WADER MIGRATION SYSTEMS IN THE EAST ATLANTIC

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The East Atlantic Flyway comprises wader populations breeding from Ellesmere Island in the west, to the Taymyr Peninsula in the east, and stretches south over the wintering grounds along the eastern side of the Atlantic Ocean to southernmost Africa. The waders using the East Atlantic Flyway, especially in the European part, have been intensively studied over the last 30 years, as is outlined in a short historical section. Some 36 specialist expeditions have been organised to study waders in parts of the flyway with few wader biologists. The paper reviews the methods used in wader migration studies, and summarises the current knowledge about breeding distribution and population sizes, the southward and northward migrations and the wintering grounds, of both coastal and inland waders. Despite the intensive level of study, no less than 14 major gaps are identified in our understanding of how waders use the flyway. Much basic work remains to be done.

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INTRODUCTION

A flyway can be defined as a distinguishable pattern of migration routes used by a group of related species. In the past, the populations of coastal waders wintering in Europe and north Africa have not been referred to as belonging to a particular flyway (Prater 1976). However, as more information on the abundance and migrations of waders along the west African coastline became available, waders which clearly belonged to the same breeding populations as those passing through or wintering in Europe, it became appropriate to define this assembly of wader populations and migratory pathways. Neither continental nor zoogeographical terms take into account the enormous north-south and west-east dimensions of migratory pathways. Altenburg *et al.* (1982) coined the term *East Atlantic Flyway* to describe the wader populations wintering in western Africa and Europe and, geographically, all the areas they use during the rest of the year.

Waders of the East Atlantic Flyway (Figure 1a) comprise populations breeding from about 70°W (Ellesmere Island) to about 110°E (Taymyr

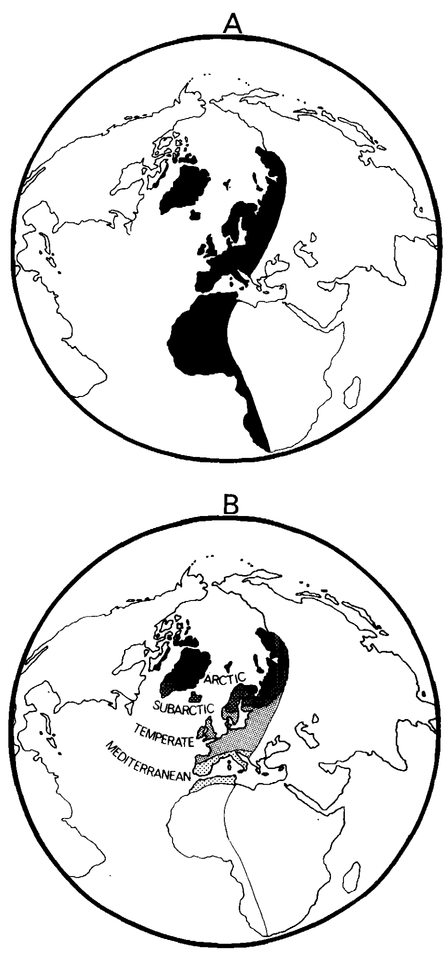

Figure 1. Geographical extent of the East Atlantic Flyway (A) and its subdivision into types of breeding area (B).

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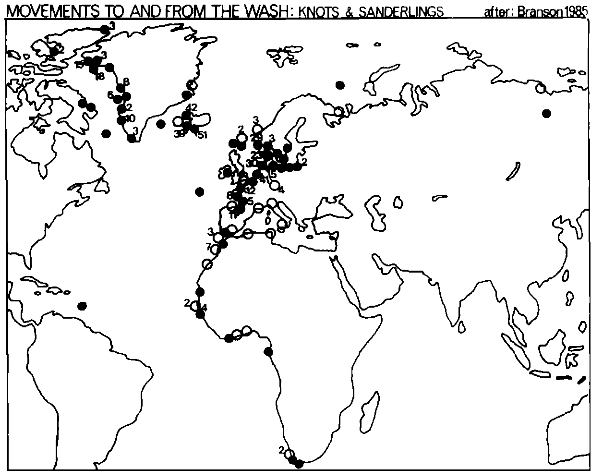


Figure 2. Summary of the overseas movements of Knots (filled dots) and Sanderlings (open dots) to and from the Wash, Great Britain (after Branson 1985). On the Wash 34 983 Knots and 6 734 Sanderlings have been newly ringed between 1959 and 1984.

Peninsula) and stretches south over the wader wintering grounds along the eastern side of the Atlantic Ocean to South Africa. It thus comprises parts of four continents (N.America, Europe, Asia and Africa) and three zoogeographical provinces (Nearctic, Palearctic and Ethiopian). The rationale for delineating the flyway as such comes from ringing studies. To illustrate this with a rather extreme example, Knots *Calidris canutus* wintering in Europe and in west and south-west Africa, have been shown to breed in respectively Greenland and NE Canadian high arctic and Taymyr Peninsula (Morrison 1975, Dick *et al.* 1975). Actually, the limits of the East Atlantic Flyway are described quite clearly by the overseas movements of Knots and Sanderlings *Calidris alba* to and from the Wash, Great Britain (Figure 2), although the Siberian element is underestimated by this. The continental boundaries of the East Atlantic Flyway are approximate (see the 'outlying' recoveries of Sanderlings and Knots in Siberia and the West Indies, Figure 2), and are not precisely described biological phenomena. Going westward in the Canadian Arctic and eastward in Europe and Africa, the numbers of wader populations that exclusively use the East Atlantic Flyway decreases. Hence there can be considerable overlap and interchange with other wader flyways (see other flyway reviews in this volume and *e.g.* Gromadzka 1981). These overlaps are not yet fully identified. For example, the extent of wader migration over the mid and east Mediterranean Sea (the Mediterranean Flyway, see Figure 21) and the links between the East Atlantic and Mediterranean Flyways, need further investigation.

Waders using the East Atlantic Flyway breed in a variety of countries, climates and habitats. Figure 1b shows the geographical extent of different types of breeding area (ecotones), *i.e.* from north to south the arctic (tundra), subarctic (arctic-alpine open country, marsh, taiga and boreal forest), temperate (moorland, marsh, meadow and broad-leaved forest) and Mediterranean (steppe, alina and maquis) ecotones. These distinctions are often used and are useful when referring to different groups of species of breeding waders.

This paper reviews the knowledge about distribution, abundance and movements of waders within the East Atlantic Flyway system. It does not review the biological correlates of, or explanations for, these phenomena: for a recent review of these see Pienkowski and Evans (1984). Waders migrating along the East Atlantic Flyway have been intensively studied for many years, and there is now a very extensive literature on the subject. A detailed description of all these studies is outside the scope of this paper, which summarises current knowledge and how it has been achieved. It highlights the gaps still remaining in our understanding of how waders use the Flyway.

A SHORT HISTORY OF FLYWAY STUDIES

During the first half of this century studies of wader biology were undertaken in relative isolation by individuals or groups in various parts of Europe. Detailed work on the breeding biology of Turnstones *Arenaria interpres* was carried out in Finland (Bergman 1946, 1958) and on the comparative ethology of waders in Germany and Denmark (Seitz 1950, von Frisch 1956, 1959, Lind 1961). The most notable early publications on the migration of waders originated from Denmark (Salomonsen 1954, 1955, Norrevang 1959), The Netherlands (Haverschmidt 1963) and Hungary (Schenk 1925). The first radar studies on wader migration were made in Great Britain by Lack (1959, 1963) and Evans (1968).

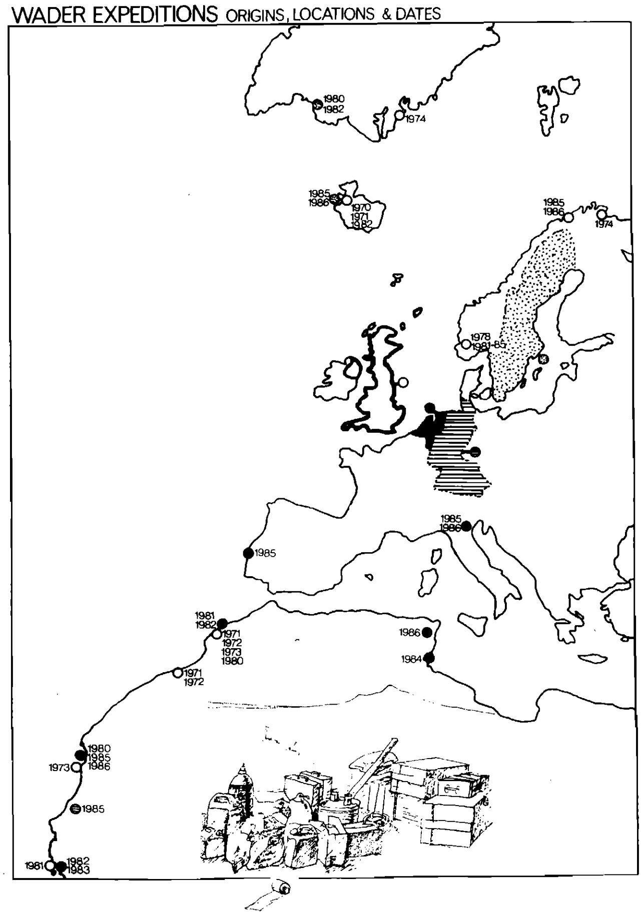


Figure 3. Summary of locations, countries of origin, and dates, of scientific expeditions with an emphasis on wader studies. See Table 1 for details and references. Different shading is used for expeditions from each country of origin, which is shaded accordingly: open, Great Britain; solid, The Netherlands; stippled, Sweden; and horizontal shading, West Germany.

The real 'flyway-work' on waders in Europe (and elsewhere) started through the activities of Clive Minton and co-workers, with the development of large-scale catching and ringing of waders on the Wash in eastern England in 1959. The annual catches rose to unrivalled sizes from 1967 onwards with the development of cannon-nets. From 1959 to 1984 the Wash Wader Ringing Group newly ringed over 163 000 waders which resulted in over 2 600 recoveries. In addition, about 1 500 waders ringed elsewhere were recaptured on the Wash (Branson 1985). The successful work on the Wash and the technical advances made there, not only stimulated similar work on other British, and overseas, estuaries, but resulted in a peculiar cannon-netters dialect (the vocabulary is explained by Minton 1980) and even a cannon-netting code of practice (Lessells *et al.* undated).

Around the same time, waterfowl counting expeditions to various localities were organised by the International Waterfowl Research Bureau (IWRB) and the then Co-ordinator of IWRB's Wader Research Group, Francois Spitz, encouraged the inclusion of wader counting in these ventures.

The increasing catching activities in Great Britain soon encouraged some groups of the more enthusiastic ringers to try to trace the waders to other parts of the world. This led to a series of wader study expeditions to different parts of the (as yet undefined) flyway. Between 1970 and 1974, Greenland, Iceland, Norway, Morocco and Mauritania were visited by British teams (see Figure 3 and Table 1), whose activities enormously increased our knowledge on the migratory movements of coastal waders.

Meanwhile the Dutch were developing plans to reclaim large parts of their intertidal Wadden Sea areas. These development threats led to a long-term (1971-1975) catching programme on the Wadden Sea island of Vlieland, to determine the function and importance of the Dutch Wadden Sea for waders (Boere 1976, Engelmoer *et al.* in prep.). Concurrently, a wader catching programme was started on the island of Schiermonnikoog (Nieboer 1972, van der Have *et al.* 1984). Although it has now been agreed that the Dutch Wadden Sea will not be reclaimed (Wolff and Smit 1984), other civil engineering works have needed the initiation of wader studies elsewhere in the Netherlands. For example the building and completion of the coastal protection works in the Delta area, has led to a series of environmental impact studies in which waders figure prominently (Baptist and Meire 1981, Leewis *et al.* 1984, Lambeck 1985).

