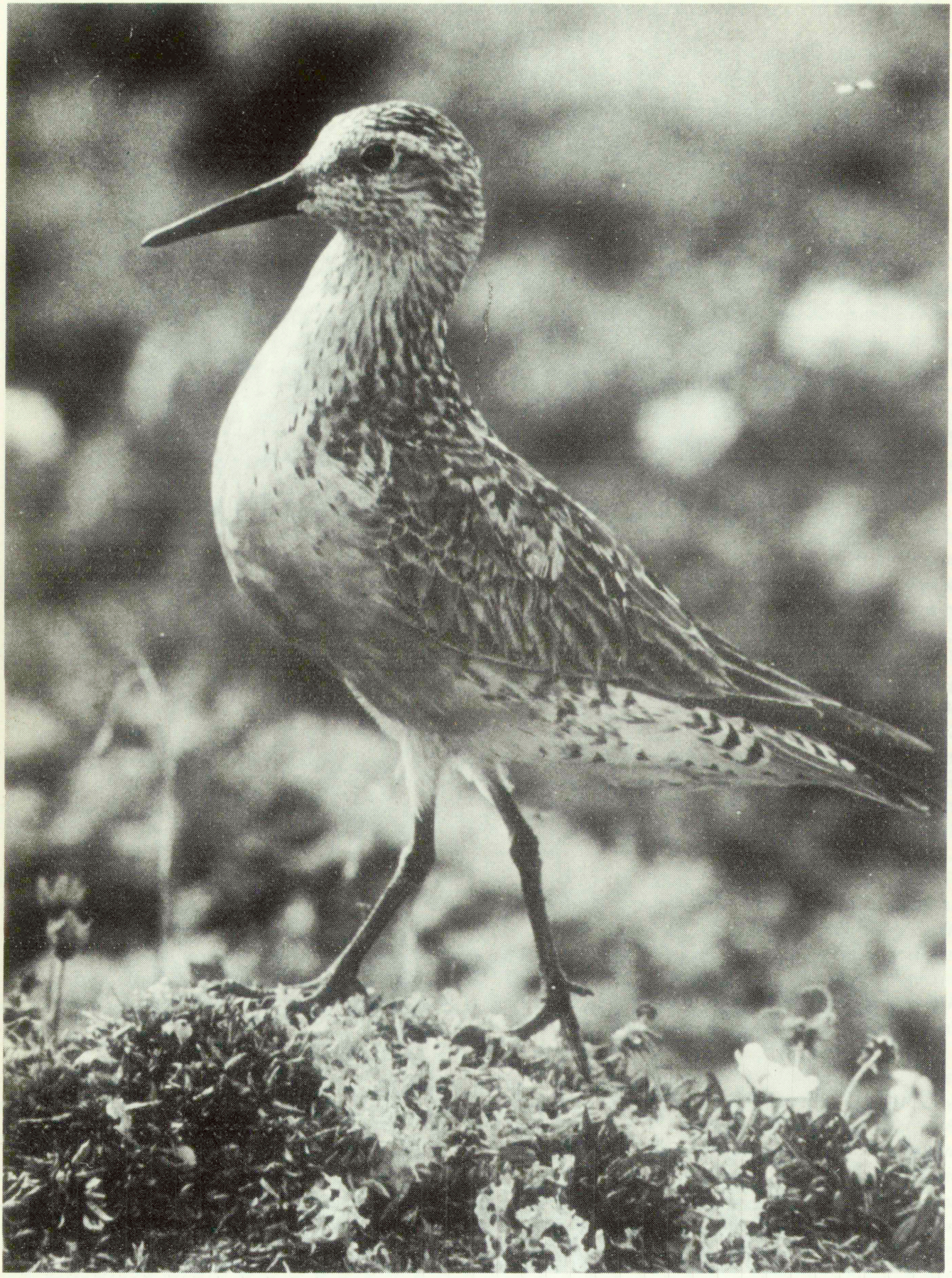

Introduction

Nick Davidson & Theunis Piersma

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'We have sought after truth, and sometimes perhaps we have found it. But did we have fun?' (Benjamin Jowett (1817 - 1893), Master of Balliol College, Oxford).

