The migration of Knots: conservation needs and implications

Nick Davidson & Theunis Piersma

Davidson, N.C. & Piersma, T. 1992. The migration of Knots: conservation needs and implications. *Wader Study Group Bull.* 64, *Suppl.*: 198-209.

In the light of the substantial recent increases in knowledge of Knots *Calidris canutus* we assess how much of the information needed to underpin national and international conservation of the species is currently available. Most of the main wintering, migration staging and breeding areas are known for most subspecies, but large gaps in even basic knowledge remain, especially for breeding areas and the non-breeding distribution of subspecies *roselaari*. Knowledge of links between elements of site networks, and the key characteristics of individual site use, is improving but patchy. There are many national and international conservation designations applied to Knots and their habitats, but the extent of site safeguard varies greatly between subspecies, location and stage in annual cycle, with breeding grounds poorest represented. Despite the extensive safeguards, there remain many threats to the maintenance of Knot populations, notably habitat loss and degredation. An overall conservation strategy for Knots must provide for safeguarding both their few widely separated non-breeding sites and very extensive areas of arctic breeding habitat. Knots are better known than many other migrant waders and provide an excellent subject for developing a flyway conservation strategy for a wader species, in line with new international initiatives for the conservation of migratory animals.

N.C. Davidson, Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough PE1 1JY, U.K.
T. Piersma, Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, and Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

INTRODUCTION

Wetlands and their wildlife are regarded as one of the world's most threatened of ecosystems. Their destruction and degredation often threatens the natural resource base used by local human populations as well as that depended on by wildlife (e.g. Dugan 1987; Finlayson & Moser 1991). Much conservation effort has been directed nationally and internationally at wetlands and their wildlife, through a wide variety of domestic wildlife conservation legislation and through international directives, conventions, treaties and agreements. A major part of the implementation and progress in international conservation, particularly for coastal wetlands, has been made through actions undertaken to safeguard migratory waterfowl and their habitats (Smart 1987; Salathé 1991).

Much of the conservation action for wetlands and waterfowl is taken by national governments by their identification and safeguarding of nationally and internationally important sites both for total waterfowl numbers and assemblages and major parts of individual populations. Increasingly there is recognition that this site-based conservation needs to be set into a 'flyway framework' of understanding the role of individual sites in the annual cycle of waders and other waterbirds. Hence the conservation of migratory birds such as waders is increasingly directed towards the maintenance and enhancement of populations in their range and distribution. This is attempted through internationally agreed principles of wise and sustainable human use of habitats throughout the flyways, used by the birds as they move between their breeding and wintering areas. Alongside this broad-based approach there is also increasing development of protection measures for individual species. These include species conservation plans, for example the White Stork *Ciconia ciconia* (Goriup & Schultz 1991) and the Greenland White-fronted Goose *Anser albifrons flavirostris* (Stroud 1992).

Conservation planning and management is most effective when founded upon a sound understanding of how the waterfowl use the areas and habitats on which they depend. In 1987 the Wader Study Group brought together a broad overview of current levels of knowledge of wader flyways worldwide, and descriptions of a variety of flyway conservation approaches from different parts of the world (Davidson & Pienkowski 1987). It concluded that there were still substantial gaps in basic knowledge about the locations of important wader wintering sites in some parts of the world, that the role and value of migration staging areas, and large-scale quantitative information about breeding grounds were even less well-known. Furthermore to develop sound conservation cases in the developed world often requires detailed information about the way in which waders use particular sites and the links between sites. This is often unavailable (Davidson *et al.* 1987; Smit & Piersma 1989).

The present volume on the migration of Knots (Piersma & Davidson 1992a) in part follows on from Davidson & Pienkowski (1987) by making a more detailed review and synthesis of the worldwide migrations and distributions of just one species. This species for various reasons has been the subject of conservation worldwide research, especially over the last 20 years. The fruits of this research permit here an assessment of the extent to which our current knowledge of the biology of Knots provides a sound basis for its conservation. The Knot is considered one of the best-known of migratory waders, and one which has a relatively simple migration system involving long flights and few major wintering and staging areas. Hence such an appraisal can help also to give insights into the state of the conservation base for other migratory wader species, and indeed for other groups of migratory birds.

In the paper we first briefly summarize some of the key features of Knot annual cycles and comment on the types of information needed to develop soundly-based conservation planning and management. We then review the current flyway and site measures applied to the conservation of Knots, assess the extent to which the different subspecies are protected at each time of year and comment on the efficacy of these safeguards.

ESSENCE OF KNOTS: GENERAL CHARACTERISTICS OF KNOT ANNUAL CYCLES

From the increasingly extensive body of knowledge included in the reviews and detailed studies of Knots elsewhere in this volume some general characteristics of how Knots use, and move between, sites during their annual cycle emerge. These identify essential elements for which provision is needed in any conservation strategy if Knots are to be safeguarded effectively throughout their range. This knowledge is listed in Table 1, and summarized below.

1. Knots make some of the longest direct migrations of any wader (and of any bird species). As a result they link countries in many parts of the world from the highest Arctic to the southern parts of Africa, South America and Australasia. Knots occur on all major coastal flyways, although they do not use the predominantly inland flyways such as those through East Africa and west and central Asia.

2. Each subspecies is dependent on just a few widely spaced staging areas, and they are therefore highly vulnerable to damage or destruction of these few places. Breaking just one link in the network may risk jeopardizing the whole migration system of a subspecies.

3. To make these long migrations involves large energetic expenditure. To meet this energy demand Knots store substantial fat reserves (up to at least

Table 1. Major characteristics of Knot populations and their migrations relevant to conservation strategy.

- Very long migrations, on all major coastal flyways;
- Dependent on a few widely spaced staging sites;
- Need abundant food to store fat rapidly for migratory flight;
- In non-breeding season entirely coastal, chiefly large areas estuaries and bays;
- Occur in large flocks on few wintering areas;
- Mollusc specialists; need to be mobile to exploit annual variations in prey abundance;
- Need severe weather refugia in colder parts of wintering range;
- Need emergency staging areas when adverse weather met on migration;
- Abundant food supply on late spring staging areas essential for storage of fat and protein reserves needed for breeding ground survival;
- Widely dispersed at low densities on arctic tundra breeding grounds;
- Small subspecific population sizes, and genetically homogeneous;
- Vulnerable to global warming and rising sea-levels.