In 1970 the Wader Study Group (WSG) was formed as a contact group of British wader-ringers. By the end of the seventies the group had developed into a truly international

Table 1. Summary of the expedition-based research on waders carried out in Greenland, Europe and northwest Africa.

Area	Year	Country of origin	Key reference
Greenland	1972	Great Britain	Green & Williams 1974
	1974	Great Britain	Green & Greenwood 1978
	1980 & 1982	Sweden	Alerstam *et al.* 1986
Iceland	1970	Great Britain	Morrison *et al.* 1970
	1971	Great Britain	Morrison & Wilson 1971
	1972	Great Britain	Morrison 1977
	1982	Great Britain	Emms & Elston 1983
	1985 & 1986	Sweden	Alerstam & Jonsson in prep.
Norway	1974	Great Britain	Leslie & Lessells 1978
	1978	Great Britain	Innes 1979
	1981 - 1985	Great Britain	Rae *et al.* 1986
	1985	Great Britain/Norway	Davidson & Evans 1986
	1986	Great Britain/Norway	Uttley *et al.* 1987
Italy	1985 & 1986	The Netherlands	Beintema 1986a
Portugal	1985	The Netherlands	Blomert *et al.* in prep.
Tunisia	1984	The Netherlands	van Dijk *et al.* 1984
	1986	The Netherlands	Beintema 1986a
Morocco	1971	Great Britain	Pienkowski 1971
	1972 & 1973	Great Britain	Pienkowski 1975
	1980	Great Britain	Moser 1981
	1981	The Netherlands	Kersten *et al.* 1983
	1982	The Netherlands	van Brederode *et al.* 1982
Mauritania	1973	Great Britain	Dick 1975
	1980	The Netherlands	Altenburg *et al.* 1982
	1985	The Netherlands	Ens 1985
	1986	The Netherlands	Project Banc d'Arguin in prep.
Senegal	1985	West Germany	Hotker 1985
Guinea-Bissau	1981	Great Britain/France	Fournier & Dick 1981
	1982	The Netherlands	Poorter & Zwarts 1984
	1983	The Netherlands	Altenburg & van der Kamp 1985

organization. This has made it possible for WSG to promote international co-operative work on the migration of waders. In 1979 the spring migration of Siberian Knots was studied by over 100 observers from 11 countries (Dick 1979, Dick, Piersma and Prokosch 1987). A similar approach has since been used in studies of the movements of wader populations throughout western Europe (Pienkowski and Pienkowski 1983), and recently, in a continuing project to study the spring migration of seven wader species along the East Atlantic Flyway (Piersma 1984, Davidson and Piersma 1986a, b) with major participants from South Africa to Greenland and Canada. The Knot project in 1979 coincided with the publication of plans to reclaim important areas for migrant Knots in the Wadden Sea of Schleswig-Holstein. This has led to a continuing programme of wader catching and other research in northern West Germany (Prokosch 1984a, b).

A very different initiative for international co-operative research came from West Germany (OAG Munster 1981, 1982). As an expansion of their extensive and innovative research into the waders using the sewage farms of the city of Munster in northern W.Germany (Harengerd, Sprunte and Speckmann 1972), this group started to organize a series of regular counts of waders on inland wetlands over much of Europe. This has since led to the capture and marking of Ruffs *Philomachus pugnax* wintering in Senegal, to document their spring movements north through Europe (Hotker 1985). In much of Europe, agricultural changes have resulted in declining breeding wader populations. This has led to studies of the causes and implications of the declines (Beintema 1983, Green 1984, Galbraith this volume). Since one of the most important meadowbird species in The Netherlands, the Black-tailed Godwit *Limosa limosa* is highly migratory, research focussing around this species have recently been carried out in its wintering grounds in West Africa (Altenburg and van der Kamp 1985).

Much of this detailed wader migration research is based on a precise knowledge of the distribution patterns of waders. Excellent and regular coverage by simultaneous counts has been achieved especially for estuarine coastal waders in Europe (Prater 1976, 1981b, Smit 1982). Southern Africa has been covered by a series of counts organized through the Western Cape Wader Study Group (Pringle and Cooper 1977, Summers *et al.* 1977, Whitelaw *et al.* 1978, Underhill 1981). Most north-west African coastal wetlands have been covered by counts made during a series of specially-organized expeditions (Trotignon *et al.* 1980, Altenburg *et al.* 1983, van Dijk *et al.* 1984, Kersten and Smit 1984, Zwarts 1984).

Apart from studies on the distribution and movements of waders in the East Atlantic Flyway system, the last 15 years have also produced many detailed and long-term studies of the population dynamics and foraging ecology and behaviour of both coastal and inland waders in relation to wetland resources. These studies have been based mainly in Britain (e.g. Evans *et al.* 1979, Goss-Custard 1980, 1983, 1985, Evans and Dugan 1984, Barnard and Thompson 1985) and The Netherlands (*e.g.* Zwarts and Drent 1981, Hulscher 1982, Zwarts and Wanink 1984).

METHODOLOGY OF FLYWAY STUDIES

Co-ordinated inland wader counts

Many, perhaps most, species of waders use inland sites during their migrations and on their winter quarters. Despite this, knowledge of the population sizes and migration biology of these inland waders is much less than that of coastal waders. Inland waders are more difficult to study than coastal waders, because during their migration periods and in winter they are spread over many inland wetlands. In contrast, coastal species often concentrate on just a few intertidal ares where they may be counted and caught comparatively easily. Inland wader resting areas are often very transitory habitats; for example, small changes in water level may have drastic effects on their suitability for waders. Hence counts from single sites are not usually representative for a wider geographical region.

The inland wader counts project (OAG Munster 1981, 1982) is a first step to overcome these difficulties. The project gathers and combines as many counts as possible from a range of inland sites over a large geographical region of western and central Europe.

The main aims of the current project are:
1. to describe the migration phenology of all wader species inland (*i.e.* when and where are the birds found?),
2. to gather information about habitat choice and management of inland waders; and,
3. to assess population trends of inland waders.

Counts of waders are ideally made once per week (for example during the weekend) from 1 March to 30 November at each of the counting sites). Counts should be as complete as possible - even numerous species like Lapwings *Vanellus vanellus* should be included. In very inaccessible sites, and for species like Snipe *Gallinago gallinago* only estimates are possible, either by extrapolation, or by indirect methods, *e.g.* from ringing results (Beintema and Muskens 1982). The most useful data come from those sites which have been observed for a number of years. Any site holding a reasonable number of waders during the migration periods may become a counting site. Inland sites like sewage farms, reservoirs, and lakes, together with wet meadows and certain arable fields, are preferred, but coastal sites are also welcomed - especially if they support some typically inland species.

Observers at 212 sites in 12 European countries are currently contributing to the project (Figure 4). The 300 volunteers count all waders about once a week from March to November on most of these sites. The counts and some data on the habitats of each site are stored on computer at the Biologische Station in Munster, West Germany.

Co-ordinated coastal wader counts

Almost all the counts of coastal waders in Europe and west Africa are made by observers on foot or in land vehicles. Only the Wadden Sea area in Denmark is regularly counted from aircraft (Laursen and Frikke 1986). In estuarine areas counts are usually made at high tide, and waders are counted as they assemble on high tide roosts. However, in some coastal areas of west Africa most waders roost in mangroves, effectively preventing counting at high tide. In such circumstances the waders are counted during low tide on sample mudflat-areas (Fournier and Dick 1981, Zwarts 1984). Counts of waders on rocky or sandy shores without extensive intertidal area, are usually carried out at low tide (Summers *et al.* 1984) or irrespective of tide (Moser and Summers 1987).

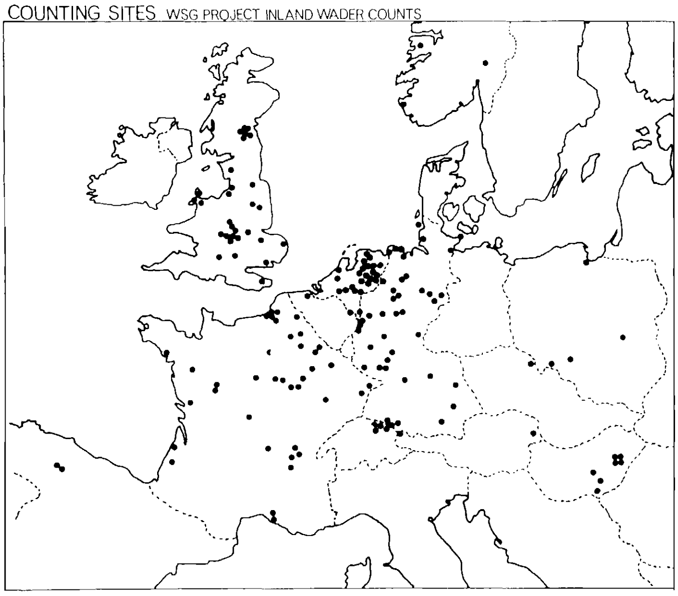


Figure 4. Locations of regular counting sites (1980-1986) in the co-operatively run WSG Project on inland wader counts, organized by the OAG Munster.

A detailed study has been carried out in The Netherlands to examine the errors of counting waders (Kersten, Rappoldt and Smit 1981, Rappoldt 1983, Rappoldt, Kersten and Smit 1985). A stochastic error is an error resulting from the 'natural' variations and uncertainties of measuring numbers. It is a measure of the relative accuracy of a single count and can be given as a percentage. When large numbers of counts are made, stochastic errors tend to average out. In contrast, systematic errors do not average out and are superimposed on stochastic errors. A systematic error implies that the numbers of a species, even in the long run, or with many spearate counts, are absolutely under- (or sometimes over-) estimated.

For flocks of waders sitting on a roost a relative stochastic error of 37% (relative standard deviation; *i.e.* standard deviation/mean x 100%) was found, independent of flock size. For waders flying in flocks to the roost, this error was much smaller (17%). The systematic error could not be quantified accurately in either situation, but is certainly less than a few tens of percent. For abundant wader species the stochastic error in the results of large-scale counts was calculated from the errors in the results of the largest occurring flocks. The addition of counts of single flocks lead to a decrease of the relative stochastic error. Calculations for the Dutch Wadden Sea showed a stochastic error of 5 to 10% in the overall counts of abundant species. For the abundant species, the studies concluded that the systematic error caused by missing birds was less than the stochastic error for single flocks (*i.e.* 37%). However, the counts of relatively scarce species, especially when individuals were widely scattered over a large area, were concluded to be very inaccurate. Such counts may indicate only the order of magnitude. In addition to the studies of Rappoldt and his co-workers, a few authors have compared counts made at low tide feeding areas with counts made on adjacent high tide roosts (Goss-Custard 1981, Engelmoer 1982, Barrett and Barrett 1984, Dominguez 1986), but with variable results, depending greatly on the configuration of each estuary and the behaviour of the birds.

Co-ordination of wader counts in Europe takes place at several levels and over several geographical areas. In many European countries there is national co-ordination of the annual midwinter counts, carried out on behalf of IWRB, e.g. in Portugal (Rufino 1979, 1984); Great Britain (Salmon and Moser 1984, 1985); France (Maheo 1985); The Netherlands (Zegers 1985); and Denmark (Meltofte 1980). Midwinter counts throughout Europe are assembled by the IWRB Co-ordinator (Smit 1983). In Great Britain, national wader counts are carried out also at other times of the year than midwinter, through the Birds of Estuaries Enquiry. In Denmark, monthly counts were made over much of the country in the period 1974-1978 (Meltofte 1981). Since 1981, between two and four co-ordinated counts of the waterbirds (waders, wildfowl, gulls, grebes) of the entire international Wadden Sea are carried out annually, organized through an ad-hoc committee of national co-ordinators, with support from IWRB (Smit 1982).

As part of the co-ordinated studies of the spring migration of waders along the East Atlantic Flyway in 1985 and 1986, large numbers of area-counts (over 400 in 1985) were carried out in Africa and Europe. These counts in spring are organized, via national co-ordinators, by the Wader Study Group.

