Breeding origins of wader populations utilizing the Dutch Wadden Sea

as deduced from body dimensions, body mass, and primary moult

RIJKSUNIVERSITEIT GRONINGEN

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door

Meinte Engelmoer
geboren op 20 mei 1954
te Leeuwarden

Promotor : Prof. dr. T. Piersma

Beoordelingscommissie : Prof. dr. P.H. Becker
Prof. dr. W.J. Wolff
Prof. dr. J. Fjeldså

Contents

Field work in ornithology is almost always the joint responsibility of many research workers, most of them being volunteers. The reason is obvious: observations made by one person at one specific location are not easily generalized. Much fieldwork in ornithology is carried out to extend our knowledge about the time-dependent spatial distribution of birds. Such knowledge builds on assessments of abundances and on ringing studies at various locations throughout the year. Ringing activities were started in the Wadden Sea by Boere on Vlieland and Nieboer on Schiermonnikoog in the early 1970s, and by Joop Jukema, Ulbe Rijpma†, Arend Timmerman, Klaas Koopman, and Piet Zegers along the mainland coast later in the 1970s and 1980s. Through the years a large amount of observational material has been produced and reported in for instance Nieboer (1972), Boere *et al.* (1973), Boere & Zegers (1974, 1975, 1977), Boere (1976), Koopman *et al.* (1982), Goede & Nieboer (1983), Boere *et al.* (1984), Van der Have *et al.* (1984), Koopman *et al.* (1985), Nieboer *et al.* (1985), Zegers (1985), Koopman *et al.* (1986), Koopman (1987), Goede *et al.* (1990), Koopman (1992), Engelmoer (1995), Zwarts *et al.* (1996b&c), Engelmoer & Roselaar (1998) and Koopman (2002).

This thesis is an attempt to update part of this material. A paper with the same title and co-authored by E. Nieboer, G.C. Boere, J. Jukema, K. Koopman, and A. Timmerman is under preparation. I am grateful to these co-authors that they allow me to submit a PhD version of this manuscript. It goes without saying that we owe a great deal to the colleagues, volunteers, and professionals, who collected the data.

The main purpose of this thesis is to make quantitative statements about the geographical breeding origins of waders captured in the Wadden Sea by comparing their wing- and culmen lengths with those of birds of known breeding origin. Quantative information about wing- and culmen lengths of birds breeding in specific areas was mainly obtained by visiting a number of zoological museums examining the collections of museum skins present there. I am very grateful for having had the opportunity to measure these skins.

When this thesis was approved some months ago, I was just too late for having the possibility to finish it with both the promotor and the co-promotor at that time Rudi Drent and Willem Schaafsma. The work should have been finished at least two months earlier. Through the years Rudi Drent has guided me until this stage. When I decided to take the final spurt he agreed and proposed to ask Willem to support me with the statistical contents. I am very grateful for their support and I would like to express my gratitude for it. It is a pity not to finish this undertaking as intended. Nevertheless I was very happy, that Theunis Piersma was willing to take over Rudi's task as promotor.

To my parents for their sincere belief

in the rewards of education
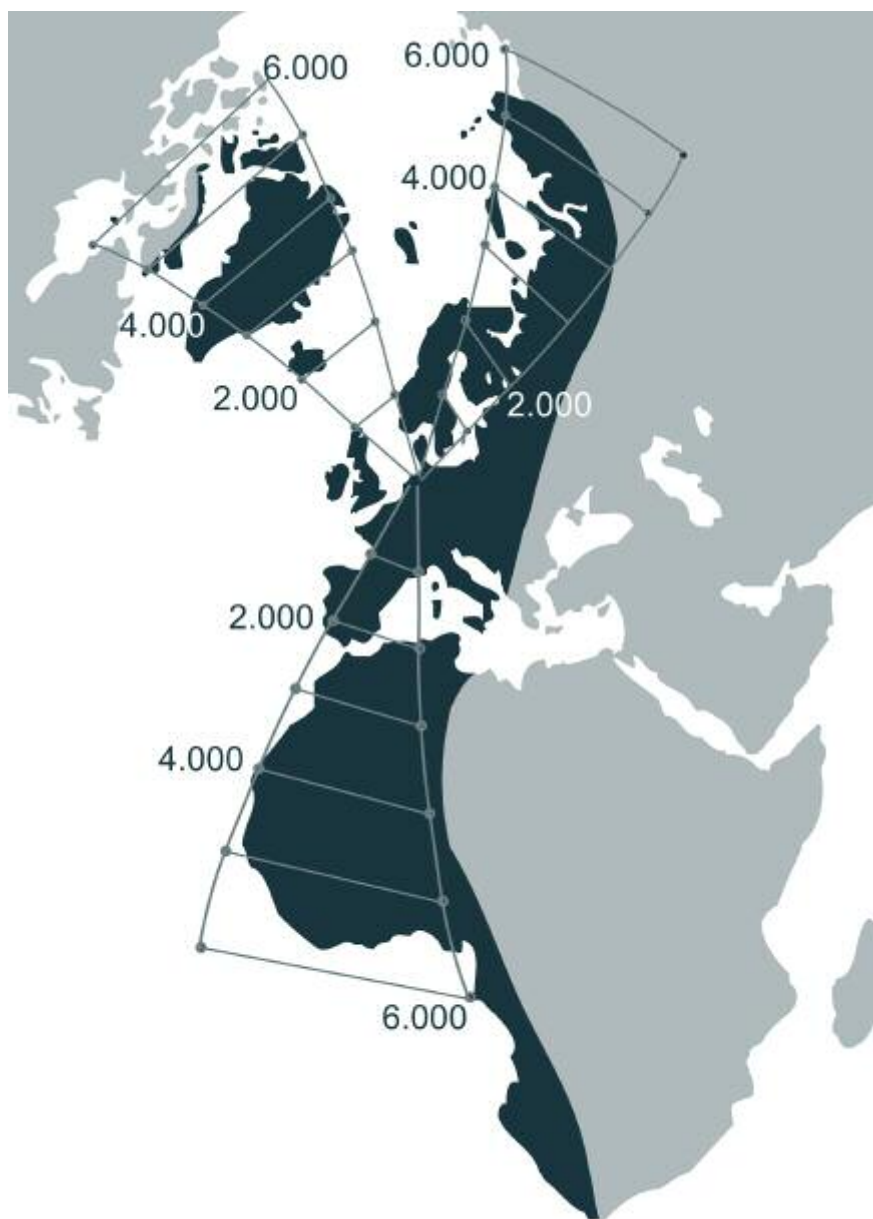
INTRODUCTION

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Figure 1: The East Atlantic flyway (in black) with the migration distances to and from the Wadden Sea according to the Great Circle routes. The migration distances are indicated with drawn lines. The figures represent the distances in kilometres.

1.1 GENERAL PERSPECTIVE

S oon after the large-scale catching studies started in the Wadden Sea, it became evident that waders in the Wadden Sea originate from a wide range of breeding grounds between Ellesmere Island in NE-Canada in the west to the Siberian Taimyr Peninsula in the east (Fig. 1, Annex 1). A continuously growing number of ring recoveries consolidates this picture (Smit & Wolff 1981, Prokosch 1988). The wide scope of breeding ranges results in large proportions of the world populations of several (sub)species temporarily using the Wadden Sea during the non-breeding season (Boere & Zegers 1974, 1975, 1977, Zegers 1985, Smit & Piersma 1989, Zegers & Kwint 1992, Meltofte *et al.* 1994, Koffijberg *et al.* 1999, De Boer *et al.* 2001, Kleefstra *et al.* 2002, Van Roomen *et al.* 2002, 2003, 2004, 2006a, 2006b). The essence is presented in Table 1.