35% of body mass) and increase muscle size to power the flight. To accumulate reserves Knots need abundant food supplies available close to the surface of sediments (because they have short bills) at times of year and in geographical locations suitable as migration staging areas. Likewise late winter food supply must have sufficiently high availability to permit Knots to fatten for flight to their early spring staging areas. Meteorological and seasonal constraints mean that Knots migrate on a tightly timed schedule and must achieve rapid rates of mass gain.

4. Outside the breeding season Knots are almost entirely coastal, occurring chiefly on large estuaries and embayments with extensive areas of muddy sand, although some do also use rocky shores. In winter (and on staging sites) they occur mostly in large flocks on fewer estuaries than most other waders. Even so, in some parts of their range such as in Britain, an important part of the world population is dispersed around smaller estuaries.

5. Knots are mollusc specialists *par excellence* and in many places depend particularly on small bivalve molluscs such as *Macoma balthica*. In temperate and tropical estuaries Knots can depend for food on only one year-class of their preferred prey, after which the molluscs have grown too big to swallow. Since spatfall and recruitment of these molluscs varies greatly from year-to-year, sufficient different and large enough sites need to be safeguarded so as to ensure that a food supply (from spatfall) is available in each year. Knots need to be mobile to be able to exploit this variable resource. Knots show this mobility in several parts of their wintering range (e.g. Britain and Patagonia). Similarly in northern staging areas (notably northern Norway) extensive spring ice cover can reduce the available area for feeding and this appears to cause more birds to use alternative staging areas. Thus Knots depend on within-season as well as between-season site networks.

6. In northern wintering areas (chiefly for *islandica* Knots) alternative wintering areas in milder parts of the wintering range need to be safeguarded as cold weather refugia.

7. Their long flights make Knots vulnerable to adverse weather conditions, notably strong headwinds *en route*. Such conditions cause Knots to exhaust their fat reserves more rapidly than is apparently anticipated. Under such circumstances Knots need alternative 'emergency' staging areas at which to pause and store additional reserves to enable them to reach their main staging destination. This phenonenon has been shown so far for *canutus* Knots pausing in western France (before trying to reach the Wadden Sea) and may occur also in *islandica* Knots pausing in west Greenland.

8. Safeguarding late spring staging areas with abundant available food is particularly important since these provide Knots with their last opportunity of compensating for shortfalls in nutritional condition induced by problems (e.g. adverse winds) earlier during migration. At such times Knots in relatively poor condition need to accelerate feeding rates to achieve elevated rates of mass gain. There is now evidence that departing from late spring staging areas in good nutritional condition increases adult survival through particularly severe weather conditions on breeding grounds, and that such periodic summer mortality (and associated low juvenile production) is a major factor influencing population dynamics.

9. In marked contrast to their non-breeding behaviour and distribution, in the breeding season Knots are widely dispersed over very large areas of arctic tundras, and breed at very low densities (e.g. 0.1 pair/ha on Taymyr, 0.01 pair/ha in most of Greenland/northern Canada range). Safeguarding breeding Knots therefore depends chiefly on broad land-use policies, rather than solely site safeguard.

10. Subspecies of Knots have small populations, even by comparison with other waders - all of which are relatively scarce in comparison with many other bird species. The most abundant Knot subspecies, *canutus*, is currently estimated at 516,000 birds. Some populations are much smaller, notable *rufa* with 125,000 birds, and *roselaari* whose population may be as small as 20,000 birds. Furthermore Knots are markedly genetically homogeneous compared to other birds, so that their plasticity may be smal which perhaps increases their vulnerability to environmental change (Baker 1992).

11. Knots worldwide may be vulnerable to several likely effects of a continuing rise in global temperatures. Rising sea-levels may reduce the extent of suitable feeding grounds on the coastal wetlands used in winter and on migration, particularly where the natural shift inland of coastal ecosystems in response to rising sea-levels is prevented by man-made sea-defences and urban and industrial developments. Some predictions of global warming also indicate a reduction in the overall areas

of arctic ecosystems, which may reduce the extent of suitable Knot breeding habitat.

An overall conservation strategy for Knots must therefore provide for safeguarding their rather few and widely separated wintering and staging sites in many different countries, ensuring that such sites are managed to retain the particular characteristics (such as those listed above) that result in their importance to Knots. But the strategy must, however, provide also for continued appropriate land use of the very extensive areas of arctic tundras that are largely remote from direct influence of most human activities.

DO WE KNOW ENOUGH TO SAFEGUARD KNOTS?

The overall features of Knot biology listed above provide guidance for the broad elements of conservation strategy for Knots. Within this framework, however, more specific information is needed about distributions and annual cycles for each population and flyway to direct conservation effort towards developing and maintaining appropriate safeguards for sites and areas used by Knots. To develop effective conservation measures, conservation planners need to know:

- Where are the sites used?
- What is the ecology and population dynamics of Knots?
- What role does each site play in the annual cycle, and how is it related to the usage of other sites on the flyway? and
- What features of each site result in it being used by Knots?

These are deceptively simple questions that are needed to underpin the identification of sites and the development of safeguard programmes. In addition further information is often essential to provide appropriate direction in the development of initiatives such as estuary conservation plans and integrated coastal zone management schemes, and in defending sites used by Knots against activities that would destroy, damage or degrade sites.

Particularly in the developed world substantial understanding and detail of how a species such as the Knot uses an estuary (which may differ between years and between estuaries) can be needed to provide a high-level case for site defence within the tight legal framework surrounding development proposals. Impact assessments for such issues, and background information for directing conservation management, often need to know:

- What pressures threaten continued usage of the site; and
- What are the constraints on site use?

Below we comment on whether current knowledge of Knot distribution and migration is sufficient to address these points. The situation is also summarized in Table 2.

Population size and trends

The only subspecies for which there is good information about both population size and trend is *islandica*, which benefits from the extensive and regular estuaries counting progammes carried out in much of its west European wintering range. These have permitted identification of a major decline in population since the early 1970s (see Davidson & Wilson 1992;

Table 2. Is knowledge of the key features of flyway use by Knots *Calidris canutus* sufficient for developing conservation action?