The results of co-ordinated counts are mostly assembled by national or international co-ordinators. To speed up the analysis of the counting results, IWRB is currently trying to set up a data-base on Texel for the midwinter, and other, count results.

Ringing - in general

The development of suitable catching techniques is an obvious prerequisite for successful large-scale ringing and migration studies. The second half of this century has seen two important innovations in bird-catching techniques in western Europe. In the 1950s the Japanese mist-nets gained popularity and made possible a huge increase in the numbers of birds ringed annually. In the 1960s the development of cannon-nets (following limited earlier use of the large rocket-nets) led, especially in the field of wader and waterfowl studies, to unrivalled catching successes. The method has proved particularly successful in capturing large flocks of roosting waders, especially on estuaries.

From the early 1970s onwards, between 30 000 and 50 000 waders have been ringed annually in north and west Europe. Since waders are relatively long-lived organisms (Evans and Pienkowski 1984), the proportion of waders along the East Atlantic Flyway carrying rings must also have increased considerably. This is reflected in the steady increase in the percentage of British wader recoveries which are listed as 'controls' (Figure 5). Over the years, this phenomenon has made wader-catching in Europe and West Africa increasingly more effective in terms of information-on-movements gained per unit catching effort. On some estuaries, very high proportions of the waders present now carry rings.

Analyses of ringing recoveries and resightings

The finding or recapture of ringed birds, particularly since the development of effective large-scale catching methods in the 1960s (see

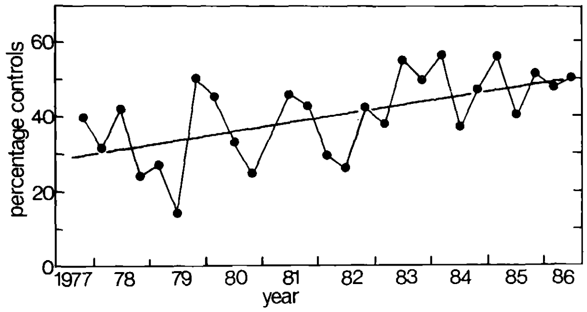


Figure 5. The increase in the percentage of 'interesting' British ringing recoveries listed as controls (*i.e.* recaptures elsewhere), r=0.55 n=27, p<0.05. Data were extracted from 'Recent recoveries of waders ringed in Britain and Ireland', in *Wader Study Group Bull.* No. 21-47. Although the criteria for an 'interesting' recovery have not been constant over the years, differing criteria are unlikely to influence the likelihood of inclusion of controls relative to other types of recovery.

above), has allowed the description of the basic framework of wader migrations along the East Atlantic Flyway. The large number of waders ringed have made the approach especially effective on this flyway. Whilst the finding of a ringed bird is clear evidence for the existence of a migration between ringing and finding locality, the absence of such a link is not usually adequate evidence for the lack of such movements. In some instances, data from ringing recoveries have therefore been combined with morphometric studies to overcome some of the difficulties (see below). Calculation of mortality and survival rates are outside the scope of this review - see Brownie *et al.* (1985) for details of methods.

An additional approach has been to use markings visible in the field, thereby removing the need for recapture and hence reducing some of the biases whilst also increasing the quantity of data likely to be generated from each captive. Generally, individual identification, based on combinations of colour-rings is inappropriate for migration studies both because of the difficulty in observing these small marks on waders, and because of the excessive rate at which the limited number of unique combinations would be used with limited return of information. Exceptions occur in the case of studies of returns to limited sites, often involving studies of survival rates and behaviour in relation to migration. The approach has proved successful for both coastal (Evans and Pienkowski 1984, Townshend 1985) and inland waders (Biologische Station "Rieselfelder Munster" 1981, Buker *et al.* n prep.). More appropriate techniques involve the use of temporary, conspicuous marks such as plumage dyes and temporary leg-flags made of flexible polyvinyl-chloride tape. Occasionally it is appropriate to supplement these markings by a permanent ring indicating, for example, age-class. These techniques have been developed for three main levels of investigation: large scale spring and autumn migrations; movements within a general wintering area; and usage of different parts of estuaries complexes.

The first extensive use of the plumage-dye technique for waders was in a study of Dunlin migration in Scandinavia by Mascher (1971). The technique was used to great effect in obtaining a remarkable number of sightings of the relatively small number of birds that were marked in the dispersed breeding situation in north-east Greenland (Green and Williams 1974, Green and Greenwood 1978). Since then, the technique has been developed extensively, particularly in WSG Projects on coastal waders (e.g. Dick, Piersma and Prokosch 1987, Davidson and Piersma 1986a, b). Dye-marking is especially effective in interpreting successive stages of a single migration system. Besides studies of coastal waders, dye-marking has been valuable in studies of the spring migration of Ruffs from Senegal into Western Europe (Hotker 1985) and of the spring migration of Black-tailed Godwits from Tunisia and Italy to the Netherlands (Beintema *et al.* 1987). It has been applied effectively in areas of the world with few earlier studies (see Morrison *et al.* this volume, Parish *et al.* this volume).

Use of visible-marking to examine movements within an estuarine complex is particularly relevant to many current cases involving proposed loss of habitat due to land-claim. Symonds, Langslow and Pienkowski (1984) investigated movements within the Firth of Forth, Scotland. Within this relatively limited area, they were able to make allowance in some analyses for observer effort in an attempt to quantify the proportions of birds moving between sites. They also made some investigations of turnover of birds within a site, an aspect also developed more intensively at spring migration staging posts by Kersten *et al.* (1983) and Moser and Carrier (1983). Kersten *et al.* (1983) and Kersten and Smit (1984) present a series of equations (modified from classical capture/recapture formulae) to calculate turnover rate and average staging times from the proportions of marked birds in the field, number of birds marked and total numbers present.

The intermediate level of study of movements within a wintering area was addressed by Dugan (1981). This approach was developed in the WSG project on movements of wader populations in Western Europe. The latter study attempts to quantify movement patterns within the western European wintering area by collating information on catching effort, to relate to ringing recoveries, and observer effort, to relate to sightings. By organising regular checks at numerous localities for visibly marked birds, the study attempts to verify negative records as well as obtaining information on the timing of movements. Preliminary results are presented by Pienkowski and Pienkowski (1983) and Pienkowski and Evans (1984). Example maps are given in Figures 13 and 19.

The potential for confusion with many colour-marking schemes in operation is considerable. WSG has therefore established a register in the East Atlantic Flyway system (Townshend, Galbraith and Thomas 1985) and the Americas (Myers *et al.* 1983). These should be consulted before embarking on new schemes. Indeed, in some countries such consultation is mandatory.

Despite the great value of ringing and dye-marking in deducing patterns of wader migration, there are several problems and limitations to the technique, even on an intensively studied flyway like the East Atlantic. The geographical distribution of recoveries/sightings is invariably biased, since the presence of recoveries indicates not only presence of birds, but also presence of humans (often hunters) able to report rings. Hence the absence of recoveries does not necessarily indicate absence of birds. Recoveries tend to concentrate on populated areas, especially those with high hunting pressures. For instance, some spring migrating Black-tailed Godwits use a route through Tunisia and Italy. Dutch Black-tailed Godwits are often reported from Italy, but never from Tunisia, suggesting that the latter might belong to eastern populations (Beintema and Brost 1986). However, in Tunisia the birds concentrate in a National Park, where they are seldom shot. Dye-marking has now shown that Dutch Black-tailed Godwits do use this area (Beintema 1986a).

There is also bias caused by the ringer. Where birds are site faithful, repeated ringing creates clusters of ringed birds and, under evenly distributed hunting pressure, clusters of recoveries. Beintema and Muskens (1982) showed that recoveries of Snipe ringed in Holland and shot in Holland were concentrated in three large clusters, suggesting a very uneven distribution of the species. However, foreign Snipe rings were much more evenly distributed. The argument can thus be reversed: in this instance the above sample one can conclude that Snipe are shown to be strongly site-tenacious.

Differences in behaviour and habitat choice also influence the probability that a bird will be reported. For example ringed Black-tailed Godwits and Ruffs are both regularly reported from Senegal, where many are shot. However in Mali waders are mainly caught with nets. Differences in flight behaviour (*e.g.* horizontal vs. vertical landing at roosts) mean that Ruffs are far more easily caught than Godwits. Consequently, Maliens catch and consume far more Ruffs than Godwits at times when both species are numerous. Hence comparison of the ratio of Godwit/Ruff recoveries from Senegal and Mali, gives a misleading idea of the relative abundance of the two species.

Since the use of particular routes by birds can never be determined from recoveries of birds ringed in only one country, the problems of bias should be reduced by using recoveries from different ringing sources. For example, 92% of recoveries of Dutch Black-tailed Godwits outside Holland are from the East Atlantic Flyway, and only 8% from a more easterly route (Beintema and Drost 1986). This might reflect just the distribution of hunters. However 95% of recoveries from central and eastern European Godwits are from the eastern route and only 5% from the Atlantic route, so qualitative conclusions can be drawn about the use of routes by the two (sub)populations.

Comparison of relative distribution of recoveries of birds from different ringing locations reveals even more: inconsistencies in patterns arise when migration is not spread evenly over the map, but instead consists of leaps, and when 'jumping patterns' of different birds are different (see Beintema and Muskens 1982 for an example).

The annual ringing total for a species is a function of the abundance of the bird, the abundance (and effort) of ringers, and the properties (*e.g.* catchability) of that species, of which the latter can be assumed to be a constant. Variation in ringing effort can be minimised by using relative ringing totals, *i.e.* by comparing the total of one species with another ringing total, *e.g.* all other birds, or of a group of (ecologically) related species. For example, in The Netherlands the contribution of ringed chicks of Redshank and Ruff to the total number of ringed chicks of 'meadowbirds' has declined steadily during the last few decades, and in the Ruff now approaches zero (Beintema 1983). This indicates that The Netherlands is losing these species as common breeders. The proportion of Snipe ringed in autumn in the totals of all inland species is declining in West Germany, steeply declining in The Netherlands, but increasing in Britain. This indicates that West Germany and especially The Netherlands are losing their function as an autumn moulting area. The birds seem to have shifted to Britain in autumn (Beintema and Muskens 1982).

Another use for ringing recoveries is to calculate the probability of recovery (PR). This is defined as the probability that a ringed bird will be reported in a given year. It is estimated by expressing the number of recoveries in a year as a fraction of the total number of rings present in the (sub)population in the same year. This total is estimated by adding surviving numbers of ringed birds from previous years to the actual ringing total of the year concerned. In year i, this total is

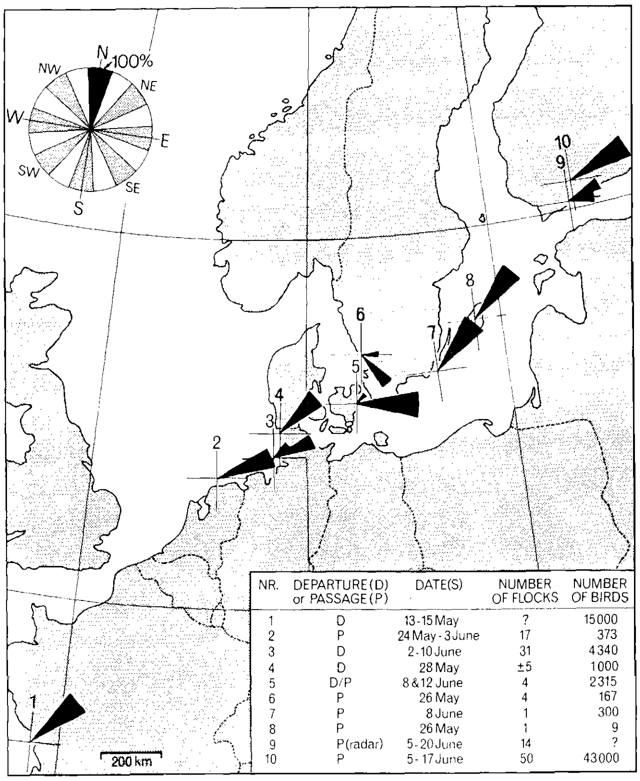
$$T = R_i + S*R_{(i-1)} + S^2*R_{(i-2)} + .. + S^n*R_{(i-n)}$$

where S is the species' annual survival of the species, R is the annual ringing total, and n is sufficiently large to ensure that no birds from year (i-n) are still alive. PR gives direct insight in historical changes in the behaviour or occurrence of both birds and hunters. In Snipe, PR has sharply declined in The Netherlands, and less so in other European countries, but there has been no change in PR in Britain. This can be explained by the shift in migration pattern mentioned before (Beintema and Muskens 1982). In the Black-tailed Godwit there is a decrease of PR in southern Europe, but an increase in Africa, mostly resulting from changes in hunting pressures. However there may be also an effect of increased migration speed in spring, caused by changes in the timing of breeding in The Netherlands. Some very simple analyses of ringing data can be valuable. Ringing (or reporting) dates give information directly on seasons of occurrence, and also on breeding season in the case of chick ringing. Imboden (1974) studied geographical variation in nesting seasons of the Lapwing in this way. In The Netherlands, ringing dates indicated markedly advanced breeding in all 'meadowbird' wader species in recent decades (Beintema *et al.* 1985).