Table 1. Estimates of the population sizes of the studied wader species in the East Atlantic flyway (Stroud et al. *2004*). The percentages of wintering along the Atlantic coast of Europe and in the W-part of the Mediterranean concern the results of January 1995 presented by Delany et al. (1999). The percentages present in the international Wadden Sea are derived from the counts presented in Meltofte et al. (1994). Information on the reliability of large-scale counts can be found in Rappoldt et al. 1985). Percentage ranges are presented for Spotted Redshank, Greenshank and Turnstone, which is due to the ranges in population size estimates of the E-Atlantic flyway.

Species		population size estimate E-Atlantic flyway	% winter W-Europe & W-Medi- terranean	% present in the international Wadden Sea			
				autumn	winter	spring	summer
Ringed Plover	*Charadrius hiaticula*	263000	20	5	0	53	1
Grey Plover	*Pluvialis squatarola*	247000	50	30	8	57	1
Red Knot	*Calidris canutus*	790000	47	45	13	55	3
Sanderling	*Calidris alba*	123000	22	11	5	16	2
Curlew Sandpiper	*Calidris ferruginea*	740000	0	1	0	0	0
Dunlin	*Calidris alpina*	2343000	53	51	11	48	1
Bar-tailed Godwit	*Limosa lapponica*	640000	16	24	7	53	2
Eurasian Curlew	*Numenius arquata*	420000	77	54	42	29	4
Spotted Redshank	*Tringa erythropus*	30-76000	2-4	9-23	0	10-25	2-5
Redshank	*Tringa totanus*	44000	28	14	4	7	2
Greenshank	*Tringa nebularia*	234-395000	0-1	4-6	0	2-3	0
Ruddy Turnstone	*Arenaria interpres*	140-213000	16-25	2-4	2-3	3-5	0

At present, a relatively clear picture exists on the functioning of the Wadden Sea in the wader migration system of the East Atlantic Flyway (Boere 1976, Smit & Wolff 1981,

Prokosch 1988, Smit & Piersma 1989, Meltofte *et al.* 1994, and Van de Kam *et al.* 1999):
When the breeding season ends, adults leave the breeding grounds in advance of the juveniles,
female waders usually earlier than male ones. They flock together preparing their migration
to the south which, somewhat amazingly, starts while the weather conditions in the breeding
region have not yet deteriorated. After arrival in the Wadden Sea, part of the population
stays for a relatively short period to recuperate and prepare for migration to the N- and
W-African wintering grounds (Annex 1), where they will moult. These are the transmigrants.
Others stay for a longer period in the Wadden Sea in order to moult into winter plumage
(post-breeding moult), followed by a variety of migration and wintering habits. Some birds
try to stay and winter in the Wadden Sea area. Others leave the moulting grounds after
having finished the post-breeding moult in order to winter in the milder parts of Europe.
Again others suspend their post-breeding moult before their departure to other wintering
grounds, where they will complete the moulting process under mild climate conditions.
It depends on the severity of the weather conditions during winter, whether waders will stay
in the Wadden Sea or leave the area in order to winter further to the west or south in Europe.
The return migration starts already by the end of February, resulting in an increase of
numbers in the Wadden Sea from March onwards. Spring departure from the Wadden Sea
strongly depends on the climate conditions at the breeding grounds: birds breeding in the
temperate and boreal climate zones depart by March or April and the ones breeding in the
high arctic depart by end May or early June.

If the term 'Wadden Sea' is used, it refers to the Dutch part. When the German and Danish
parts are not excluded, this is expressed by using the term 'international Wadden Sea'.
Throughout this text the notion 'post-breeding period' or 'post-breeding' is used, even
though it is somewhat strange when used in contexts with non-breeding birds.
It refers to the period between mid June, when Spotted Redshank start to return from their
breeding grounds, to end November, when all adults have finished moulting. It thus spans
both summer and autumn. In this text 'winter' covers the period December, January, and
February. The 'pre-breeding period' starts in March, when waders return to the Wadden Sea
from their wintering grounds and ends by early June, when the last high arctic migrants have
left the Wadden Sea, even though Ringed Plover, Eurasian Curlew, and Redshank already
start to breed in the area by April.

1.2 AIMS OF THIS STUDY

Through the years many studies have been made to quantify the time-dependent spatial distribution of wader populations in relation to age, sex, breeding area, moult, and body mass. This thesis elaborates on a series of papers dealing with the function of the Wadden Sea in the yearly wader migration cycles and with the breeding origin of waders visiting this area (in particular: Nieboer 1972, Boere *et al.* 1973, Boere 1976, Nottrot 1981, Smit & Wolff 1981, Boere *et al.* 1984, Van der Have *et al.* 1984, and De Goede *et al.* 1985). This paper includes an effort (1) to compare measurements of staging populations in the Wadden Sea with the measurements of known breeding populations, (2) to improve the comparability of the measurements obtained on the breeding grounds with the ones obtained during migration and winter, and (3) to evaluate numerical assessments of probability based on the morphometric comparisons. Our main purpose is to make inferences about the breeding origins of waders captured in the Wadden Sea on the basis of their morphology, wing- and culmen length in particular. Therefore, the observational material from both the catches in the Wadden Sea and the museum measurements (largely based on measurements of wing- and culmen length of skins in museum collections throughout the world), as well as the statistical methodology of Engelmoer & Roselaar (1998), will be updated and extended. Nearly all observational material about waders collected in the Wadden Sea between 1970 and 2000 is incorporated. The methodology is extended by introducing a simple but convenient method for estimating proportions in a population composed of birds from different breeding origins based on the wing- and culmen lengths of a 'sample' of birds captured from the mixed population. Behind all our work is the desire to describe and evaluate the observational material made available by all those who were involved in counting and catching activities in the Wadden Sea area.

With respect to the *wader counts*, attention will be paid to three major sources of variation in the time-dependent spatial distribution of twelve wader species in the area (Fig. 2). The first source of variation concerns the long-term trends over the years. Yearly fluctuations in mortality and productivity will have effects on staging numbers in the Wadden Sea area. Secondly, there is the seasonal variation with certain species or populations being more abundant during winter and others during spring migration. Thirdly, there is the spatial variation within the Wadden Sea illustrating preferences for feeding and roosting areas.

With respect to the *catching results*, The same sources of variation will be discussed. By measuring birds caught additional information is obtained with respect to the spatial and temporal variation of wader populations. Some specific topics are as follows:

	Long-term changes	Seasonal variation	Spatial variation
Staging numbers	figs. 15, 17	Table 1, Fig. 17	Table 13
Age composition	tables 16, 17, 18 Fig. 19	Table 14, Fig. 18	Table 14
Primary moult	figs. 21, 23	Table 16,	figs. 20, 22, 23
Body mass		energy reserves figs. 24 through 28	moulters Table 21
		flight ranges figs. 29, 30	
Breeding origin			
Ringed Plover		Table 22	
Grey Plover		Table 23	Table 24
Knot		Table 22, Fig. 34	
Curlew Sandpiper		Table 26	
Dunlin	tables 27, 28 figs. 37, 38	tables 27, 28 Fig. 37	tables 27, 28 figs. 37, 38, 39
Bar-tailed Godwit		Table 29	tables 30, 31
Curlew		tables 32, 33	
Redshank		Table 34, Fig. 43	Table 34, Fig. 43

Figure 2: The three major sources of variation analysed in this paper with respect to the population numbers staging in the Wadden Sea and to the population composition estimates with respect to age composition, primary moult, body mass and breeding origins. Presented are the numbers of the relevant figures and tables.