Topic	Level of knowledge				
	canutus	*islandica*	*rufa*	*rogersi*	*roselaari*
Population size & trend	☺☺	☺☺☺	☹	☹	☹
Breeding location	☺☺	☺☺	☺☺	☹	☹
Non-breeding location	☺☺☺	☺☺☺	☺☺	☺☺	☹
Site roles & links	☺☺☺	☺☺☺	☹	☹	-
Key features of sites	☺☺☺	☺☺☺	☺☺	☹	-
Pressures on sites	☺☺☺	☺☺☺	☹	☹	-
Constraints on site use	☺☺	☺☺	☹	☹	-

Level of knowledge: ☺☺☺ good, ☺☺ fair, ☹ poor, - none

Boyd 1992). Annual indices calculated since 1971 for the U.K. wintering population have shown only a slow increase in numbers. Although there is increasing evidence that it was severe weather during late spring and early summer that led to the early 1970s population decline, the reasons for the only slow recovery are less clear. Little else is known about the factors affecting the population dynamics of *islandica* Knots, and almost nothing about population trends in other subspecies.

The population estimate for *canutus* Knots is based on infrequent (and sometimes incomplete) counts of birds wintering in West Africa, supported by interpretation of spring counts on the Banc d'Arguin (Piersma *et al.* 1992).

For the other three subspecies there are still considerable uncertainties about the population sizes, let alone trends in populations, since not all wintering and staging sites are believed to have been identified (see below). Some information about population trends in *rufa* comes from the International Shorebird Survey (ISS) (Howe *et al.* 1989), but largely from the USA - outside the main wintering range of the subspecies.

In general, therefore, very little is known of the factors that affect the population dynamics of most Knot populations, except that weather on migration and breeding grounds may be a key factor affecting the populations. Very little is known about whether Knot populations are currently artificially depressed as a consequence of earlier (or current) human pressures such as hunting. Hunting in the second half of the 19th century is known to have had a major impact on many wader species (notably the Eskimo Curlew *Numenius borealis*; Gollop *et al.* 1986). Many waders are still hunted extensively for food in many parts of south-east Asia and this hunting is believed to have contributed to population declines in some species (Parish & Howes 1990). Tubbs (1991, in press) has recently speculated that the populations of several waders in Britain are only now recovering from extensive wildfowling pressure that continued until the mid-20th century. Habitat loss and damage is also regularly implicated as a pressure on Knot populations (e.g. Davidson *et al.* 1991), but the extent to which these factors have affected population dynamics remains to be clarified.

Site locations, usage and links

The location of wintering and migration staging sites of *islandica* and *canutus* in Iceland, western Europe and Africa now appear to be clearly identified, and population sizes on known sites at different times of year generally tally well (Davidson & Wilson 1992; Piersma *et al.* 1992). Even for these best-known subspecies, there have, however, been major site discoveries within the last 10 years. These include the presence of large spring Knot populations in Balsfjord in northern Norway (Strann 1984), and that this site and Porsangerfjord is used *islandica* Knots (Davidson *et al.* 1986). For *canutus* the major wintering area Archipélago dos Bijagos in Guinea-Bissau was not discovered until 1981 (Fournier & Dick 1981). Furthermore there remains uncertainty about whether *canutus* Knots fly directly from the Wadden Sea to Siberia in spring, or whether some stage in the White Sea area. Recent discoveries about the body size of *canutus* breeding on the Taymyr Peninsula in Siberia also raise a possibility that some *canutus* may overwinter amongst *islandica* Knots in western Europe.

There remains more uncertainty about the breeding grounds of *islandica* and *canutus* Knots. Godfrey (1992) has only recently confirmed that *islandica* Knots breed across a much larger area of the Canadian Arctic than was previously supposed, but the precise location of the main centre of their breeding is not yet clear. International studies, many since 1985, have confirmed that high densities of *canutus* breed on the Taymyr Peninsula, largely within 50 km of the coast, but there remains uncertainty about whether another part of the *canutus* population breeds further inland in Yakutia (Piersma *et al.* 1992).

For *rogersi* we know nothing about the location or use of autumn staging areas north of Australia (Barter 1992). Although many Knots have been found in autumn in the Gulf of Carpentaria in northern Australia, the extent to which this area is also a wintering site or used during spring migration, perhaps by birds wintering in southern Australia, is not clear. In spring the area of China around the mouth of the Yellow River is a staging area, but the numbers using this site and whether there are other staging sites is unknown (Barter 1992). There is also very little known of the extent and population densities in the breeding area now considered by Tomkovich (1992) to be the Chukotski Peninsula in east Asia.

Similarly, the main locations of the staging sites in North America and wintering areas in South America are known for *rufa*, much of the detail of the latter

coming in the last five years (Morrison & Ross 1989). There are nevertheless uncertainties over the precise location and extent of both autumn and particularly spring staging sites in South America, especially in northern Brazil. Although it is clear that birds migrate from North to South America and from there to Patagonia the sites and routes used in this latter part of the migration are very uncertain. There is also a major discrepancy in the total population estimate between winter and spring suggesting the presence of other undiscovered major staging areas for *rufa* (Morrison & Harrington 1992). The extent and patchiness of *rufa* breeding areas in northern Canada are also very poorly known.

There is a further major uncertainty surrounding the small wintering population of Knots in the southern U.S.A. and central America. Its population size and wintering grounds are very poorly known, and it seems that this population may now be called *roselaari*, which is thought to breed in Alaska and on Wrangel Island (see Baker 1992; Piersma & Davidson 1992b). Nothing is known of the migration routes and staging areas used by the *roselaari* breeding population, nor whether any overwinter amongst *rogersi* Knots in Australasia. Furthermore although part of this population is thought to breed in northern Alaska, very few nests have been found and the size and distribution of the breeding population is not known.

Finally two major coastal wetland systems in southern Alaska, the Copper River Delta (Isleib 1979) and the Yukon-Kuskowim Delta (Gill & Handel 1990), have been reported to hold over 100,000 Knots in late spring. These are presumed to be *roselaari* heading for Wrangel Island and northern Alaska and/or *rogersi* en route to the Chukotski Peninsula, but little more is known. It is not clear, for example, whether the two deltas are used simultaneously (i.e. perhaps a total of over 200,000 birds). The two deltas might instead be used as alternative sites in different years (cf. the usage of Balsfjord and Porsangerfjord in Norway; Strann 1992).