Analyses of morphometric data

Species breeding over large areas often show variations in body dimensions across their breeding range. These variations sometimes permit the approximate breeding areas of birds captured on migration or on the wintering grounds to be traced. In morphometric studies on waders, bill-length and wing-length have been most extensively used, although both (especially wing-length) are subject to various errors, including seasonal variation, inter-observer error, and shrinkage of museum specimens (Engelmoer *et al.* 1983). More recently, total head (=head-plus-bill) length (Green 1980) and the length of the tarsus-plus-toe (Piersma 1984) have proved valuable additional measures in these analyses. Both have the advantage of being fairly easy to measure in the field, but suffer the disadvantage of fewer existing data than more traditional measures.

However, since size variations are often only slight, most morphometric analyses yield only 'statistical conclusions' rather than identify the breeding areas of individual birds and so are used mostly to supplement and interpret



NR.	DEPARTURE (D) or PASSAGE (P)	DATE(S)	NUMBER OF FLOCKS	NUMBER OF BIRDS
1	D	13-15 May	?	15000
2	P	24 May - 3 June	17	373
3	D	2-10 June	31	4340
4	D	28 May	±5	1000
5	D/P	8 & 12 June	4	2315
6	P	26 May	4	167
7	P	8 June	1	300
8	P	26 May	1	9
9	P(radar)	5-20 June	14	?
10	P	5-17 June	50	43000

Figure 6. Departure or passage directions of presumed Siberian Knots along the European coast in the spring of 1979 (from Dick, Piersma and Prokosch 1987). The inset gives the details of the observations at each site.

analyses of ringing recoveries. In studies of migration along the East Atlantic Flyway the morphometric approach has been applied successfully to Ringed Plover *Charadrius hiaticula* (Taylor 1980), Knot (Dick *et al.* 1976, 1987, Davidson *et al.* 1986), Purple Sandpiper *Calidris maritima* (Atkinson *et al.* 1981, Boere *et al.* 1984), Dunlin *Calidris alpina* (Pienkowski and Dick 1975) and Redshank *Tringa totanus* (Hale 1973, Furness and Baillie 1981, Summers 1985). A comprehensive study to determine the breeding origins of waders occurring in the Dutch Wadden Sea, which is using morphometric data extensively as an indicator of breeding location, is currently being undertaken by Engelmoer and his co-workers (Engelmoer 1984, Engelmoer *et al.* this volume).

Departure directions

Wader flocks departing from stop-over sites are often very conspicuous, especially in spring. Birds call loudly before and during flight. Flocks often depart by first spiralling upwards, and then flying in a fairly straight line whilst still gaining height. Compass bearings from direct observations of departing or passing flocks have proved helpful in interpreting the migration pathways of different breeding populations of Knots through western Europe. An example of the departure and passage directions of Siberian Knots at different sites in spring is shown in Figure 6. Flight directions of departing or passing flocks tracked by radar, have the advanatage that pathways can be tracked for longer distances than by direct observation, and has proved a powerful tool for understanding migration routes (*e.g.* Alerstam *et al.* 1986).

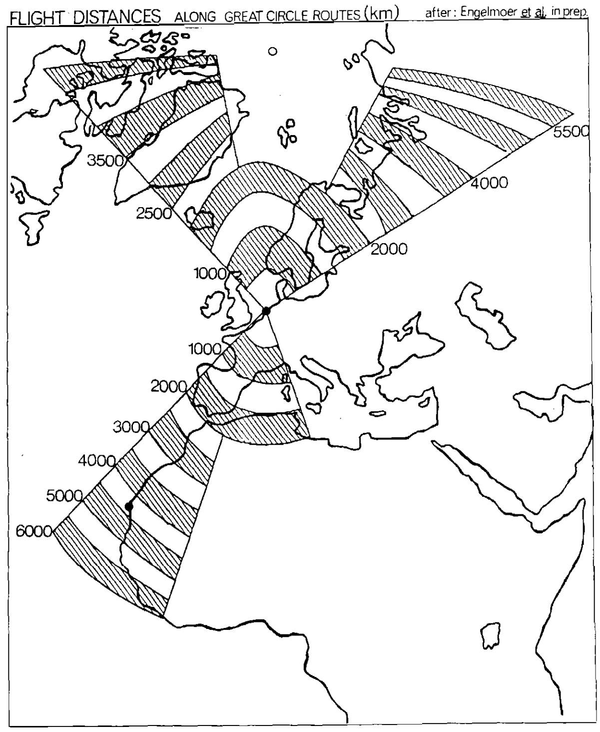


Figure 7. Great circle distances between the Dutch Wadden Sea and elsewhere along the East Atlantic Flyway (from Engelmoer *et al.* in prep.).

Nutrient reserves and flight ranges

Before embarking on migratory flights, waders store fat, at times amounting to 50% of their total body mass. The fat reserves are then used as fuel on their flights. These large fat loads are often sufficient for non-stop flights of several thousand km (see Figure 7 for an example of flight distances along great circle routes - the shortest routes between two points - on the East Atlantic Flyway). Relating the quantity of fat carried by a wader as it departs on migration to the rate at which the fat is then used up, allows the flight range of the birds to be predicted. Hence the likely location of the next staging area, the breeding grounds or the wintering grounds of the birds can be tentatively identified. This approach has been widely used, usually as an adjunct to interpretation of morphometric and ringing recovery findings, in assessing the migration systems of waders along the East Atlantic Flyway (*e.g.* Summers and Waltner 1979, Davidson and Evans 1986, Koopman 1986, Dick, Piersma and Prokosch 1987). However, despite the attraction of the method, it has a great many limitations, both in the use of flight range formulae, and in accurately measuring the size of fat reserves at departure and arrival on migration. These are reviewed by Davidson (1983, 1984).

Waders store and use muscle protein as well as fat during their migrations (Davidson and Evans in press), so that lean (fat-free) mass also varies seasonally. Hence fat loads must usually be measured by laboratory analysis of carcasses rather than predicted from body size and total mass. Fat and protein are accumulated very rapidly before migration, so a sample for flight range analysis must be obtained very shortly (one or two days at most) before a known migration departure. Such sampling is very difficult and has so far seldom been achieved.

Despite the caution needed in applying flight range analysis to studies of wader flyways, analysing the extent of the gain of fat, or even total mass, before each migration has been invaluable in identifying the broad migration strategy (or strategies) used by some wader species along the East Atlantic Flyway. Such analyses can reveal whether birds are making a few long-distance or many short-distance flights during their migration. In Knots (Figure 8) the approach has identified 4 strategies used on different parts of their spring migration along the East Atlantic Flyway. These are a) long flights using up much of a large fat reserve, *e.g.* Banc d'Arguin to France; b) long flights using up only part of a large reserve *e.g.* northern Norway to Ellesmere Island; c) short flights using up much of a small reserve *e.g.* western France to the Wattenmeer; and d) short flights using only part of a large reserve *e.g.* western Britain to Iceland.

Flight range calculations predict that waders migrating along the East Atlantic Flyway in spring arrive after most migrations with a substantial amount of fat reserve remaining (see Figure 8). This phenomenon is now being confirmed by the few direct observations of arrival condition (*e.g.* Davidson and Evans 1986, in prep.). Particularly for waders such as Knot that make only a few long migrations, flight range predictions do correspond broadly with the distribution of known staging and breeding areas (Figure 8).

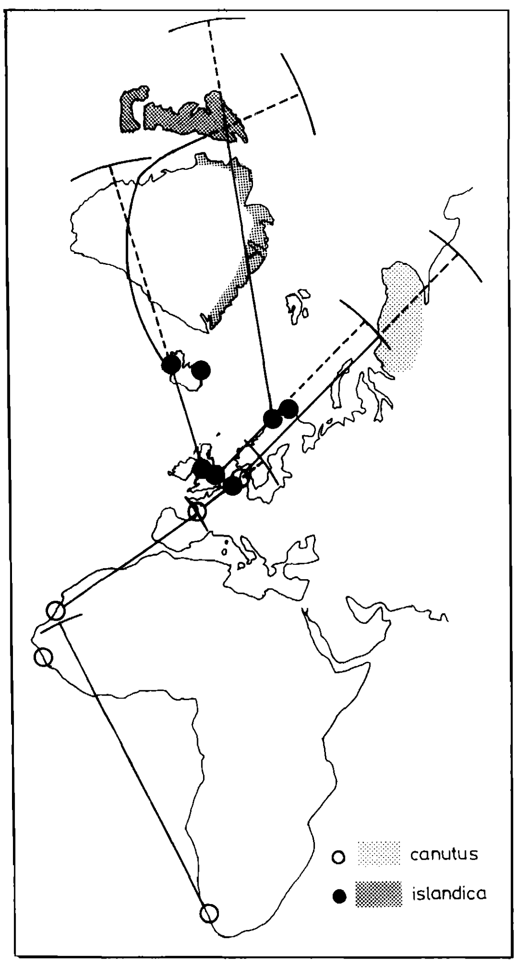


Figure 8. Predicted flight ranges of Knots during their spring migration to their breeding grounds, in comparison with the known wintering and staging areas (open and closed circles) and breeding grounds (shaded) of each population. The excess of predicted range over the distance between sites is shown as a dashed line. Revised after Davidson (1984), Davidson and Evans (1986), Davidson *et al.* (1986) and Dick, Piersma and Prokosch (1987).

Financial backing of the research

The largest part of the costs of the research described in this chapter - and indeed throughout this volume - were met by the workers concerned providing their own time, and meeting their own costs, in terms of travel and equipment. This applies to the counters, other observers, and ringers. Whilst the co-ordinating activities of national ringing schemes are in many countries supported by state funds, the prime cost, that of the ringing activities, is generally met by the volunteers concerned. Without this pool of willing, skilled labour, very few of the studies described here would have been possible.

When the need for gap-filling required expedition work, outside funding became essential however, even though the man-power was provided voluntarily, generally by students. Unfortunately student expeditions are often assumed *a priori* to be incapable of producing worthwhile scientific results and research councils were often reluctant or totally unwilling to consider supporting them. Thus funding for this stage of investigation was obtained from university funds, charitable trusts, ornithological bodies, and, sometimes, commercial firms. Some of the later student expeditions managed to obtain research council funding in cases where a senior scientist was prepared to lend his name to the project, often on the basis of trust rather than direct involvement.

The most recent stage of development has involved large scale co-ordinated projects. In many cases, the scale of co-ordination has meant that such activity is impossible on a voluntary basis. The tendency has thus been to fund the employment of professional scientists as co-ordinators of a vast voluntary work effort. This co-operative approach has proved highly effective.