1. *Analysis of data with respect to geographical breeding origin.* The measurements of individuals of known origin were obtained from skins of birds shot in the breeding area and present in museum collections throughout the world. The results of an earlier study concentrated on the differences in measurements between breeding areas for various wader species separately (Engelmoer & Roselaar 1998). In principle, it is possible to estimate the population composition of mixed wader populations with the statistical characterization (in terms of means, standard deviations, and correlations) of the population distributions of measurements. The underlying statistical analyses consist of comparisons between the measurements of birds of the mixed Wadden Sea population and the statistics characterizing the breeding wader component-populations. We make statements about the time- and space- dependent proportions of birds from different breeding areas present in the Wadden Sea. For that purpose some multivariate methods

were used. Since the methodology, described in Engelmoer & Roselaar (1998) was not always useful, we shall have to develop some alternative methodology.

2. *Age composition.* Van der Have *et al.* (1984) and Swennen (1984) already showed that juveniles and adults select different areas when visiting the Wadden Sea. Thus, age composition will be different at the various sites.

3. *Primary-moult patterns.* As moulting adults tend to stay longer in the Wadden Sea than non-moulting adults after arrival from the breeding grounds, attention has to be paid to primary-moult patterns prior to mass analysis.

4. *Body mass.* Smit & Wolff (1981) presented statistics with respect to masses of several species captured on the island of Vlieland. Since then additional data were collected at other sites and analysed for Oystercatcher (Koopman *et al.* 1985, Zwarts *et al.* 1996c), Purple Sandpiper (Boere *et al.* 1984), Dunlin (Van der Have *et al.* 1984, De Goede *et al.* 1985, Goede *et al.* 1990), Bar-tailed Godwit (De Goede *et al.* 1985, Piersma & Jukema 1990), and Redshank (Koopman *et al.* 1982). The masses of adults will be analysed in relation to primary moult. The results are discussed in relation to the population composition estimates.

DATA AND BASIC METHODS

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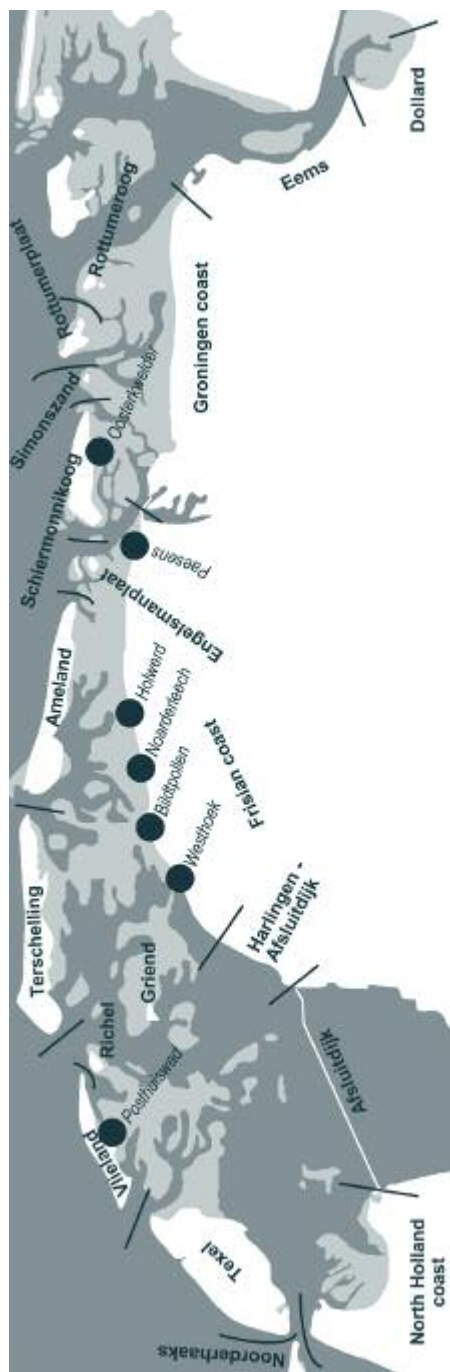
Figure 3: An overview of the study area. The white areas are not inundated at high tide, the light grey ones are covered at high tide and exposed at low tide (the intertidal zone), and the dark grey ones are also covered at low tide (the subtidal zone). The black circles indicate the major trapping sites of waders. The drawn lines separate the various counting areas mentioned in Fig. 4.

This sort of broad-scale studies over a 30-year period may be corrupted by measurement errors and mis-classifications. During these years, I experienced two major sources of errors. The first one concerns erroneous notes taken during nightly catching activities and the second one occurs when converting field forms into computer files. As a result, some birds will have been assigned to wrong species, age, or sex category. Or their measurements may have been reported wrongly, etc. Therefore, both the field- and computer data were critically examined. I did my utmost to provide appropriate corrections.

Nearly all computations were performed with SPSS (Norušis 1992a, b & c, Sybex 1996, Norušis 1998).

2.1 STUDY AREA

The Wadden Sea covers 272,000 ha. About 234,000 hectares are legally designated for nature protection (Van den Tempel & Osieck 1994, Heath & Evans 2000). The largest part of the area consists of intertidal areas covered by the sea at high tide and exposed at low tide (Fig. 3). These mudflats are the main feeding grounds of the species studied. At rising tide, waders move from the feeding grounds to their roosting areas near the flood line. Nearly all waders were captured with mist-nets, during these high-tide flights, at the following catching sites: on Vlieland the Posthuiswad (53°15N 4°58E), on Schiermonnikoog the Oosterkwelder (53°28N 6°10E), and along the Frisian mainland coast Westhoek (53°17N 5°33E), Bildtpollen (53°18N 5°37E), Noarderleech (53°20N 5°45E), Holwerd (53°23N 5°52E), and Paesens (53°24N 6°08E). Detailed descriptions of these catching sites are given by Nieboer (1972), Boere *et al.* (1973), Boere (1976), Koopman *et al.* (1982 & 1985), and Goede *et al.* (1990). The first two catching sites are located in the pioneer zones of the salt-marshes on the barrier islands Vlieland and Schiermonnikoog. Both sites have sandy mudflats and salt-marshes with the Oosterkwelder-site being more sandy than the one on Vlieland. The last four sites are located in the salt-marshes along the Frisian mainland coast. These sites have clayish mudflats skirted by salt-marshes.