Other features

From this appraisal it becomes clear that although enough is known to direct conservation action at many of the major Knot sites worldwide, there are still sites on most flyways for which there is uncertainty about the identity the the birds present, the precise nature of the role of the site in the birds' annual cycle, or the extent of the area used (especially for breeding areas). Furthermore there appear to be undiscovered Knot sites on most flyways.

With there still being some considerable gaps in the most basic information about the locations and migrations of Knots, it follows that answers to the more detailed questions needed to safeguard individual sites are known even now for only a few parts of the migration system. It is also likely therefore that for other wader species site location information is unlikely to be more comprehensive. For those species with less clearcut migration systems overall understanding of site usage, flyway links and constraints is probably poorer, although comprehensive flyway-wide appraisals are generally lacking.

Similarly, although patterns of human pressure on Knots are not yet clear worldwide, there are known to be many places in which Knots occur that are under intense pressure of habitat damage and loss, and a variety of other anthropogenic activities (see e.g. Davidson *et al.* 1991). Such information about individual sites and general problems is, however, often enough to direct the general principles of the habitat safeguard that is essential to conserve birds such as Knots.

HOW ARE KNOTS CONSERVED?

Although there is a need for more detailed knowledge on which to base conservation coverage of Knots throughout their world range, there are already many forms of conservation applied to areas in which Knots occur, and in some cases these places are designated specifically for their Knot populations. Here we briefly describe some of these measures, and then attempt to assess the extent to which they afford safeguard to Knot populations.

There are a wide variety of conservation measures taken in different countries that contribute to providing safeguards for parts of Knot populations. Many of these are site-related designations, some specifically intended to provide wildlife conservation cover for habitats and migrant waterfowl populations. Others are landscape designations providing broad land-use safeguards often compatible with maintaining nature conservation interest. Some measures are operated through domestic legislation; others are placed through non-statutory safeguards such as nature reserves managed by voluntary nature conservation bodies. There is often considerable variation between countries in the ways in which conservation is delivered, and in the strength of safeguards achieved by the suite of conservation measures.

In addition an increasing number of countries are party to international conventions such as the *Ramsar Convention* on wetlands especially as waterfowl habitat, the *Berne Council of Europe Convention* on the conservation of European wildlife and natural habitats and the *Bonn Convention* on the conservation of migratory species of wild animals, and international law such as the *European Communities 1979 Directive* on the conservation of wild birds and the *1992 Directive on the conservation of habitats and species*. Other international conservation agreements are bilateral agreements between countries sharing migratory bird populations (Biber-Klemm 1991). Major international measures that apply to parts of the worldwide Knot populations are listed in Table 3. For more general descriptions of the application of these measures, and their relevance to migratory waders see Davidson & Pienkowski (1987), Davidson *et al.* (1991), Salathé (1991) and Biber-Klemm (1991).

Some measures have considerable relevance to the conservation of Knots. One such is the *Western Hemisphere Shorebird Reserve Network* (WHSRN) which has become a highly successful international, but non-statutory, mechanism for raising support and awareness of the importance of key wetland sites for American waders since its inception in 1985 (see Myers *et al.* 1987). WHSRN now has four categories of reserves: hemispheric, international, regional and endangered species, and by 1991 there were 12 hemispheric, 4 international and 1 regional WHSRN reserves covering about 1.5 million hectares (Hunter *et al.* 1991). Several WHSRN reserves are very important coastal wetlands for *rufa* Knots, notably the Copper River Delta in Alaska, Delaware Bay in the eastern U.S.A. and Lagoa do Peixe, Brasil, and the WHSRN network appears to provide a major contribution to safeguarding *rufa* Knots during their non-breeding season.

Table 3. International conservation measures and agreements relevant to waders and their habitats.

A. Worldwide
- Ramsar Convention (1971)
- World Heritage Convention (1972)
- CITES (1973)
- Bonn Convention (1979)

B. Europe/Africa/West Asia
- Berne Convention (1979)
- EEC Wild Birds Directive (1979)
- African Convention (1968)
- EC Habitats and Species Directive (expected '92)

C. East Asia/Australasia
- Bilateral agreements:
- U.S.A., Japan, China, Australia, India, ex-U.S.S.R.
- e.g. JAMBA (Japan-Australia Migratory Birds Agreement)

D. Americas
- Protection of Migratory Birds Convention (1916)
- Protection of Migratory Birds & Game Mammals Convention (1936)
- Western Hemisphere Convention (1940)
- U.S.-Japan Migratory Birds Convention (1976)
- U.S.-U.S.S.R. Migratory Birds Convention (1976)
- Western Hemisphere Shorebird Reserve Network (WHSRN) (1985)
- North American Waterfowl Management Plan (NAWMP) (1986)

Other international designations also make a major contribution to Knot conservation, notably the Ramsar convention. By 1992 there were a total of over 500 Ramsar-listed wetlands distributed amongst the 52 contracting countries worldwide. Figure 1 shows the distribution of Ramsar sites supporting Knot populations. Worldwide there are 24 Ramsar sites that are internationally important for Knots (each supporting >1% of a biogeographic population), and a further 24 sites in which Knots regularly occur in smaller numbers.

With over 5% of all Ramsar sites being important for Knots it would seem that the species is well covered by this international designation. Figure 1 shows, however, that coverage, which in part reflects the geographical distribution of contracting parties to the Convention, is not equally distributed across Knot migrations systems. Except that many important parts of the Australasian wintering range of *rogersi* Knots are Ramsar sites, almost all the Ramsar sites of importance to Knots are on the East Atlantic Flyway and so support *canutus* and/or *islandica* subspecies. In total, 14 (58%) of Ramsar sites internationally important for Knots are in Britain and the southern North Sea, so supporting migrant and wintering *islandica* and migrant *canutus*. A major part of the wintering population of *canutus* in the Banc d'Arguin, Mauritania, is also within a Ramsar site. There is very little Ramsar site coverage for the Western Hemisphere subspecies *rufa* and *roselaari* (Figure 1), and the dispersed breeding populations of all subspecies are afforded little safeguard by this site-based designation.