One of the most encouraging developments in recent years has been the increasing willingness of national research or conservation bodies to contribute to the funding of international projects. This recognition that international migrant populations require international research and co-ordinated conservation measures, is overdue and very welcome. The existence of international resources, such as those within the Commission of the European Communities, has also been helpful in this regard.

BREEDING GROUNDS

Distribution

In the European part of the East Atlantic Flyway about 37 wader species breed regularly. Figure 9 shows the species densities of breeding waders over much of Europe. The number of species is highest in Fennoscandia and decreases south- and westwards. The species composition also changes considerably from north to south. For example, Portugal has only four wader species in common with Finland (see Piersma 1986 for further details).

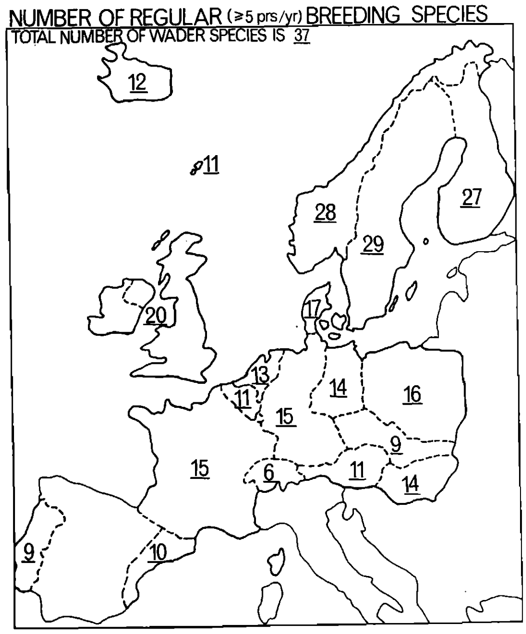


Figure 9. Species densities of breeding waders in different European countries (compiled from Piersma 1986: Table 2).

Abundance

A review of population size estimates of waders breeding in Europe, northeast Greenland and Ellesmere Island has recently been published by the Wader Study Group (Piersma 1986). Figure 10 shows how the waders are quantitatively distributed over this enormous area. A total of 6.6 million wader pairs are estimated to breed in the area reviewed. Waders wintering in coastal habitats number 1.7 million pairs, and originate more from countries in or along the Atlantic Ocean (notably Iceland), than waders wintering in inland habitats. The majority of inland-breeding waders (4.8 million pairs) originates from Fennoscandia.

Iceland appears to be especially important for the European breeding populations of Ringed Plover, Golden Plover *Pluvialis apricaria*, Purple Sandpiper, Dunlin (*schinzii* race), Snipe, Black-tailed Godwit (*islandica* race), Whimbrel *Numenius phaeopus*, Redshank and Red-necked Phalarope *Phalaropus lobatus*. For southern breeding species such as Black-winged Stilt *Himantopus himantopus*, Stone Curlew *Burhinus oedicnemus*, Collared Pratincole *Glareola pratincola* and Kentish Plover *Charadrius alexandrinus*, Portugal and Spain are very important breeding grounds. Fennoscandia is the major breeding area in Europe for the tringid sandpipers (Common Sandpiper *Actitis hypoleucos*, Green Sandpiper *Tringa ochropus*, Wood Sandpiper *Tringa glareola*, Spotted Redshank *Tringa erythropus* and Greenshank *Tringa nebularia*). Fennoscandia also supports the largest breeding populations of mainland Europe of many other species. The Netherlands is a major breeding area of Oystercatcher, Avocet *Recurvirostra avosetta*, Lapwing *Vanellus vanellus* and Redshank, and has about 85% of European breeding Black-tailed Godwits. Great Britain has the largest breeding population of Lapwings in Europe, and has also a large population of Oystercatchers, the largest temperate populations of Ringed Plovers and Golden Plovers, the only remaining large population of temperate breeding *schinzii* Dunlins, and the only large populations of Woodcock *Scolopax rusticola* and Curlew *Numenius arquata* outside Fennoscandia.

By comparison with the 6.6 million pairs of breeding waders in Europe, Meltofte (1985) estimated only 100 000 pairs (of different species composition) breeding in high-arctic Greenland and Ellesmere Island, although he indicated that this is likely to be an underestimate.

Although population size estimates of varying accuracy are now available for a large part of Europe, a most obvious gap in knowledge is that we do not know even approximately, how many of the waders that use the East Atlantic Flyway breed in the enormous area of the USSR and in the countries around the Mediterranean Sea.

Not only is it important to determine population sizes at any one moment, but it is also important to understand trends in the size of breeding populations. A start has been made in Britain with the British Trust for

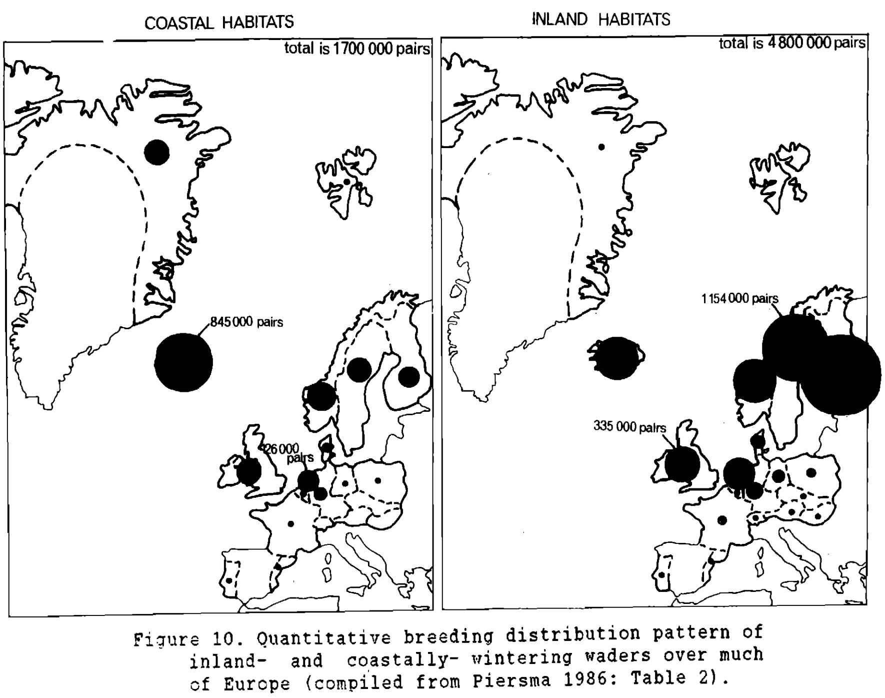


Figure 10. Quantitative breeding distribution pattern of inland- and coastally- wintering waders over much of Europe (compiled from Piersma 1986: Table 2).

Ornithology's Waterways Bird Survey, which covers a few species of waders (Marchant and Hyde 1980, Taylor and Marchant 1983) and the Lowland Wader Survey (Smith 1986). In Friesland (The Netherlands) there are annual data on breeding wader densities on protected plots totalling 45 000 ha (Peetsma 1980. Fokkema *et al.* 1986). It would be of clear value to international nature conservation to monitor breeding wader populations in selected sites in Europe. The absence of such data is a second important gap in knowledge.

Productivity

Although a breeding area may be important in terms of breeding densities, its nature conservation value lies ultimately in the contribution the area makes towards future generations, *i.e.* the relative local breeding productivity of a particular species (see discussion by Witt 1986 and Beintema 1986b). Breeding productivity is commonly assessed as fledging success per pair, or fledglings per breeding attempt, but its estimation is full of methodological pitfalls (see *e.g.* Pienkowski 1984). Although productivity has been measured in several species and places, few studies have yet attempted to compare breeding success at several localities along a species' breeding range. Pienkowski (1984) studied Ringed Plovers at breeding sites in north-east England and in north-east Greenland, but was unable to investigate completely differences in annual breeding schedules, strategies and components of breeding performance. No author has ever compared breeding productivity per unit area in different parts of a wader's breeding range in Europe.

THE SOUTHWARD MIGRATION

Inland waders

Most species leave their breeding area from the end of June onwards until the end of August. Some waders breeding in temperate regions may start migration considerably earlier, even as early as the end of May. One of these species, the Lapwing, has a pre-moulting migration which does not necessarily lead directly to the south or to the wintering grounds. Adults generally migrate earlier than juveniles (for information see Glutz von Blotzheim, Bauer and Bezzel 1975, 1977). The time periods in which birds resting on migration may be found in European wetlands differ greatly between species, although the peak for most species is in August. Migration periods in European inland sites are much shorter than on the coast. Waders inland are much more dispersed than on the coast, concentrations of more than at least a few hundreds of birds of any species are rare in western Europe. There are often great annual variations in resting numbers, which partly result from the great ecological instability of most of the sites.

Migration routes and strategies are poorly understood for most species. In general, estimates of the breeding populations (Piersma 1986) are much higher than the totals of the counts in central and western European resting sites, indicating that many birds must use eastern migration routes, or cross central and western Europe without pausing. There is circumstantial evidence for the number of resting sites used per migratory trip. For many species, no differences in the timing of the migration peaks in southern, western and central Europe could be found (see Figure 11 for an example of Wood Sandpipers *Tringa*

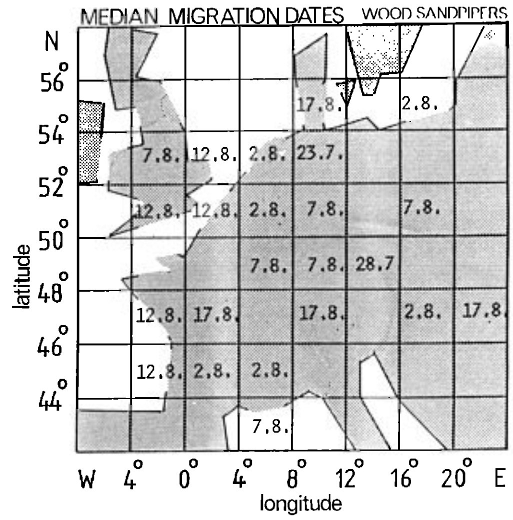


Figure 11. Timing of autumn migration of Wood Sandpipers in Europe (median dates: from OAG Munster 1987).

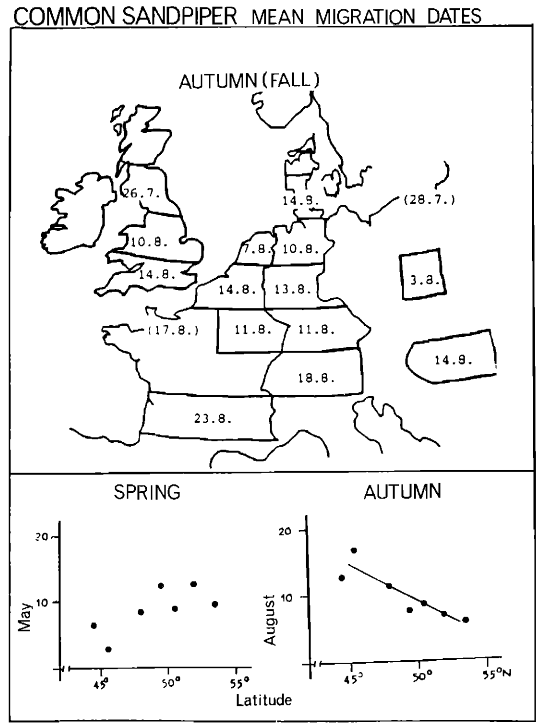


Figure 12. Timing of the autumn migration of Common Sandpipers over much of Europe (compiled from OAG Munster 1982, 1984).

glareola). This indicates that most birds of such species either rest in central, or in western, or in southern parts of Europe, but at not more than one site in the whole of this region, *i.e.* long-distance migrations. Weight analyses show that Wood Sandpipers, for example, resting in central Europe are theoretically able to reach their wintering quarters in Africa by non-stop flights (OAG Munster in prep. a). In contrast to the species mentioned before, mean migration dates of Common Sandpipers *Actitis hypoleucos* are later at southerly latitudes (Figure 12), suggesting migration in shorter hops.