2.2 SPECIES SELECTION AND THEIR BREEDING DISTRIBUTION

Species selection for this thesis is based upon the availability of catching results. Only species captured in good numbers will be analysed: Ringed Plover *Charadrius hiaticula*, Grey Plover *Pluvialis squatarola*, Red Knot *Calidris canutus*, Curlew Sandpiper *Calidris ferruginea*, Dunlin *Calidris alpina*, Bar-tailed Godwit *Limosa lapponica*, Eurasian Curlew *Numenius arquata*, Redshank *Tringa totanus*, Greenshank *Tringa nebularia*, and Ruddy Turnstone *Arenaria interpres*. Sanderling *Calidris alba* and Spotted Redshank *Tringa erythropus* will also be included, since both regularly occur in the Wadden Sea and in spite of the fact that they were only rarely caught. The Oystercatcher *Haematopus ostralegus* is not included in this study, even though it is regularly captured and a regularly occurring species in the region. The main reason is that our data would not add substantially to the picture already known from earlier publications (Ens 1992, Blomert *et al.* 1996, Goss-Custard 1996, Kersten 1997, Heg 1999). Some publications on Oystercatchers (e.g. Zwarts *et al.* 1996a, b, c & d) were partly based on measurements and mass-data obtained by the catching activities of ringers involved in the present paper.

The breeding distribution of the species involved is presented on species' maps inserted in the back flap. These maps were based upon the maps presented in Engelmoer & Roselaar (1998) with additional information from Prokosch *et al.* (1993), Underhill *et al.* (1993), Hustings & Van Dijk (1994), Schekkerman & Van Roomen (1995), Tomkovich & Soloviev (1996), Valle & Scarton (1996), Whitfield *et al.* (1996), Tulp *et al.* (1997), Belik (1998), Blokhin (1998), Butiev & Lebedeva (1998), Byrkjedal & Thompson (1998), Gilyazov (1998), Gromadzka & Ryabitsev (1998), Lappo (1998), Lappo & Tomkovich (1998), Lebedeva (1998), Mischenko & Sukhanova (1998), Morozov (1998), Nikiforov (1998), Nikolaev (1998), Ryabitsev & Alekseeva (1998), Samigullin (1998), Tulp *et al.* (1998), Zekhuis & Tempelman (1998), Zubakin *et al.* (1998), Khomenko *et al.* (1999), Exo & Stepanova (2000), Gilg *et al.* (2000), Tomkovich *et al.* (2000). Whatever distribution maps for the (sub)arctic region are produced, three major handicaps must be kept in mind. Firstly, in our maps only confirmed breeding and the generally accepted large breeding ranges are presented. Confirmed non-breeding in well-studied areas is not presented, even though such is just as valuable. Secondly, confirmed breeding might indicate large as well as low breeding densities. Thirdly, the breeding distribution maps are based upon published records covering nearly the whole 20th century, whilst the population levels as well as the breeding ranges have changed considerably during this century (for instance Tomkovich 1992, Gilyazov 1998, Lebedeva 1998).

2.3 WADER COUNTS

Many bird counts have been carried out in the Wadden Sea since the end of the 1960s. Such counting results are always based on counts made by observers present at a specific location on various dates. They certainly provide knowledge about the changes in numbers of the populations per species present at that specific location. In order to obtain a more global perspective, counting programs have been designed involving simultaneous observations by different observers throughout the international Wadden Sea or -in case of midwinter counts- throughout the world. Apart of these *simultaneous counts*, also *local counts* were performed, e.g. when a person repeatedly counted only one counting area (e.g. Engelsmanplaat) or a group of people only repeatedly counted a selection of *counting areas* (e.g. the barrier islands). The Wadden Sea is divided in 19 different counting areas (Fig. 3). Catching activities differ from counting activities, which is why the counting areas do not correspond with the locations of the catching sites.

Many local counts originate from Griend and Engelsmanplaat: areas with wardens during summer (Fig. 4). As a consequence, high numbers of records occur during May, June, and July in the 1970s and 1980s (Fig. 5). In total, 84 simul-taneous counts were performed between July 1972 and June 1999, with the following frequencies per month: January 26, February 3, March 6, April 5, May 12, June 2, July 2, August 4, September 8, October 6, November 7, and December 3. The counted numbers resulting from these simultaneous
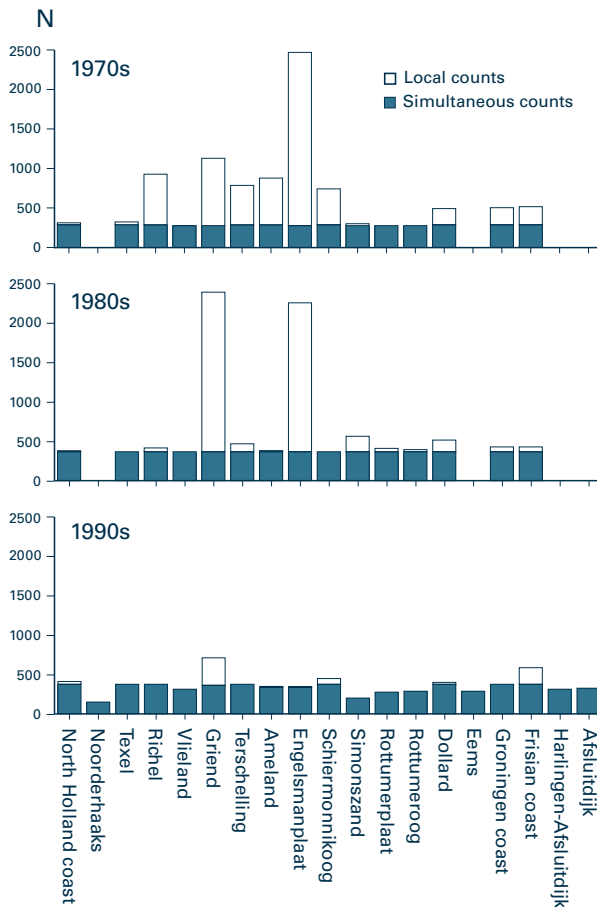
Figure 4: The number of records per counting area, collected since the 1970s, in the wader counts-database used in this study. Distinction is made between the records obtained with simultaneous counts or with local counts.

counts were presented in Boere & Zegers (1974, 1975, 1977), Zegers (1985), Zegers & Kwint (1992), Meltofte *et al.* (1994), Smit & Zegers (1994), Koffijberg *et al.* (1999), and De Boer *et al.* (2001).

The counting results of twelve wader species, collected in the Wadden Sea during the 1970s, 1980s and 1990s, are analysed. The resulting database includes 26,882 entries, of which 11,292 originate from local counts and 15,590 from simultaneous counts. Each entry represents the numbers of birds counted present per species, counting area, and date. It is sometimes impossible to count a species, due to a series of reasons. It is of some interest in this respect to note that the number of entries per species ranges from 2,153 in the Sanderling to 2,296 in the Ruddy Turnstone.
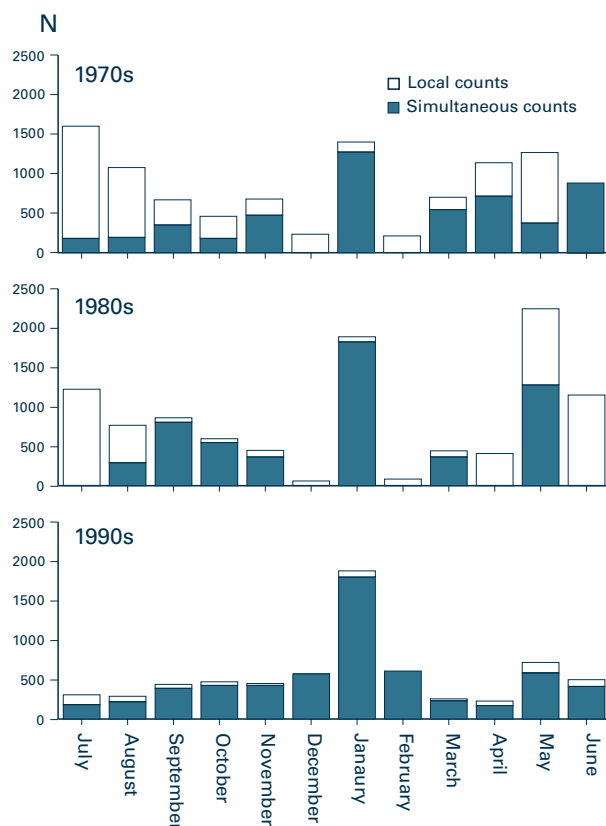
Figure 5: The number of records per month collected since the 1970s in the wader counts-database used in this study. Distinction is made between records obtained with simultaneous counts or with local counts.