Clearly there is great variation at national level in the extent to which the habitats important for Knots are safeguarded by the various international desig-

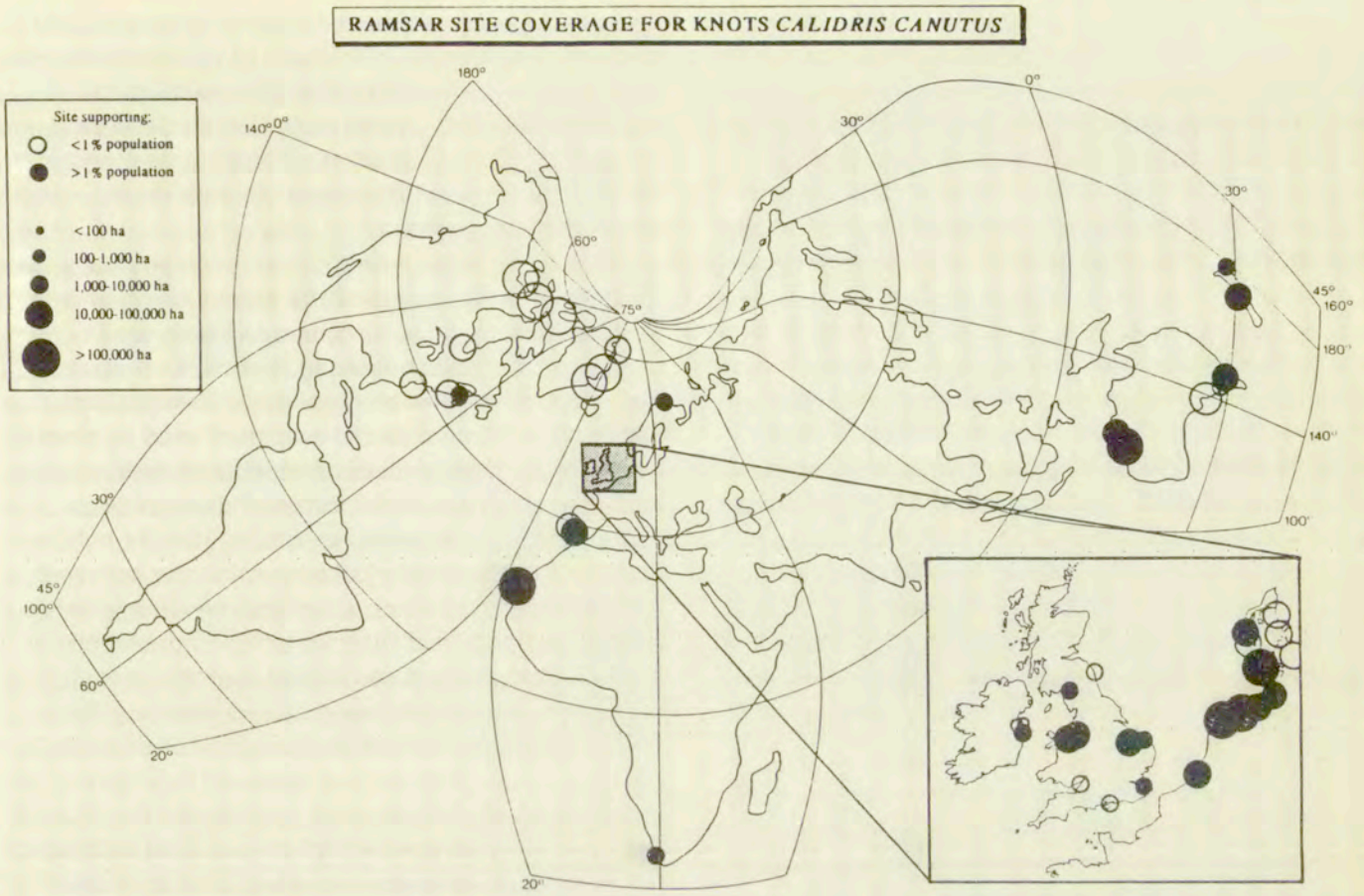

Figure 1. The distribution and size designated Ramsar sites (wetlands of international importance) that regularly support more than 100 Knots. Filled symbols show sites that are internationally important for a Knot population (i.e. the site supports >1% of a biogeographical population). Note that some sites support Knots in more than one season, some support populations of both *canutus* and *islandica* Knots, and some provide only partial coverage for the coastal sites used by Knots.

nations. In Europe the international conservation of migratory waterfowl is achieved through both the Ramsar Convention and the EEC Wild Birds Directive. Amongst the measures in this directive, member states are required to designate Special Protection Areas (SPAs) for migratory waterfowl such as Knots to ensure their survival and reproduction within their area of distribution. In The Netherlands, Germany and Denmark almost all the international Wadden Sea is designated as Ramsar/SPA sites so affording safeguard to almost all migratory *canutus* and many staging and some wintering *islandica*. In Britain the pattern is more complex. At present about 56% of the British wintering population of *islandica* (38% of the international population) is within designated Ramsar/SPA sites in midwinter (Davidson *et al.* 1991). However many more Ramsar and SPA sites in Britain await designation, and Stroud *et al.* (1990) estimated that overall 97% of the British wintering population (63% of international population) are within the proposed SPA network in Britain. Many of these British estuaries of importance to Knots are, however, already listed as Sites of Special Scientific Interest (SSSIs), the main British statutory nature conservation designation, and parts of the network also fall within many of the other statutory and non-statutory conservation designations (see e.g. Davidson *et al.* 1991). Similarly most of the important areas of habitat for Knots in southern Australia are safeguarded, whilst two of the major areas in north-east Australia are Ramsar sites (Lane 1987).

No detailed assessment of the extent to which Knots are afforded conservation assessment throughout their range has been made. Figure 2 presents a first broad attempt to make such an assessment. This confirms the pattern described for just Ramsar sites: that there is great variability between subspecies and within a subspecies at different times of year. Some subspecies, notably *rufa* and *rogersi*, are poorly safeguarded (at least by site designations) at most or all times of year. For others such as *roselaari* knowledge of the sites used is too poor to allow an assessment of conservation coverage. *Canutus* seems to have most

consistent cover, with over two-thirds of the population within conservation sites throughout most of the annual cycle - largely because of designations covering the Wadden Sea and Banc d'Arguin. Similarly *islandica* is well protected on wintering and staging areas in western Europe, but there is little or no site protection on late spring and early autumn staging in Iceland and Norway.