The migrations of birds have fascinated naturalists and scientists for centuries. During this time many explanations, often as outlandish as those proposed to account for the disappearance of dinosaurs, have been given to account for the sudden seasonal appearance and disappearance of bird populations. Although some ideas, such as the hibernation of swallows at the bottom of lakes, have yet to be supported by scientific evidence, others have proved to be more accurate. Wildfowler-naturalists such as Abel Chapman were writing with great perception in the late 19th century about the migrations of waders and wildfowl that breed in more northerly latitudes (e.g. Chapman 1889). Such people showed considerable understanding of the significance of seasonal variations in the fatness of waders and its significance to both their migrations and winter survival.

Once scientific ringing began in the 20th century our understanding of the origins and destinations of migrant birds increased dramatically and waders were used as dramatic examples of long-distance migration. For example Landsborough Thompson (1939) described waders as '... migratory in the very highest degree, performing journeys from their breeding-grounds in high northern latitudes to the extremities of the southern continents. The Knot is an example of a sandpiper of which this is true ...'.

For waders the leap in knowledge has been particularly large since the advent of first rocket-nets and then cannon-nets in the late 1960s. Operation of cannon-nets is a social skill. To catch and ring large flocks of waders requires the co-operation of an often large team of people, and it has often involved co-operation between professional scientists and amateur ornithologists. As described by William Dick in his foreword to this volume, such co-operation has subsequently been extended to international collaborations along whole migration flyways. This international communication between wader-workers in many countries is a particular feature of wader research. Indeed collaboration is an essential research tool if we are to understand the migrations of such mobile birds since it is practically impossible for a single researcher to collect the necessary data along the migration route so as to understand the migration phenology of such birds. This co-operative spirit, much of it facilitated through the role of the Wader Study Group, is especially well demonstrated by studies of Knots *Calidris canutus*. Indeed *canutus* subspecies Knots were the subject of the first international project co-ordinated by the Wader Study Group (Dick 1979).

Knots have been highly prized for centuries. Indeed they are supposed to have gained both their common and scientific names from King Canute's partiality to the flesh of the Knot, although alternative derivations come from the Knots tendency to stand 'Canute-like' in the edge of the waves and from their characteristic 'cnut' calls. During the medieval times many Knots and other waders were caught on estuaries such as the Wash and sold for the table. The dark flesh and fattiness of Knots, so characteristic of a long-distance migrant, made them a favoured meal, and there are even records from the 16th century of Knots being held in captivity and fattened for the table on a diet of grain - a curious parallel with the migration and energetics studies on captive Knots now being made (Piersma *et al.* 1991).

More recently many ornithologists and bird-watchers have been attracted to Knots, perhaps for many reasons. Knots have proved to be one of the most elusive of waders, especially in finding their breeding grounds and even then in finding their nests. Nethersole-Thompson & Nethersole-Thompson (1986) described the Knot as 'the blue riband wader that has tantalised and defeated so many great nest hunters' and Bent (1927) summarized the problem: 'Arctic explorers were baffled in their attempts to find the nest; and the eggs were among the greatest desiderata of collectors. This is not to be wondered at, however, when we consider the remoteness of its far northern breeding grounds, its choice of its nesting sites on high inland plains, its widely scattered nests, and its habit of sitting very closely on its eggs and not returning to them after flushing.'

The nest of the Knot was amongst the last of the European-migrant waders to be found. It was the only species that eluded Seebohm (1901) during his expeditions to Siberia, although we now know that when Seebohm reached the mouth of the Yenisei River in 1877 he was close to Knot breeding grounds on the Taymyr Peninsula.

Exactly who first found breeding Knots is rather uncertain. The first undoubted confirmation of breeding came as late as 1876 and then surprisingly from the northern extreme of their breeding range: Feilden (1877) found newly-hatched chicks at 82°33'N in northern Ellesmere Island, although Feilden comments that in 1820 Knots were reported as nesting in great numbers on Melville Island, much further south in the Canadian Arctic. The first nest seems to have been found in 1886 on the New Siberian Islands (Birulya 1907), and on the Taymyr Peninsula in Siberia the first nest was found in 1901 (Walter, reported in Bannerman 1961). A more detailed account of the search for Knot nests has been published recently by Vaughan (1992).

The circumstances surrounding the discovery of the first New World Knot nest adds to the romance of the species. On his return from reaching the North Pole, Peary overwintered at Cape Sheridan in northern Ellesmere Island. The following spring, in 1909, the Peary expedition found and photographed two nests a few kilometres to the south, close to Floeberg Beach where Feilden had first found Knot chicks. Even then, the discovery was not published until eleven years later and after Peary's death (Feilden 1920).