In some *Calidris* and a few *Tringa* species there are differences between migration routes, and possibly migration strategies, of juveniles and adults. Adults of these species are almost

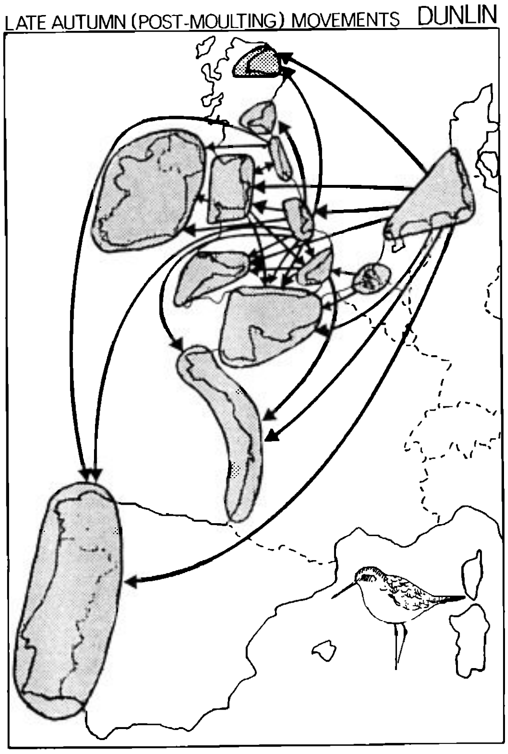


Figure 13. Summary of the late autumn (post wing-moult) movements of northern Dunlin (*C.a.alpina*) in western Europe. Only connections for which there is direct evidence from the exchange of marked birds are shown (from Pienkowski and Pienkowski 1983).

exclusively found in coastal habitats, whereas inland sites hold juveniles only (OAG Munster, unpublished). Much basic descriptive work remains to be done on autumn migration patterns of inland waders.

Coastal waders

Pienkowski and Evans (1984: Table 1) have summarised the timing of the autumn migration (and the location of autumn moulting areas, wintering areas and timing of spring migration) of waders along the East Atlantic Flyway. Waders leave the breeding areas from the end of July onwards. There are only slight differences in timing between different latitudes. In general, adults leave the breeding grounds before juveniles, and so the autumn arrival of juveniles on European staging sites is rather later than the arrival of adults. The numbers of waders staging in the European estuaries generally reaches peak numbers in September (Prater 1981a, Smit and Wolff 1981), when both adults and juveniles have returned from their northern breeding grounds.

Most individual waders seem to make use of a series of coastal wetlands when migrating from breeding to wintering grounds. How the series of available sites are connected in the movements of one species is illustrated in Figure 13 for northern Dunlins (*Calidris alpina alpina*), from the results of recent colour-marking studies in western Europe. Figure 13 shows that after leaving the moulting areas concentrated in the Wadden Sea, different groups of Dunlins move in a complex pattern between the different European estuaries.

Although most of the knowledge probably already exist to outline the patterns of autumn-movements of most other species of waders in these general terms, there is still much scope for filling many of the important details.

Post-breeding moult

The post-breeding moult is the most energetically most costly moult period in the annual cycle of waders wintering in northern temperate ans subtropical areas, since both the flight and body feathers are replaced. Some wader populations start the post-breeding moult after arrival on their wintering grounds, either in western Europe or Africa. Other populations interrupt their autumn migration to moult on staging areas before continuing the flight to their wintering grounds (*e.g.* Dunlin, Figure 13; Boere 1976, Pienkowski *et al.* 1976), or even moult their flight feathers whilst continuing their migration (Pienkowski *et al.* 1976). An inland species like the Black-tailed Godwit moults the majority of flight and body feathers whilst still on the breeding grounds (van Dijk 1980). Although most wintering areas of waders have at least some moulting populations, within the East Atlantic Flyway system the international Wadden Sea clearly fulfills a major role as a moulting centre (Boere 1976, Smit and Wolff 1981, Pienkowski and Pienkowski 1983).

In accordance with their overall non-breeding distribution, the populations of waders from inland habitats generally moult their flight feathers over more dispersed areas than the coastal species. Detailed moult studies are now available for many wader species of the East Atlantic Flyway (see reference list in Ginn and Melville 1983), but there is a clear need for review of the major moulting sites of waders along the East Atlantic Flyway, especially from a nature conservation point of view.

WINTERING GROUNDS

Inland waders

During winter, the open habitats of inland Europe (meadows and arable fields) harbour large populations of a few wader species; Golden Plover, Lapwing and Curlew. No comprehensive counts of the undoubtedly numerous Lapwings have ever been made but counts are available for Golden Plovers (Figure 14, van Eerden and Keij 1979, Fuller and Lloyd 1981) and Curlews (A.J.van Dijk in prep.). In November a total of 700 000 Golden Plovers have been located in Denmark, northern West Germany, The Netherlands and Great Britain (Figure 14). Quite a few more are predicted to overwinter elsewhere (notably Ireland, Hutchinson 1979). Hence some information is available, but awaits interpretationin an international (flyway) context. However, especially for Lapwing and Curlew, much more counting and analyses remains to be done.

In Africa most of the inland waders winter in more vegetated habitats than their northern counterparts, and this is one of the reasons they are much more difficult to 'map' quantitatively. Apart from the general distribution maps of the species (Moreau 1972, Urban, Fry and Keith 1986) there is extremely little information on wintering densities and total population sizes. Only recently has one attempt been made to quantify the numbers of inland waders in Senegambia and in Guinea-Bissau (Altenburg and van der Kamp 1985, 1986). Figure 15 shows the resulting quantitative distribution of wintering Black-tailed Godwits. Most were located in the areas of small wet ricefields. Table 2 shows

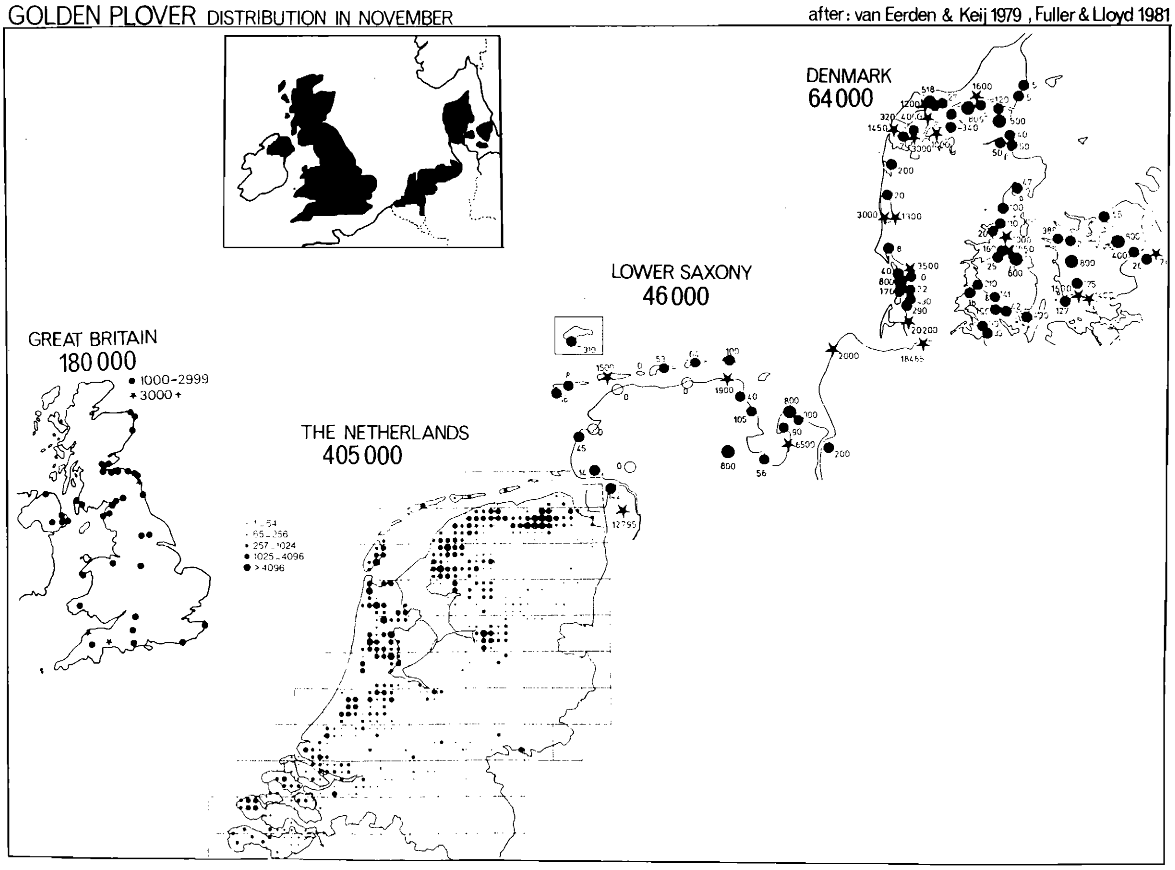


Figure 14. Distribution of Golden Plovers in part of north-west Europe in November. Note that dot size and the maps are not to the same scale between countries (from van Eerden and Keij 1979, and Fuller and Lloyd 1981).

the estimated total numbers of wintering waders in the wet ricefields of Guinea-Bissau, obtained by sampling part of the available habitat. Apart from Black-tailed Godwits, large numbers of Collared Pratincoles, Little Stints *Calidris minuta*, Ruffs *Philomachus pugnax* and Wood Sandpipers were found. To enhance our understanding of the winter distribution of inland waders in Africa, there is enormous scope for similar studies elsewhere on the continent.

Coastal waders

Coastal waders wintering in the estuaries of western Europe have been well covered by counts. A first summary of their quantitative

Table 2. Estimated numbers of waders wintering in the ricefields of Guinea-Bissau (*i.e.* half of the total area of wet ricefields in coastal West Africa). From Altenburg and van der Kamp (1986).