As for Ramsar site coverage, overall conservation site coverage is poorest during the breeding season, when Knots are dispersed at low density over large high arctic areas. Such dispersed populations are not readily safeguarded by designating sites, since even very large areas such as some national parks and Ramsar sites in arctic Canada hold only small parts of the population. An exception is *roselaari* whose breeding grounds on Wrangel Island are a strongly protected nature reserve. Similarly a large part of the known breeding grounds of *canutus* are currently also planned to form the Great Arctic Reserve Taymyr with a similarly strong level of protection.

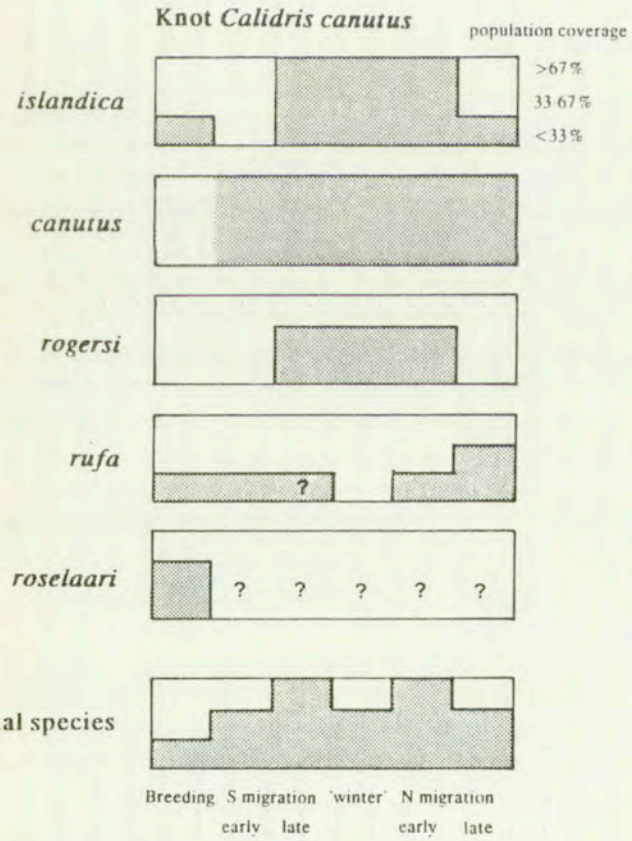

Figure 2. Estimated proportions of Knot populations occurring within designated conservation sites during different stages of their annual cycle. Conservation designations include both domestic and international designations. The light shading for breeding *canutus* indicates a large nature reserve designation currently proposed to cover a substantial part of their known Siberian breeding range (P. Prokosch pers. comm.).

Overall, because *canutus* and *islandica* numerically dominate the species, the levels of protection for the species as a whole are best in late southwards migration and early spring migration as birds pass through northern hemisphere staging areas, and at no other time of year is more than two-thirds of the population safeguarded.

This analysis has assessed the extent to which site designations intended to conserve Knots are in place, but this does not mean that all such places are safe from further anthropogenic damage and destruction. Many types of wetlands used by Knots have already been under continued pressure of drainage, land-claim and other forms of damage and degradation for centuries, particularly in the northern hemisphere. Partly as a consequence, the domestic and international conservation framework applied to coastal wetlands and their waterfowl populations is highly developed in these places, but this does not necessarily seem to act as a strong deterrent for further land-claim and other damage. For example Davidson *et al.* (1991) have assessed land-claim pressures on British estuaries, and found that there is a continuing piecemeal loss of estuarine habitats for many purposes such as rubbish and spoil disposal, marinas and leisure developments, road schemes, barrages, and docks and ports. Further habitat losses are affecting parts of estuaries identified as SSSIs and those estuaries known to be internationally important. Such patterns of land-claim are not consistent with international committments to the sustainable use of coastal wetlands and the maintenance and enhancement of migratory waterfowl populations embodied in the Ramsar Convention and EEC Wild Birds Directive.

No similarly comprehensive assessment for all parts of the flyway network of Knots has yet been made. It is clear, however, that many places vital to Knots are facing a wide range of pressures and threats which include not just direct habitat loss but also recreational disturbance, dredging and over-shellfishing, and hunting for food destruction of mangroves in tropical wintering areas. For example, even in the Wadden Sea there has been recent extremely heavy exploitation of Cockles *Cerastoderma edule* and Mussels *Mytilus edulis* which appears to have severely depleted bivalve mollusc populations, destroyed undisturbed sediments and may have forced migrant Knots to feed on less-preferred food (T. Piersma pers. obs.). There have also been some substantial areas of habitat loss through land-claim and the construction of sea defences in parts of the Wadden Sea in recent years.

There are known to be pressures on many other parts of the range of Knots. For example there are currently very great threats to coastal wetlands in many east Asian countries, largely through very extensive land-claims for industry and agriculture, and also from hunting of waders for food (Parish 1985). Pressures on sites of vital importance to Knots are not restricted to these populous areas in middle latitudes. Parts of the upper shores of key staging areas in northern Norway have, for example, been recently lost through road construction, and parts of South American wintering grounds of *rufa* Knots may be affected by industrial developments and pollution (P. González pers. comm.). There are long-standing proposals for a tidal power barrage on the Bay of Fundy, and more recently a barrage scheme for part of James Bay, both places being important autumn staging areas of *rufa* Knots.

Although Knots breed in some of the most remote areas of the world even these places are not entirely safe from human pressures. Extension of oil exploration and production facilities may threaten parts of the Alaskan breeding grounds of presumed *roselaari* Knots (Bildstein *et al.* 1991). Furthermore Prokosch & Hötker (1992) list a wide variety of human threats, including increased coastal shipping, waste disposal from settlements, physical damage to tundra by vehicles, mineral exploitation and increasing hunting tourism, in the Taymyr breeding range of *canutus* Knots.

A further source of potential pressure on all Knot populations comes from the effects of any continuation in global warming. In some parts of the Knot's range there are increasing concerns about currently rising sea-level and its effect of squeezing intertidal shores into increasingly restricted areas against sea defences (e.g. Davidson *et al.* 1991). It is not yet clear however the extent to which sizes, locations and suitability of staging and wintering areas would be altered by an accelerated and more widespread rise in sea-level, nor the extent to which arctic tundra breeding areas may be constricted by changing arctic climates.