Wader counts were analysed with respect to the three sources of variation mentioned earlier. Long-term trends since the season 1975/76 were provided by SOVON Bird-research Netherlands (Van Roomen *et al.* 2005 & 2006a) and were produced with the computer program TrendSpotter (Visser 2002). The second source of variation concerns monthly changes. Monthly averages per species were calculated and presented separately for the 1970s, 1980s, and 1990s. Spatial variation in numbers between the 19 counting areas is the third source of variation over the years. Spatial variation was quantified by calculating the mean number of birds per species and counting site for six different periods: July - August, September - November, December - February, March - April, May, and June.

The mean number was obtained by averaging over the counting days for a given period. The mean numbers of the 19 sites were added together, after which the proportions (expressed as percentages per site) were calculated (see Chapter 5).

2.4 PROCESSING WADERS

Nearly all data of waders captured (either by mistnet, cannonnet, or dazzle-light netting) in the Wadden Sea area during the 1970s and 1980s will be analysed in this study (Fig. 6). About half of the information from the 1990s is included as well, but the results of more recent work still have to be brought together and/or computerized, e.g. the catching efforts of De Roos on Vlieland, much of the work of the NIOZ-team catching throughout the Wadden Sea, some years of work of the Calidris-group on Schiermonnikoog, some data-sets of RUG-projects and the results obtained by Doevendans & Hendriksma from some sites along the mainland coast. We decided not to wait until all information from the 1990s was ready for analysis because one of the purposes of this thesis is to provide ideas about future analyses. Further delay would affect the usefulness of these ideas. In total, 32,446 waders were captured and

Figure 6: The number of waders included in this study and captured since the early 1970s on Vlieland, the Frisian coast and Schiermonnikoog.

Species	Vlieland	Frisian coast	Schiermon- nikoog	Elsewhere Wadden Sea	Total	% first winter birds
Ringed Plover	78	176	50	1	305	55.5
Grey Plover	285	448	366		1099	26.3
Red Knot	376	1095	775	2	2248	35.8
Sanderling	317	1	3		321	3.1
Curlew Sandpiper	153	169	16	1	339	52.8
Dunlin	4284	4938	9072	31	18325	25.9
Bar-tailed Godwit	662	954	874	219	2709	6.3
Eurasian Curlew	446	390	117	76	1029	17.4
Spotted Redshank	3	23	17	9	52	40.4
Redshank	1534	2442	482	231	4689	29.6
Greenshank	151	16	105		272	17.3
Ruddy Turnstone	893	140	25		1058	22.4
Total	9182	10792	11902	570	32446	25.4

measured (Table 2). The captured birds were processed as soon as possible after being caught. The data are based upon the catching activities of (1) G.C. Boere and P.M. Zegers mainly on Vlieland (*N*= 8,892), (2) E. Nieboer, mainly on Schiermonnikoog (*N*= 11,933), and (3) J. Jukema, K. Koopman, U. Rijpma, A. Timmerman, and P.M. Zegers, mainly along the Frisian mainland coast (*N*= 11,621).

Most birds were captured with mist-nets (*N*= 28,171). On Vlieland also cannon-nets (*N*= 2,842), catching cages (*N*= 273), and dazzle-lightning techniques (*N*= 92) have been used (described by Boere 1976). Along the Frisian mainland coast another 966 waders were trapped with so-called 'wilsternets' (Koopman & Hulscher 1979). The capturing method of the remaining 102 birds was not registered. Most birds were captured during late summer and autumn (Fig. 7). The activities generally diminished during winter and were resumed during spring. The main reason for the decrease of the activities during winter are severe weather circumstances and the reduced presence of waders in the area.

Sex

When possible, sex was determined according to Minton (1971) and Prater *et al.* (1977). Only 2,913 of the 32,446 waders captured were sexed, because of lack of distinguishing features. Of the birds sexed, 2,688 were Bar-tailed Godwits. In this species both sexes can be distinguished easily, since males are smaller than females, have different bill colour throughout the year and a bright red breeding plumage.

Age

When possible, age was determined according to Minton (1971) and Prater *et al.* (1977). The classification of age is based on plumage characteristics, being the colouration of feather fields, the presence of buff fringes or boldly spotted margins on coverts or the colour of bills and legs. The juvenile characters differ per species and are clearly presented in Prater *et al.* (1977). The field system of age determination followed the official EURING terminology: full-grown (*N*= 417), first calendar year (*N*= 7,025), after first calendar year (*N*= 19,168), second calendar year (*N*= 1,425), after second calendar year (*N*= 4,406), third calendar year (*N*= 1), and fourth calendar year (*N*= 4).

For the purpose of this publication this system was simplified to three partly overlapping age-classes. The first age-class concerns 'juveniles'. These are the first calendar year birds of the field system and can only be classified as such until December 31st. The 'first winter birds' are the second age-class. They include juveniles, first calendar year birds and second calendar year birds as long as they can be recognized as such. In these wader species, the recognition of second calendar year birds becomes gradually impossible as they undergo their moult during the summer of their second calendar year. The third age class 'adults' includes birds, classified in the field system as 'after first calendar year' when captured between July 1st and December 31st or as 'after second calendar year' when captured between January 1st and June 30th. The data of the 417 full grown birds were not used in age-specific analyses, since they might be first winter birds as well as adults.