Collared Pratincole	50 000 - 75 000
Black-winged Stilt	2 000 - 4 000
Little Ringed Plover	200 - 500
Little Stint	10 000 - 20 000
Ruff	50 000 - 75 000
Black-tailed Godwit	110 000 - 120 000
Snipe	750 - 1 250
Spotted Redshank	500 - 1 000
Marsh Sandpiper	2 500 - 5 000
Greenshank	2 500 - 5 000
Green Sandpiper	100 - 500
Wood Sandpiper	25 000 - 50 000
Common Sandpiper	2 000 - 5 000

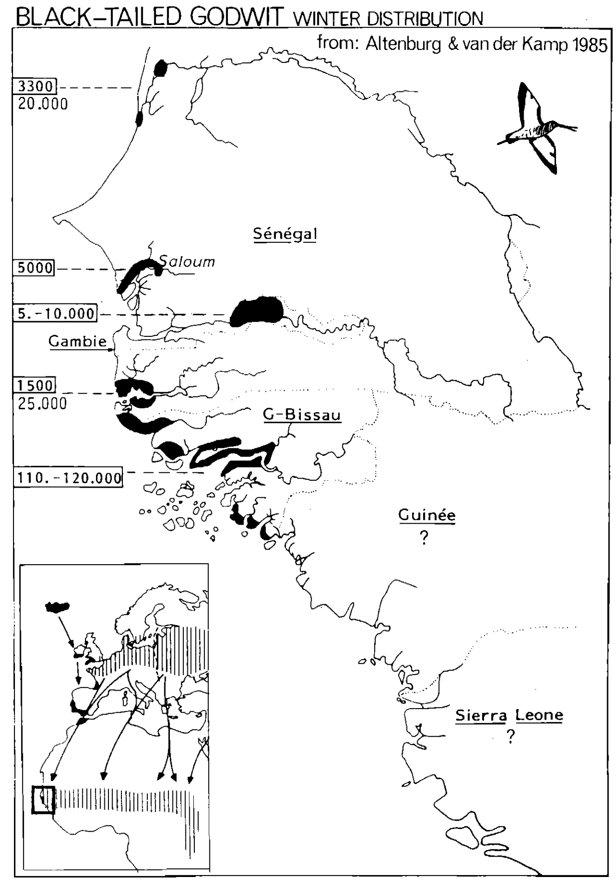


Figure 15. Quantitative distribution pattern of Black-winged Godwits wintering in Senegal, Gambia and Guinea-Bissau in the winter 1983/1984 (from Altenburg and van der Kamp 1985).

distribution was presented in 1969 and revised in 1975 (Spitz 1969, Prater 1975). Estuarine waders in Great Britain are covered in detail by Prater (1981a) and in Ireland by Hutchinson (1979). The waders wintering in the Wadden Sea areas of The Netherlands, West Germany and Denmark are reviewed by Smit and Wolff (1981). Many of the important coastal wetlands of western Africa have meanwhile also been covered once or twice, and a first overview of all the information was provided by Altenburg *et al.* (1982). Subsequently, additional information for a few other important coastal sites (notably Guinea-Bissau) have become available (Fournier and Dick 1981, Zwarts 1984), and the summaries of the winter distribution and numbers of waders along the East Atlantic Flyway have been updated a few times (Altenburg *et al.* 1983, Smit 1983, Piersma 1985). However, in none of these compilations is there information from anywhere in the Gulf of Guinea. Counts of some of the coastal areas have become available recently: in Ghana (MacDonald 1978, Hepburn 1986, Ntiamoa-Baidu pers. comm.) and Sierra Leone (Tye and Tye, this volume). Figure 16 summarises the current knowledge of the distribution of estuarine coastal waders in midwinter, along the entire East Atlantic Flyway. (A detailed review updating this information is currently in preparation by C.J.Smit on behalf of IWRB.) Figure 16 shows that waders are concentrated along the southern North Sea, and in westernmost Africa. More than half of the total number of coastal waders of the East Atlantic Flyway winters in West Africa. As far as the waders of estuarine areas are concerned, it is only the Gulf of Guinea where a lot of coastline remains to be covered by counts.

Athough the estuarine coasts of Europe are currently well covered, little is yet known about the wintering numbers along the non-estuarine open shores of Europe. Scattered information exists for the Belgium and Dutch coastlines (Meininger and Becuwe 1979) and parts of the Norwegian coast (Rov 1984). A comprehensive survey has recently been undertaken along the enormously long shores of Great Britain (Moser and Summers 1987, Figure 17). This survey found that the open shores

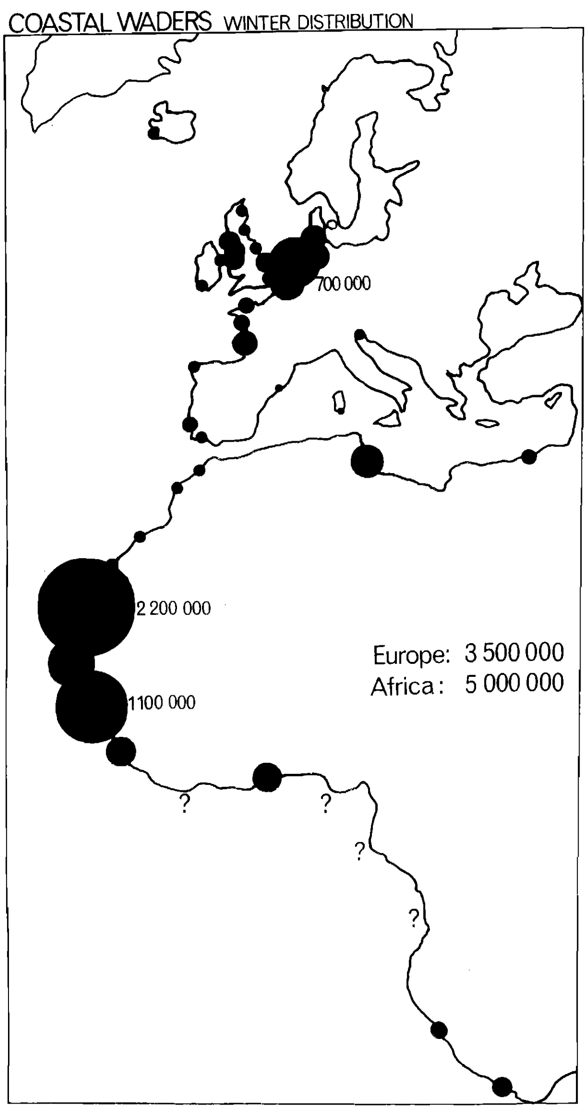


Figure 16. Quantitative distribution pattern of coastal waders in midwinter along the East Atlantic Flyway (compiled from many sources; see Smit (in prep.) for listing). The surfaces of the dots are scaled to wintering numbers.

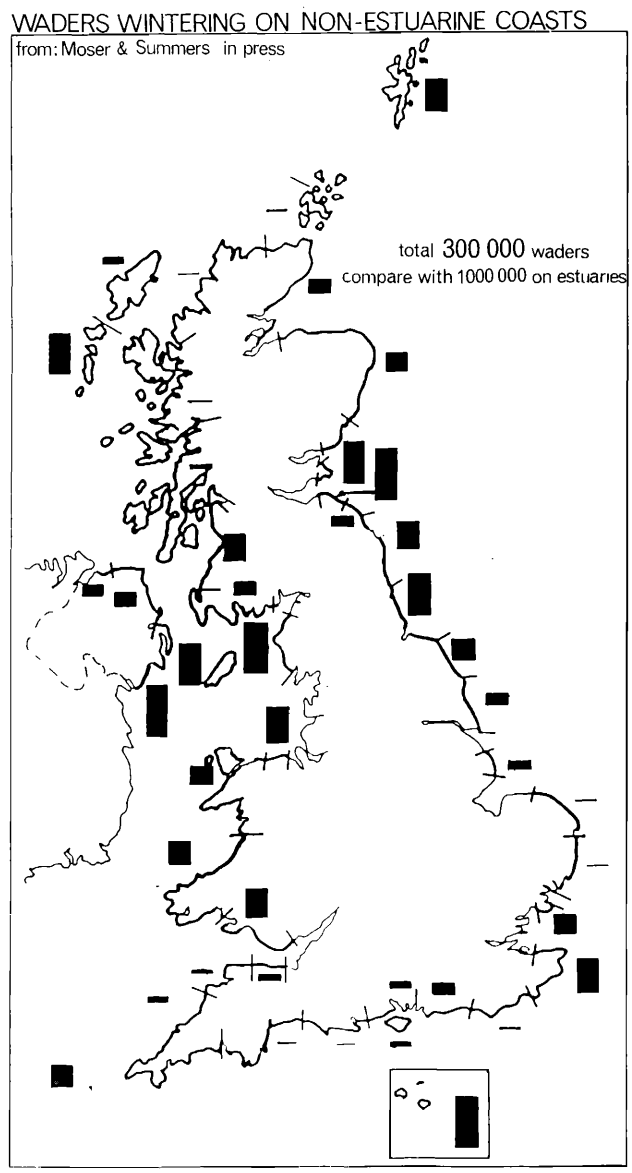


Figure 17. Relative densities of waders wintering along the non-estuarine open shores (thick lined coasts) of Great Britain in the winter 1984/85 (after Moser and Summers 1987).

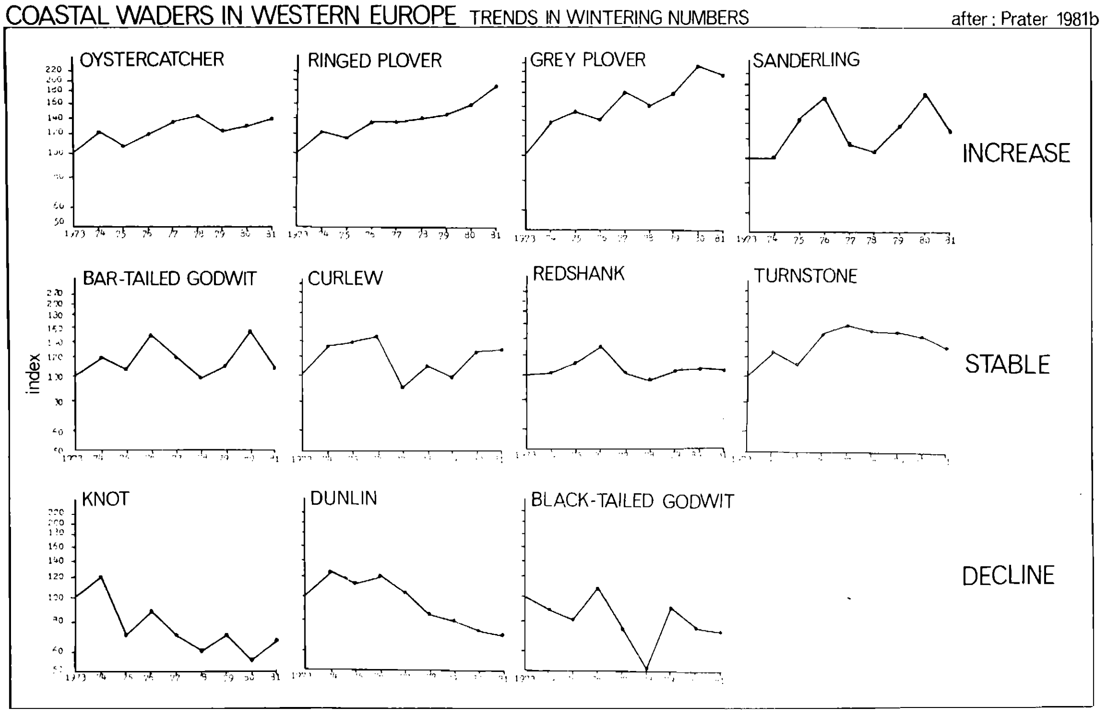


Figure 18. Population changes of coastal waders wintering in western Europe, from 1973/74 to 1980/81 (after Prater 1981b).

harboured at least 300 000 waders. This is 33% of the number wintering in the British estuaries, and 23% of the revised British total. Other European non-estuarine coastlines, notably in Ireland (M.E.Moser pers. comm.) are expected to hold also large numbers of wintering waders. (For Africa the same is true, but the practicalities of doing comprehensive surveys seem as yet unsurmountable.) This is yet another area of research where many new discoveries can be made.

Since the majority of the European estuaries are covered by counts each winter, it is possible to use these counts to calculate trends in the sizes of the wintering populations. This kind of analysis is performed annually for the British estuaries (Salmon and Moser 1985), but the only existing analysis on the scale of western Europe is that by Prater (1981b, Figure 18) over the period 1973-1981. This analysis showed that 4 species increased, 4 others remained stable and 3 species (Knot, Dunlin and Icelandic Black-tailed Godwit) declined in numbers. Such analysis extended to recent years is now overdue. Interpretation of such trends would be helped considerably if more was known about trends in the breeding population levels (see above), and if comparable series of counts could be obtained for coastal waders at the major sites in west Africa (*e.g.* Banc d'Arguin, Archipelago dos Bijagos).

Oversummering

In several wader species a large proportion of the first winter birds remains the northern summer on the wintering grounds and do not, or only partly, migrate (Elliott *et al.* 1976, Beintema and Drost 1986, Summers *et al.* 1987). The survival of this stock of juveniles is of obvious importance for future generations of waders. However, there is only little, and scattered, information on the size and composition of the summering populations, both in western Europe and Africa (*e.g.* Smit and Wolff 1981, Robertson 1981). A survey of the summering populations of waders on the wintering grounds throughout the flyway has not yet been made. Such information is likely to be important for nature conservation.