Since the spectacular migrations undertaken by waders such as Knots are one of the world's biological wonders, the maintenance of such a phenomenon is perhaps as important a conservation goal as the maintenance of the species involved. Brower & Malcolm (1991) have suggested recently that some migratory organisms may be able to survive even after being forced to abandon their migratory habits though, for example, the removal of key sites in a migratory network. Migratory wader populations such as Knots may, however, be unlikely to adopt rapidly a non-migratory lifestyle should key sites in their flyway network be removed since this would prevent birds from moving between their wintering and breeding grounds. Such arctic-breeding species could not survive on their breeding grounds through the arctic winter. Nor would there seem to be large enough areas of suitable breeding habitats around coastal and inland wetlands to support many birds of the displaced populations.

Destruction of key elements in their flyway site network may thus lead at best to greatly reduced population sizes and at worst to the destruction of the species. The conservation challenge for Knots in the future therefore needs to be focussed on maintenance of flyway networks.

KNOT CONSERVATION IN THE FUTURE

It seems that despite the many safeguards currently in place, Knot populations are under continued threat throughout their world range. Perhaps partly in response to such perceptions, there are a variety of recent further international initiatives aimed at flyway conservation of waders and other migratory birds. These include the IUCN Global Wetlands Programme and ICBP's Migratory Birds Conservation Programme, WHSRN, an East Asia Flyway Network co-ordinated by the Asian Wetland Bureau, the International Wadden Sea Secretariat and a variety of other projects further reported by Salathé (1991). There are also numerous national iniatives such as in the U.K. the RSPB Estuaries Campaign (Rothwell & Housden 1991) and the Joint Nature Conservation Committee's Coastal Review following up NCC's Estuaries Review (Davidson *et al.* 1991).

Of particular significance to attempts to conserve Knots is the future is the proposed *Western Palearctic Waterfowl Agreement* (WPWA) currently nearing completion under the terms of the Bonn Convention. This agreement will provide a mechanism for co-ordinating and linking conservation action on the two major flyways in the Western Palearctic, and provides a framework for developing co-ordinated species and population conservation strategies (Netherlands Ministry of Agriculture, Nature Management and Fisheries 1991). The first action plan under the WPWA focusses on ducks, geese and swans (the Anatidae), and other inter-

national species action or management plans under development are for the Slender-billed Curlew *Numenius tenuirostris* the White Stork (Goriup & Schultz 1991) and the Greenland White-fronted Goose (Stroud 1992). None are currently under way for coastal waders.

One way of developing effective future safeguards for Knot populations worldwide may therefore be to develop an international flyway conservation plan for Knots. This might be facilitated through the approach set out in the Western Palearctic Waterfowl Agreement, and using the model of the other species conservation plans such as those listed above. Certainly we are better placed to define the elements of such a plan for the Knot than for many other species. The information brought together in this present volume provides an essential basis for initial development of such a conservation plan, and has indicated where there remain key gaps in the understanding of Knot biology, some of which are substantial (Piersma & Davidson 1992b). Such a plan would need to be set also the content of broader based international and national assessments of features of conservation status, human activities and threats, and other conservation strategy developments, as outlined by Davidson *et al.* (in prep.).

A great deal of effort is expended worldwide to conserve coastal wetlands and their wildlife. Knots have a pan-global distribution and away from their breeding grounds Knots are entirely characteristic of the large and most internationally important areas of coastal soft shores, yet they also highlight the vital links between this globally threatened habitat and the vast and fragile arctic tundras on which they breed. There can be few bird species better suited to fly the flag of international coastal and estuarine wetland conservation than the Knot.

ACKNOWLEDGEMENTS

We thank all the participants in the 1989 workshop on the migration of Knots for their substantial contributions to increasing the understanding of the conservation needs of Knots. We particularly thank Mike Pienkowski, Phil Rothwell, Hugh Boyd, David Stroud, Peter Prokosch and Hermann Hötker for stimulating discussions during the preparation of this paper.

REFERENCES

Baker, A.J. 1992. Molecular genetics of *Calidris*, with special reference to Knots. *Wader Study Group Bull.* 64, *Suppl.*: 29-35.

Barter, M. 1992. Distribution, abundance, migration and moult of the Red Knot *Calidris canutus rogersi*. *Wader Study Group Bull.* 64, *Suppl.*: 64-70.

Biber-Klemm, S. 1991. International legal instruments for the protection of migratory birds: an overview for the West Palearctic-African Flyways. *ICBP Technical Publ.* 12: 315-344.

Bildstein, K.L., Bancroft, G.T., Dugan, P.J., Gordon, D.H., Erwin, R.M., Nol, E., Payne, L.X. & Senner, S.E. 1991. Approaches to the conservation of coastal wetlands in the Western Hemisphere. *Wilson Bull.* 103: 218-254.

Boyd, H. 1992. Arctic summer conditions and British Knot numbers: an exploratory analysis. *Wader Study Group Bull.* 64, *Suppl.*: 144-152.

Brower, L.P. & Malcolm, S.B. 1991. Animal migrations: endangered phenomena. *Amer. Zool.* 31: 265-276.

Davidson, N.C., Strann, K.-B., Crockford, N.J., Evans, P.R., Richardson, J.R., Standen, L.J., Townshend, D.J., Uttley, J.D., Wilson, J.R., & Wood, A.G. 1986. The origins of Knots *Calidris canutus* in arctic Norway in spring. *Ornis Scand.* 17: 175-179.

Davidson, N.C. & Pienkowski, M.W. (eds.) 1987. The conservation of international flyway populations of waders. *Wader Study Group Bull.* 49, *Supplement*.

Davidson, N.C., Pienkowski, M.W., Myers, J.P. & Moser, M.E. 1987. Future directions for the research and conservation of flyway populations of waders. *Wader Study Group Bull.* 49, *Suppl.*: 149-150.

Davidson, N.C., Laffoley, D.d'A., Doody, J.P., Way, L.S., Gordon, J., Key, R., Drake, C.M., Pienkowski, M.W., Mitchell, R. & Duff, K.L. 1991. *Nature conservation and estuaries in Great Britain*. Nature Conservancy Council, Peterborough.