The percentages first winter birds per catching effort and per site were calculated. Such an effort can be a catching night with mistnets as well as a catching day with cannon- or wilsternets. Data-analysis was then restricted to samples with five or more birds. If, for a specific species, sample sizes were too small, the catching results were combined
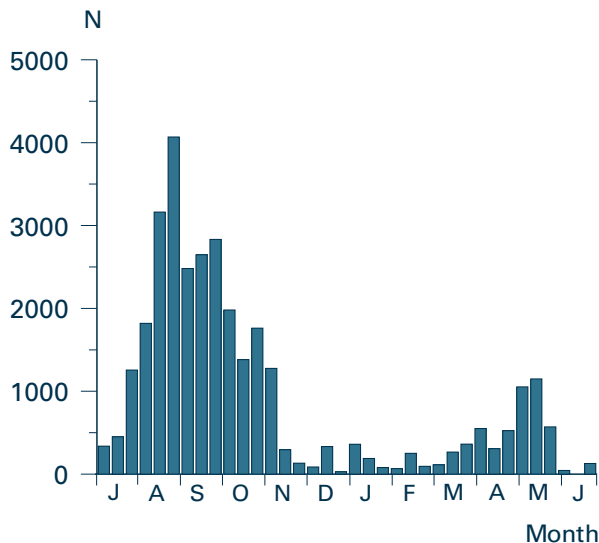

Figure 7: The number of waders captured per month from July through winter to June. The results from all three trapping sites and all years are combined.

with the ones of neighbouring catching nights or -days. Such a combination of catching nights (or days) is called a 'catching period'. By doing so, more samples could be added to the database. Sometimes a gap of one or two nights (or days) had to be allowed within the same catching period. A new catching period was defined to start when there was a gap in the catching activities for at least three nights (or days). Age-data from the three major catching sites Vlieland, the Frisian coast, and Schiermonnikoog were not combined. Similarly, sites along the Frisian coast were not combined either, since (1) they are generally about 20 km apart from each other and (2) some of these sites hold smaller populations than others, which might be related to different percentages first winter birds. The numbers of samples are presented in Table 3. In the data-analyses, the percentages first winter birds of a particular catching night or period will be considered as point estimates. For reasons of efficiency, the mean percentages of first winter birds were already presented in Table 2.

It is of interest from an ecological perspective, to study the variation in percentages juveniles and/or first winter birds. Therefore, the spatial and temporal variation in age composition on the various catching sites in the Wadden Sea is analysed (see later) to validate and extend findings of earlier studies, e.g., Roselaar (1979), Prokosch (1981), Van der Have *et al.* (1984), Swennen (1984), Summers & Underhill (1987), Mason (1988), Underhill *et al.* (1989), Ebbinge (1992), Boudewijn & Ebbinge (1994), Rybkin (1998), and Madsen *et al.* (1999). These studies had concluded, that adults and juveniles tend to adopt different migration schedules, routes, and staging grounds, both during post-breeding and spring. Also, Minton (2003), Clark *et al.* (2003 & 2004), and Gunnarsson (2006) focus on the biases associated with estimating age composition during autumn migration and winter and try to deal with these biases, since standardized estimates would be very useful in the large-scale monitoring of wader breeding success. Several of these studies and many others have shown, that the estimates of age composition vary with time and space, with juveniles arriving generally later than adults on the passage grounds, and with different habitat choices between both age-groups both during passage and wintering. In addition, small samples tend to contain relatively more juveniles than large ones (Van der Have *et al.* 1984, Swennen 1984, Gunnarsson 2006) and also relatively more juveniles are trapped with mist nets than with cannon nets (Goss-Custard *et al.* 1981, Insley & Etheridge 1997). To test these claims, our age-data collected during post-breeding will be analysed with respect to month, catching site, and sample size by using species-dependent GLM-analyses. Percentages first winter birds obtained with cannon nets will be excluded in the analyses, since nearly all birds were trapped with mist nets. The residual percentages first winter birds obtained, representing that part of the variation in productivity which is not explained by the three mentioned factors, are averaged per post-breeding season resulting in maximally 32 averages per species between 1967-1999. These seasonal mean residuals have been weighted for sample

Table 3. The number of samples, which were collected in the Wadden Sea between 1967 and 2000. A single sample concerns the percentage first winter birds for a given species and site per catching effort or per combination of catching efforts (details in section 2.4 - age). For instance, in September 22 estimates of the percentage first winter birds were gathered on Schiermonnikoog. 'V' stands for Vlieland, 'F' for the Frisian coast and 'S' for Schiermonnikoog.

Species	Site	July	August	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
Ringed Plover	V	-	9	1	-	-	-	-	-	-	-	-	-
	F	-	6	7	-	-	-	-	-	-	-	-	-
	S	-	5	5	-	-	-	-	-	-	-	1	-
Grey Plover	V	-	1	9	11	5	-	1	1	1	2	4	-
	F	-	11	11	10	2	-	-	-	-	-	14	-
	S	1	30	22	23	4	-	-	-	-	-	1	-
Red Knot	V	-	4	11	5	1	-	1	-	1	-	-	-
	F	4	15	7	4	-	1	2	2	-	-	-	-
	S	2	16	27	12	-	-	-	-	-	-	-	-
Sanderling	V	-	2	1	-	-	-	-	-	-	-	-	-
	F	-	-	-	-	-	-	-	-	-	-	-	-
	S	-	-	-	-	-	-	-	-	-	-	1	-
Curlew Sandpiper	V	6	14	4	-	-	-	-	-	-	-	-	-
	F	-	9	5	-	-	-	-	-	-	-	-	-
	S	-	1	-	-	-	-	-	-	-	-	-	-
Dunlin	V	16	42	35	37	12	1	7	-	9	6	7	-
	F	7	49	40	31	9	-	3	6	11	19	18	-
	S	17	105	83	78	18	2	-	-	1	25	23	-
Bar-tailed Godwit	V	1	8	7	8	9	1	3	2	9	3	4	-
	F	1	9	1	-	-	-	-	-	-	3	50	-
	S	8	34	20	13	5	-	-	-	-	8	24	-
Eurasian Curlew	V	1	1	7	5	2	1	4	2	6	1	-	-
	F	4	1	6	8	2	-	-	5	-	2	1	-
	S	1	6	12	11	-	1	-	-	-	2	-	-
Spotted Redshank	V	-	-	-	-	-	-	-	-	-	-	-	-
	F	-	-	-	-	-	-	-	-	-	-	-	-
	S	-	-	1	1	-	-	-	-	-	-	-	-
Redshank	V	13	24	12	15	7	5	8	-	7	5	5	1
	F	20	45	27	17	4	3	3	4	1	13	10	-
	S	5	28	16	8	8	-	-	-	-	-	-	-
Greenshank	V	3	2	-	-	-	-	-	-	-	-	-	1
	F	-	-	-	-	-	-	-	-	-	-	-	-
	S	3	15	6	-	-	-	-	-	-	-	-	-
Ruddy Turnstone	V	2	10	4	2	2	1	1	1	2	1	5	-
	F	-	2	-	-	1	1	2	-	1	-	2	-
	S	1	2	2	3	-	-	-	-	-	-	-	-

size and were related to a set of indices referring to (1) breeding circumstances (weather conditions, food), (2) conditions during migration (weather, condition adults during pre- and post-breeding migration, and condition juveniles during post-breeding migration) and (3) winter conditions (severe weather, food). The following indices were used:

1. *The Siberian Brent Geese productivity cycle.* Several arctic breeding waders have a 3- to 4-year cycle in their productivity pattern, which -for Siberian wader populations- might be reflected in the Brent Geese productivity pattern (Madsen *et al.* 1999, SOVON Ganzen- en Zwanenwerkgroep 1997, 1998 & 1999, and own data). Commonly, the idea behind the cyclicity of this productivity pattern is, that non-breeding years happen to occur in poor lemming years causing the predators to shift their diet from lemmings to birds' eggs and pulli. In years with many lemmings predators can cling to their preferred prey, being lemmings. Therefore, if a species in the Wadden Sea originates mainly from the Siberian breeding grounds, correlation with the Brent Geese productivity pattern might be expected. Tomkovich & Soloviev (1999 - 2004) also give insight in the breeding conditions in relation to the productivity.