Even since then Knot nests have proved very difficult to locate and the breeding distribution remains patchily known. Even now major new discoveries are being made or anticipated. For instance it now seems possible that there are major undiscovered Siberian breeding areas (see Tomkovich 1992 in this volume). Also in this volume Godfrey (1992) describes a major breeding area extension in northern Canada. Enough is known of their breeding areas, however, to confirm that Knots are one of the most high arctic of breeding waders. Until recently very few ornithologists had travelled far north enough to meet breeding Knots. Knots' breeding plumage of bright russet underparts and spangled back blends perfectly with the browns and greys of early-season tundra. Such plumage is, however, seen by most ornithologists only briefly in late spring before birds migrate to the Arctic, and then again in early autumn as the birds return to moult. The large flocks of 'red' Knots on their spring staging areas such as Delaware Bay, the Wadden Sea and northern Norway are a remarkable sight. In spring Knots often seem to be even more excited than the researchers studying them, and from a distance the sound of a large flock singing and twittering resembles that of a tantalizingly distant waterfall.

On their wintering grounds an individual Knot in its winter plumage of soft grey seem to have little to excite the enthusiasm of ornithologists, yet here they make up for an individually dowdy appearance with spectacular behaviour. Away from their breeding areas Knots congregate in very few places in the world. These are almost invariably large areas of soft intertidal flats, chiefly estuaries and embayments, that support the abundant molluscs upon which Knots specialize for food. The size and inaccessibility of these places makes Knots often difficult to find and observe closely, but when located Knots are a spectacular sight. Knots gather in larger and more densely packed flocks than almost any other wader species. Roosting flocks can number tens of thousands, and when they fly to and from their roosts a flock at a distance resembles a swirling cloud of smoke. On the tidal flats feeding flocks appear like mobile grey carpets.

Although they are rather small compared to many other migrant waders and wildfowl - Knots generally weigh 120 - 200 g - Knots make some of the longest-distance migrations of any migrant bird. Knots breed as far north as there is land, to within 800 km of the North Pole in the Canadian Arctic (83°N), and migrate to overwinter as far south as New Zealand,

southern Africa and Tierra del Fuego (55°S), only 3,000 km from the South Pole. Studies in the 1970s on Knots migrating along the East Atlantic Flyway (Dick *et al.* 1976; Dick 1979; Dick *et al.* 1987) revealed a relatively simple migration pattern in which Knots make a few long-distance non-stop flights between wintering grounds, staging areas and breeding grounds.

The apparent simplicity and extreme nature of the Knot's migration has made it an attractive species for research within the world of waders, and also as a subject of broader-based research into bird migration and the energetics of survival and annual cycles. Studies of Knots, and other long-distance migrants such as Bar-tailed Godwits *Limosa lapponica* are now contributing to our understanding of the costs and benefits of migrating.

Since the investigations in Europe and West Africa in the 1970s there have been many further studies of Knots worldwide. As well as more research on the two subspecies *islandica* and *canutus* that occur in western Europe and Africa there have also been great advances in understanding of Knots migrating to South America, and even more recently about Knots in Australasia and the birds breeding in Siberia. Recent opportunities for international research on the Taymyr Peninsula in northern Siberia are producing particularly exciting information which, as described later, is set to make major changes to interpretation of the migration patterns of Siberian-breeding populations.

Arising from discussions amongst wader-workers at the 19th International Ornithological Congress in Ottawa in 1986 was a consensus that it would be useful to bring together Knot-workers from around the world to review the considerable recent advances in our understanding of the migration systems of Knots. In September 1989 the Wader Study Group (WSG) Annual Conference and the International Waterfowl Feeding Ecology Workshop (arranged under the auspices of the International Waterfowl and Wetlands Reseach Bureau in association with WSG) were held jointly in Ribe, Denmark. This provided the appropriate forum for a meeting about Knots, since it was attended by many wader-workers from around the world. During this week of meetings a workshop was held (on 21/22 September 1989) on 'Recent advances in understanding Knot migrations'. This volume is derived from that workshop.

The workshop aimed to review and compare the current knowledge of the migration systems of each subspecies of Knots, to hear reports of recent and future research on Knots around the world, and to identify gaps in the knowledge that remained to be investigated. It proved a valuable forum at which much new information was presented.