THE NORTHWARD MIGRATION

Inland waders

The timing of northward migration of inland waders is species-dependant. Some waders breeding in the temperate zone start migration very early (February). Most of those breeding in Scandinavia reach their migration peaks in central Europe in late April or early May (Hilden 1979); Siberian breeders are even later (Glutz von Blotzheim, Bauer and Bezzel 1975, 1977). The period of passage in Europe is usually quite short, often a few weeks only (Harengerd, Prunte and Speckmann 1973). As during the southward migration period, birds of most species are dispersed over many different resting sites (exceptions are Ruff and Black-tailed Godwit) and there are large annual fluctuations of resting numbers in many of these sites.

Migration routes and migration strategies are poorly understood for most of the species. Migration patterns of some species such as for Black-tailed Godwit and Ruff may be quite complex. Birds of both these species, which spend the winter in Senegal, may go either directly to France and the Netherlands, or stop in Italy. Some of the birds resting in Italy are later found on Dutch resting sites, and others in the East Germany and Poland. There is considerable evidence for loop migration patterns for some species like Little Stint and Curlew Sandpiper (see below) as well as for the Ruff. Ruffs, certainly those wintering in Senegal, use western Europe wetlands in spring but not at the same extent in autumn. Hence they probably migrate on a more eastern route in autumn. Numbers of stopping sites used

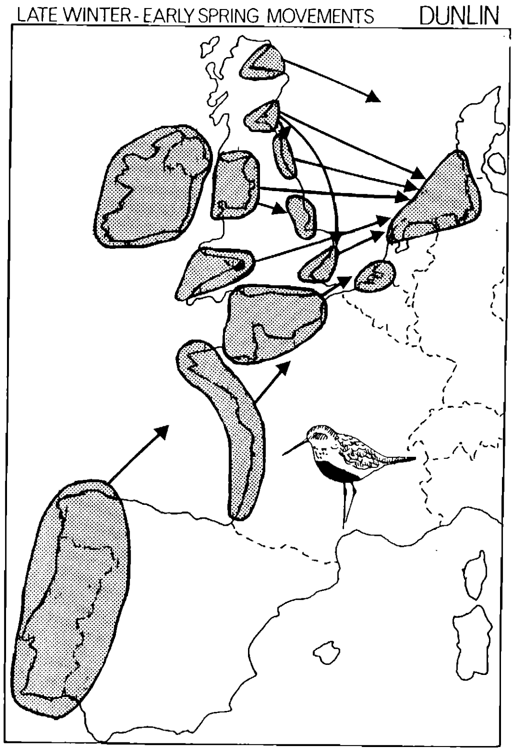


Figure 19. Summary of the early spring movements of northern Dunlin (*C.a.alpina*) in western Europe. Only connections for which there is direct evidence by the exchange of marked birds are indicated (from Pienkowski and Pienkowski 1983).

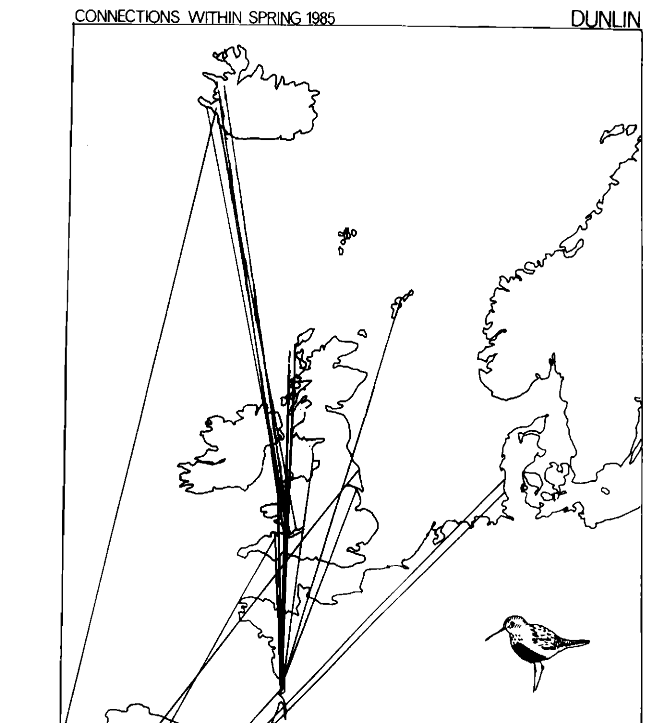


Figure 20. Summary of the spring movements of individual southern Dunlins (*C.a.schinzii*) from west Africa to Europe and within western Europe (Piersma in prep.).

during a spring migration are largely unknown for most species. Colour-marking of Ruffs has indicated that birds wintering in Senegal probably go directly to central Europe (OAG Munster in prep. b).

Coastal waders

A summary of the timing of spring migration of the coastal waders of the East Atlantic Flyway is provided by Pienkowski and Evans (1984: Table 1). Although detailed fieldwork and analyses of the spring migration of several wader species have been undertaken in recent years, resulting in some published analyses (Ferns 1980a, b, 1981a, b, Dick, Piersma and Prokosch 1987), there is a need for an up-to-date overview of the migration patterns of coastal waders along the East Atlantic Flyway. An example of the migration patterns of two subspecies of Dunlins is given in the Figures 19 (*C.a.alpina*) and 20 (*C.a.schinzii*). The *alpina* race concentrates in the Wadden Sea before departing in April to the north Fennoscandian and Soviet breeding grounds. The *schinzii* population winters in west Africa and returns to the breeding grounds on Iceland with stops in western Morocco and Portugal (though not shown in this sample), France and Great Britain. Some of the birds in Figure 20 apparently fly to the Baltic breeding sites (probably also stopping over along the way from the Banc d'Arguin). Both figures show only *proven* *intra*-seasonal movements of individuals during one migration, illustrating the effectiveness of extensive colour-marking work.

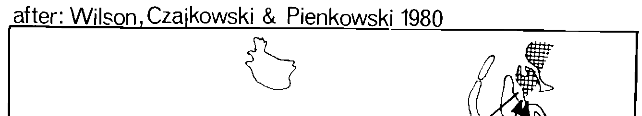


Figure 21. Schematic summary of the migration system of Curlew Sandpipers in Europe and Africa, showing the links between the East Atlantic and Mediterranean Flyways (after Wilson, Czajkowski and Pienkowski 1980). Breeding grounds are indicated by cross-hatching; wintering grounds by hatching, and the migration staging sites are circled.

BREEDING WADER SPECIES NUMBERS after: Alerstam et al. 1986

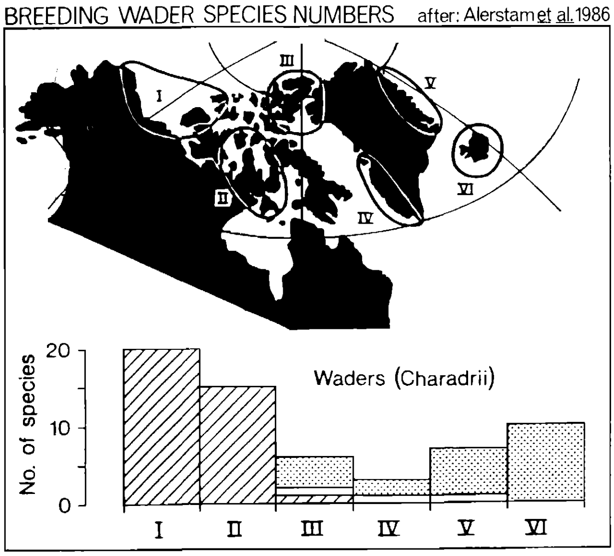


Figure 22. Species densities of breeding waders in different regions around the North Pole. Species wintering in the New World are indicated by hatching. East Atlantic Flyway species are stippled and unshaded is resident species with poorly known migration habits (from Alerstam *et al.* 1986).

Not all waders migrate along the seaboards of western Europe. Some species, like Little Stints and Curlew Sandpipers probably move more inland (many seemingly crossing the Sahara) from west African coastal wetlands (see *e.g.* Ens 1985: his Figure 6 shows a resighting in Malta of a Curlew Sandpiper dye-marked on the Banc d'Arguin, Mauritania). The probable pattern is illustrated in Figure 21 for Curlew Sandpipers and shows how this species may move between the two flyways. Although of great importance to our understanding about what natural entities we have to deal with in flyway conservation, there are no data on the details and extent of interchanges between the East Atlantic and the Mediterranean Flyways.

Stopover sites and breeding distribution

This paragraph links the first (breeding grounds) with the last (the northward migration) sections of this review of current knowledge about wader migration along the East Atlantic Flyway. From studies of arctic birds migrating over the Greenland ice-cap in spring, Alerstam *et al.* (1986) have proposed that the gap in the circumpolar breeding distribution of many species of waders (see Figure 22) may be explained by the limitations on successful spring migration imposed by the staging areas. The limitations are suggested to be due to competition for resources on the staging areas, and the distance to the breeding grounds. This view implies that successful occupancy of outlying breeding areas is only possible when high-quality stopover areas are available. This is thus an illustration of one possible bottleneck in the annual cycle of migrating wader populations. There may be many more. A sophisticated management of migratory bird populations, more than anything else, requires knowledge about such bottlenecks. As well as filling the gaps in distributional knowledge (patterns) identified in this review, it is therefore of great importance to continue the detailed ecological research aimed at understanding what makes a species do what it does.

THE MAJOR GAPS IN KNOWLEDGE

In this review we have shown that, despite the fact that the wader populations and migrations along the East Atlantic Flyway are heavily researched and relatively well-known, there are many large and important gaps that still remain. The review has identified the following 14 major gaps in knowledge of waders on the East Atlantic Flyway. These are listed below in the same order as the sections of the review:

1. Population sizes of waders breeding in the USSR and in the countries around the Mediterranean.
2. Changes in the population sizes of European breeding waders.
3. Geographical variations in breeding productivity per pair, and per unit area, over species' ranges in Europe.
4. Autumn migration patterns of inland waders.
5. The relative importance of different coastal moulting sites along the East Atlantic Flyway.
6. The winter distribution over Europe of open-habitat inland waders (Golden Plovers, Lapwings and Curlews).
7. Numbers of waders wintering in inland areas in Africa.
8. Numbers of wintering coastal waders along the Gulf of Guinea (from Guinea to Angola).
9. Numbers of waders wintering along the non-estuarine coasts of Europe (and Africa).
10. Population fluctuations of waders wintering in coastal west Africa.
11. Size and composition of the oversummering wader populations along the East Atlantic Flyway.
12. Spring migration patterns of inland waders.
13. Migratory pathways of the waders wintering in coastal west Africa.
14. Connections involving migrating waders between the East Atlantic and Mediterranean Flyways.

These 14 major gaps in knowledge are of different kinds. The last concerns the delimitation of the actual flyway. Others refer to gaps in rather advanced knowledge about population processes (nos. 2, 3, 10, 11). It should be realised however, that apart from its intrinsic biological importance, this sort of information is also a basic requirement for sound and well-founded nature conservation and management practices. The (perhaps) largest gaps in knowledge about the East Atlantic wader flyway are still the lack of some kinds of simple distributional knowledge (1, 6, 7, 8, 9). There is much scope yet for pure description, even in this part of the world. The last type of missing information concerns the moulting and migration patterns and strategies of waders (4, 5, 12, 13). This information is required to define the crucial importance of single sites in the annual cycle of waders (moult), and also the inter-connections of all these sites (migration). The very fact that migrant waders use series of wetlands in the course of a year has the greatest implications for developing effective management and conservation strategies. To ensure their survival, the conservation of entire chains of suitable wetlands is required.

There remains enormous scope for both field and desk studies on the wader migration systems of the East Atlantic Flyway. We want to emphasize here that as well as collecting new data, there is a need also for comprehensive and innovative syntheses of information that is already available, both in published and unpublished forms.

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