2. *Numerical changes in wader abundance.* The long-term trends of wader numbers both in the Netherlands and on the British isles, are used according to Van Roomen *et al.* (2005 & 2006a), Collier *et al.* (2005), and Cranswick *et al.* (2005). The changes from one year to the other in the wintering populations might reflect the relative influence of productivity and mortality, but also emigration and immigration might be of influence on the yearly changes.

3. *Climate Wadden Sea.* The strength of the preceding winter in the Wadden Sea as represented by the winter index of IJnsen (IJnsen 1988, Camphuysen 1998). A seasonal winter index is defined as w= $0.00275*v^2 + 0.667*y + 1.111*z$ with 'v' being the number of days that the minimum temperature stays below 0°C, 'y' the number of days that the maximum temperature stays below 0°C and 'z' the number of days that the minimum temperature stays below -10°C from November throughout March. This winter index practically ranges between 0 and 100 as far as the Wadden Sea is concerned. Temperatures registered in De Bilt (NL) by the Royal Dutch Meteorological Institute were used for this exercise.

4. *The North Atlantic Oscillation.* Several authors advocate the role of the North Atlantic Oscillation (NAO) in ecological processes in the northern hemisphere including breeding performance (a.o. Sims *et al.* 2001, Post & Forchhammer 2001, Thompson & Ollason 2001, Gjerdrum *et al.* 2003, Post & Forchhammer 2004, Vähätalo *et al.* 2004, and Vik *et al.* 2004). The difference between the atmospheric pressures at sea level on Gibraltar and in SW-Iceland is often used as the index of strength of the NAO. This index is varying in a rhythm of about 30 years and can be both positive and negative. A positive value

reflects a larger difference than normal and is associated with relatively warm and wet winter conditions in Europe and relatively cold and dry winter conditions on Greenland and Iceland. A smaller difference than normal provides a negative value of the NAO-index and is associated with opposite climate conditions: a relatively cold and dry winter in Europe. A positive index value during summer is associated with good breeding conditions in N-Europe and Siberia and relatively bad circumstances on the Nearctic breeding grounds. With a negative index the situation is conjectured to be opposite. Such effects might be visible in our estimates of percentages first winter birds or juveniles. Three sets of NAO-indices were used, since climatic circumstances affect the living conditions of waders during winter, spring migration as well as during breeding. The index figures were obtained from the websiteof the Climatic Research Unit of the University of East Anglia (www.cru.uea.ac.uk).

Morphometrics

Wing-, culmen-, and tarsus lengths were measured according to Minton (1971) and Prater *et al.* (1977). The method of measuring 'maximum' wing length was used by measuring in mm while straightened and flattened against a ruler (Fig. 8). Wing lengths were standardized to the moment of breeding (June) as will be explained in Section 4.2.
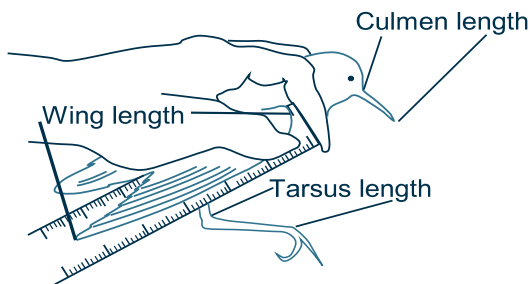
Figure 8: The methods used to measure maximum wing length, culmen length and tarsus length.

Culmen length was measured from the feather edge at the base of the culmen to the bill tip, taken with vernier calipers to the nearest 0.1 mm. Tarsus length was measured from the middle point of the joint between tibia and tarsus at the rear of the leg to the middle point of the joint between tarsus and middle toe in front of the leg and taken with vernier calipers to the nearest 0.1 mm. Both wing- and culmen lengths were measured in 26,401 cases.

In 6,654 cases tarsus lengths were measured as the third variable, but they lacked standardization. Other measurements taken were: total head length (6,360 cases), tarsus- & toe length (448 cases; the length of stretched tarsus plus middle toe), tail length (169), length of first secondary (29) and culmen height (18). Only wing- and culmen length were selected for analysis due to the lack of standardization in tarsus lengths, the incompatibility with museum measurements for total head and tarsus & toe, and the too small sample sizes for the other measurements (tail, culmen height, first secondary).

Body mass

Most birds were weighed soon after catching using spring balances. The measured masses (in grams) were corrected for time since capture. Special attention is given to the methods used for the analysis of body masses in Chapter 3.

Primary moult

Wader populations arriving in the Wadden Sea after the breeding season have varying moult patterns and schedules. These patterns may provide useful information on the function of various areas in the Wadden Sea for these populations. The progress of primary moult is characterized in such a way, that useful information is obtained about flight capabilities. When the birds were processed, the stage of moult was characterized according to Snow (1970) and Ginn & Melville (1983) by scoring each primary between one and five, depending on their state of moult. Usually, moult scores of the ten primaries are summed up, resulting in a score ranging from 0 (all old) to 50 (all new). This may result in a loss of relevant information, since, e.g., moult-score 23 might concern, both, a large gap in the wing (e.g. 5553211100 as ordered from the inner to the outer primary) as well as a small gap (e.g. 5555300000). Gaps become larger when more primaries are replaced simultaneously. The flight ability of a bird with small gaps might be less reduced than that of a bird with large gaps. Gap sizes can be deduced from the scores per primary. In addition it may be useful to produce calculations

Table 4. Relative feather masses of the primaries (sum 1 through 10 = 100) used to calculate Percentages Feather Mass Grown (PFMG) and gap sizes following Underhill & Joubert (1995) and Redfern (1998). See text for details.

Species	Primary									
	1	2	3	4	5	6	7	8	9	10
Ringed Plover	3.2	4.1	5.3	6.9	8.6	10.7	12.4	14.4	16.1	18.2
Grey Plover	3.2	4.1	5.3	6.9	8.6	10.7	12.4	14.4	16.1	18.2
Red Knot	3.6	4.4	5.5	6.9	8.6	10.5	12.0	14.1	16.1	18.4
Sanderling	4.0	4.7	5.6	6.8	8.4	10.2	12.0	14.0	16.2	18.1
Curlew Sandpiper	4.0	4.8	5.7	7.0	8.6	10.4	12.0	13.9	15.6	18.0
Dunlin	4.0	4.9	5.7	6.9	8.5	10.2	11.8	13.7	15.8	18.4
Bar-tailed Godwit	3.8	4.7	5.8	7.3	8.8	10.5	12.1	13.8	15.5	17.6
Eurasian Curlew	3.9	5.1	6.3	7.5	8.9	10.7	12.2	13.8	15.1	16.5
Spotted Redshank	5.0	5.7	6.7	7.7	9.1	10.6	11.8	13.1	14.2	16.1
Redshank	5.0	5.7	6.7	7.7	9.1	10.6	11.8	13.1	14.2	16.1
Greenshank	4.4	5.1	6.0	7.3	8.8	10.4	12.1	13.7	15.4	16.9
Ruddy Turnstone	4.2	4.7	5.9	7.2	8.7	10.4	12.0	13.7	15.4	17.9