Our original intention in holding the workshop was to reach an assessment of the similarities and differences in migration strategy between subspecies of the Knot. This proved, however, to be a premature objective given the extent of the gaps in our understanding of the migrations of some Knot subspecies. Nevertheless, the information brought together at the workshop and in this volume has permitted a first attempt at a comparison of some of the features of the distribution and migrations of the Knot subspecies. This assessment forms part of the final section of this volume.

The structure of this volume closely follows that of the workshop it reports. The volume contains a total of 28 papers. It starts with four papers that describe the origins and distributions of Knot subspecies from a variety of viewpoints. The second section provides brief reviews of the migration system of each of the four subspecies (*C. c. canutus*, *C. c. islandica*, *C. c. rufa* and *C. c. rogersi*) that were recognized at the time the workshop was held. There then follow 18 reports of recent research on Knot migrations, all of which cover the two subspecies *canutus* and *islandica* during various times of year - perhaps a measure of the amount of research effort currently being expended on these subspecies. These sections include also two papers summarizing the extensive data collected in the early 1970s on Knots migrating through western Iceland (Morrison & Wilson 1992; Wilson & Morrison 1992). Although widely referred to for providing major clarification of the migrations of *islandica* Knots, much of this material has not previously been published. The volume is rounded off with two summary papers, the first giving a synthesis of the migrations and annual cycles of the various subspecies and suggested future directions for research on Knots. The second discusses conservation implications of our current knowledge about Knot distribution and migration.

Most of these papers are versions of those presented at the workshop. This collection of published papers differs, however, in several ways from that presented at the workshop. First, to provide a more comprehensive coverage of the subject we have

included several invited papers from people unable to attend the workshop. Second, and perhaps inevitably in a subject as active as Knot research, there have been some major and startling discoveries in the 2.5 years since the workshop was held. Some of these are a direct consequence of questions raised during the workshop (see e.g. Godfrey 1992). This has resulted in the need to update some of the papers. Perhaps most intriguing is Tomkovich's (1992) review of the subspecies in Siberia in which he identifies a fifth subspecies (*roselaari*), and throws doubt of the presumed location of the breeding areas of the *canutus* subspecies. Without delaying the publication of this volume even further it has, however, not been possible to fully integrate all this new information into all the papers.

The various subspecies of Knots have been described by a great variety of English names, many of which are not really appropriate. The *islandica* subspecies is often called the 'Nearctic Knot', but this is not very helpful since there are two subspecies that breed in the Nearctic (*islandica* and *rufa*). To avoid ambiguity we refer, where necessary, to *islandica* as the 'European-wintering Knot'. Similarly we refer to the *canutus* subspecies as the 'Afro-Siberian Knot', although the precise location of its breeding area now seems unclear (Tomkovich 1992). The *rufa* subspecies traditionally has been known as the 'Red Knot' in North America. This is unfortunate since in plumage colour this is the palest and least red of the subspecies, but we have nevertheless retained this common usage in those papers that refer to *rufa*. The *rogersi* subspecies also is known as the 'Red Knot' where it occurs in Australia (and as the 'Lesser Knot' in New Zealand) - a more appropriate title since this is a much redder subspecies. Furthermore in Australia there is a need to distinguish *C. canutus rufa* from the Great Knot *C. tenuirostris* which also overwinters there. In general, however, we use the subspecific scientific names throughout these proceedings to give unambiguous distinction between subspecies.

It may seem extravagant to devote an entire volume of over 200 pages to the migrations of just one species. We believe, however, that the Knot is a species that provides an excellent subject for investigating broad biological phenomena, so that the lessons to be learnt from understanding Knot migrations have a much wider application than just for this species. Furthermore, innovative research often depends for its success on the enthusiasm and excitement of researchers. Wader-workers often form enthusiastic and communicative flocks, and the studies of Knots and their migrations that are reported in this volume amply illustrate the success of this strategy for the survival of healthy research.

This volume provides a progress report on Knot research, but it is clearly not the end. Perhaps inevitably, Knot migrations are proving much less simple than was believed, and there are certainly many more exciting discoveries to be made about this enigmatic species. We hope that this volume will provide help, direction, and stimulation to researchers to discover more about Knots and other waders. For example, there is this tantalizing little-known Great Knot .....

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