisal. If Taymyr birds are wintering in western Europe then they might use north Norwegian spring staging sites along with part of the Nearctic *islandica* population. Use of these staging sites might explain the observations of spring migrant Knots along the Murmansk coast (P.S. Tomkovich pers. comm.). Whatever the migration system of the Taymyr birds proves to be it will almost certainly lead to a substantial modification of our understanding of Knot migration along the East Atlantic Flyway.

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