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

Davidson, N.C., Rothwell, P.I. & Pienkowski, M.W. in prep. Towards a flyway conservation strategy for waders. In: Hötker, H. *et al.* (eds.), Migration and international conservation of waders. *Wader Study Group Bull., Supplement*.

Dugan, P.J. 1987. Socio-economic considerations in protecting shorebird sites in the developing world: some priorities and implications for the direction of future research. *Wader Study Group Bull.* 49, *Suppl./ IWRB Special Publ.* 7: 146-148.

Finlayson, M. & Moser, M. (eds.) 1991. *Wetlands. Facts on File*, Oxford.

Fournier, O. & Dick, W.J.A. 1981. Preliminary survey of the Archipel dos Bijagos. *Wader Study Group Bull.* 31: 24-25.

Gill, R.E., Jr & Handel, C.M. 1990. The importance of sub arctic intertidal habitats to shorebirds: a study of the central Yukon-Kuskokwim Delta, Alaska. *Condor* 92: 709-725.

Gollop, J.B., Barry, T.W. & Iversen, E.H. 1986. *Eskimo Curlew. A vanishing species?* Spec. Publ. 17,

Saskatchewan Natural History Society, Regina.
Goriup, P.D. & Schultz, H. 1991. Conservation management of the White Stork: an international need and opportunity. *ICBP Technical Publ.* 12: 97-127.
Godfrey, W.E. 1992. Subspecies of the Red Knot *Calidris canutus* in the extreme north-western Canadian arctic islands. *Wader Study Group Bull.* 64. *Suppl.*: 24-25.
Howe, M.A., Geissler, P.H. & Harrington, B.A. 1989. Population trends of North American shorebirds based on the International Shorebird Survey. *Biol. Conserv.* 49: 185-199.
Hunter, L., Canevari, P., Myers, J.P. & Payne, L.X. 1991. Shorebird and wetland conservation in the Western Hemisphere. *ICBP Technical Publ.* 12: 279-290.
Isleib, M.E. 1979. Migratory shorebird populations on the Copper River Delta and eastern Prince William Sound, Alaska. *Stud. Avian Biol.* 2: 125-130.
Lane, B.A. 1987. *Shorebirds in Australia.* Nelson, Melbourne.
Morrison, R.I.G. & Ross, R.K. 1989. *Atlas of Nearctic shorebirds on the coast of South America*, 2 Volumes. Canadian Wildlife Service Spec. Publ., Ottawa.
Morrison, R.I.G. & Harrington, B.A. 1992. The migration system of the Red Knot *Calidris canutus rufa* in the New World. *Wader Study Group Bull.* 64, *Suppl.*: 71-84.
Myers, J.P., Morrison, R.I.G., Antas, P.Z., Harrington, B.A., Lovejoy, T.E., Sallaberry, M., Senner, S.E. & Tarak, A. 1987. Conservation strategy for migratory species. *Amer. Scientist* 75: 18-26.
Netherlands Ministry of Agriculture, Nature Management and Fisheries. 1991. *Final draft of the Western Palearctic Waterfowl Agreement and Action Plan with Explanatory Notes and Management Plan.* Ministry of Agriculture, Nature Management and Fisheries (Directorate for Nature Conservation, Environmental Protection and Wildlife Management), 's Gravenhage, The Netherlands.
Parish, D. 1985. Threats to wader populations in East Asia. *Proc. 3rd East Asian Bird Protection Conf.*: 211-214. Wild Bird Society of Japan, Tokyo.
Parish, D. & Howes, J.R. 1990. Waterfowl hunting and management in S.E. Asia. Pp. 128-131 in: Matthews, G.V.T. (ed.), *Managing waterfowl populations.* IWRB, Slimbridge.
Piersma, T. & Davidson, N.C. (eds.) 1992a. The migration of Knots. *Wader Study Group Bull.* 64, *Supplement.*
Piersma, T. & Davidson, N.C. 1992b. The migrations and annual cycles of five subspecies of Knots in perspective. *Wader Study Group Bull.* 64, *Suppl.*: 187-197.
Piersma, T., Prokosch, P. & Bredin, D. 1992. The migration system of Afro-Siberian Knots *Calidris canutus canutus*. *Wader Study Group Bull.* 64, *Suppl.*: 52-63.
Prokosch, P. & Hötker, H. 1992. The Great Arctic Reserve - large-scale nature protection in northern Siberia. *Wader Study Group Bull.* 65: in press.
Rothwell, P. & Housden, S. 1991. *Turning the tide.* Royal Society for the Protection of Birds, Sandy.
Salathé, T. (ed.) 1991. *Conserving migratory birds.* ICBP Technical Publ. 12, Cambridge.
Smart, M. 1987. International conventions. *Wader Study Group Bull.* 49, *Suppl./IWRB Special Publ.* 7: 114-117.
Smit, C.J. & Piersma, T. 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. Pp. 24-63 in: Boyd, H. & Pirot, J.-Y. (eds.), *Flyways and reserve networks for water birds.* IWRB Special Publ. 9, Slimbridge.
Strann, K.-B. 1984. Vartrekk at Polarsniper. *Krykka* 7: 4-6.
Strann, K.-B. 1992. Numbers and distribution of Knot *Calidris canutus islandica* during spring migration in north Norway 1983 - 1989. *Wader Study Group Bull.* 64, *Suppl.*: 121-125.
Stroud, D.A., Mudge, G.P. & Pienkowski, M.W. 1990. *Protecting internationally important bird sites.* Nature Conservancy Council, Peterborough.
Stroud, D.A. 1992. *Greenland White-fronted Goose Anser albifrons flavirostris International Conservation Plan.* Draft working document: full plan, version January 1992. National Parks & Wildlife Service, Ireland/-IWRB.
Tomkovich, P.S. 1992. An analysis of the geographical variability of Knots *Calidris canutus* based on museum skins. *Wader Study Group Bull.* 64, *Suppl.*: 17-23.
Tubbs, C.R. 1991. The population history of Grey Plovers *Pluvialis squatarola* in the Solent, Southern England. *Wader Study Group Bull.* 61: 15-21.
Tubbs, C.R. 1992. The William Mudge diaries. *Wader Study Group Bull.* 65: in press.