based on the concept of 'relative feather mass' (Summers 1980, Underhill & Zucchini 1988, Underhill & Summers 1993, Underhill & Joubert 1995, and Redfern 1998). The outermost primary in a wing is larger and has more mass than the innermost one. If the mass of all primaries is set equal to 100 and when mean masses of the individual primaries are known, relative masses per primary can be calculated. In this study, the relative feather masses calculated by Underhill & Joubert (1995) will be used (Table 4). For Ringed Plover, Eurasian Curlew, and Spotted Redshank the relative feather masses of resp. Grey Plover, Whimbrel, and Redshank were taken. The Percentage Feather Mass Grown (PFMG) is defined as the sum of relative feather masses of all ten primaries and is calculated with the relative feather mass-data of moulting primaries presented by Redfern (1998). He converted the moult scores as follows: moult score 0 to 0% of the relative feather mass of a primary feather prior to moulting, score 1 to 0.6%, score 2 to 7.6%, score 3 to 31% , score 4 to 73% and score 5 to 100%. A wing with only old primaries is equivalent to PFMG 0 and one with exclusively new primaries has PFMG 100. A Redshank with a field score 5553211100 has a PFMG of

$$5.0 + 5.7 + 6.7 + 0.31*7.7 + 0.076*9.1 + 0.006*10.6 + 0.006*11.8 + 0.006*13.1 = 20.7$$

Redfern's (1998) data can also be used to calculate gap size during primary moult. Birds with completely full-grown primaries have a gap-size value of 0, irrespective whether these primaries are old or new. A flightless bird without any primaries will have gap size 100. The more primaries start growing then, the smaller the gap becomes. Relative masses of the primaries and their various moult stages can then be used to quantify the gap size. In the example of the Redshank with score 5553211100 the gap size is

$$(1-0.31)*7.7 + (1-0.076)*9.1 + (1-0.006)*10.6 + (1-0.006)*11.8 + (1-0.006)*13.1 = 49.0$$

The mean start and duration of primary moult was estimated with the help of dr. J. Van der Meer by using non-linear regression. In order to obtain these estimates the number of birds involved per species, year, catching site, day number and score of relative feather mass grown (RFMG explained below) were grouped. The model consists of three stages: (1) a bird is not yet moulting, (2) a bird is moulting, and (3) a bird has finished its primary moult. The probability to catch a non-moulting bird is decreasing in the course of the season, while the probability of catching a bird which has finished its primary moult is then increasing. When the feather masses are taken into account the speed of moult appears to be rather constant (Underhill & Zucchini 1988, Underhill & Summers 1993, Underhill & Joubert 1995), whilst such is not evident when moult scores are used. This is due to the fact that the last and largest primaries to be moulted are the outer ones. Consequently, more feather mass

has to be replaced. Thus the non-linear model described below approaches reality better than predictive models based on the S-shaped relationship between moult scores and time. The start of the primary moult, the variation in start, and the duration of primary moult are estimated from the model by iteration starting from a-priori estimated species-specific values. The non-linear regression model was initially calculated by Van der Meer (unpubl.) and formulated in SYSTAT-syntax command language. In SPSS it is written as:

(RFMG = 0)*(1-CDFnorm((daynumber-start)/s)) +
(RFMG>0 & RFMG<1)*(duration*exp(-(daynumber-start-rmass*duration)**2) / (2*s**2)) /
(sqrt(2*4*artan(1.))*s)) +
(RFMG = 1)*CDFnorm((daynumber-start)/s)

With 'RFMG' the relative feather mass grown is meant. The PFMG is in percentages ranging between 0 and 100, which is the only difference with the RFMG ranging between 0 and 1. 'CDFnorm' is the standardized cumulative frequency for the normal distribution, which returns the probability that a random variable with mean 0 and standard deviation 1 would be less than the specified numeric value. 'Daynumber' is the number of days between 1 July and the day of catching. 'Start' is the mean starting date of primary moult to be estimated in the model. 'S' is the mean variation (expressed as the standard deviation) in the start of primary moult to be estimated. 'Duration' is the mean duration of primary moult to be estimated.

METHODS USED TO STANDARDIZE BODY MASSES

3
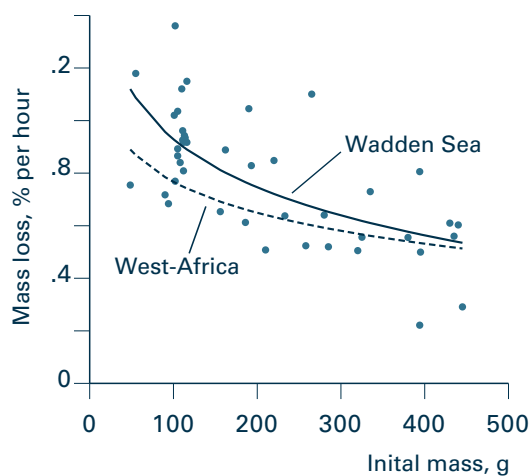
Figure 9: Rate of mass loss per hour in waders during captivity in the Wadden Sea as based on the repeated weighing of individual waders. The closed circles and solid line represent the Wadden Sea data. The statistics with derived equation are presented in the text. The dotted line represents the W-African situation according to Zwarts et al. *(1990).*

An important purpose of weighing waders in large-scale catching studies, is to study their energy reserves in order to learn more about the major periods of arrival and departure. It is obvious that in spite of the enormous amount of data collected, our approach falls short with respect to more direct, experimental, techniques used to understand migration energetics by e.g. Engel (2005).

The spatial and temporal variation in body masses of waders in the Wadden Sea throughout the non-breeding season is large. The body mass of an individual bird varies considerably, much more than its structural size. Factors causing these variations are obvious: daily feeding patterns in relation to the tidal rhythm, different migration strategies, or different patterns of winter fat accumulation. Since birds are usually not weighed immediately after catching, Boere (1976) and others studied the loss of body mass during the period of captivity. We apply corrections to the body masses measured, under the assumption that the body mass at the moment of catching is the relevant one. The corrections depend on structural size. The body mass data thus obtained will be analysed in Chapter 8 with the aim to quantify energy reserves in order to learn more about the major periods of arrival and departure and to increase our understanding of bird migration.

3.1 MASS LOSS DURING THE PERIOD OF CAPTIVITY

Mass loss during captivity is generally defined in terms of percentage loss of initial mass per hour (for instance Boere 1976, Goede & Nieboer 1983, Zwarts *et al.* 1990). In the earliest data-sets mass loss corrections were taken at 1% per hour for all species with a maximum of 7% (if seven hours or more elapsed between catching and weighing). Only the corrected values were reported. Koopman (1986) reported a mass loss in captive Ruffs of 0.75% per hour. Zwarts *et al.* (1990) showed that, not unexpectedly, large-sized species had a lower rate of mass loss than small-sized species. They provided the following formula for the % mass loss per hour : mass loss = 1.55 - 0.17*ln(initial mass) where initial mass is expressed in grams. The Wadden Sea data set contains 42 captured waders, which were weighed soon after catching and re-weighed at least half an hour later. These data confirm the trend shown by Zwarts *et al.* (1990) (Fig. 9). The relationship was quantified by studying the regression of mass loss % per hour using linear regression with the logarithm of initial mass as explanatory variable:

loss % per hour= 2.145 - 0.264*ln(initial mass) R^2= 0.443, df= 42, *F*= 32.624, *P*< 0.000)

Relatively small-sized waders captured in the Wadden Sea appear to have a more substantial mass loss than waders captured on the W-African wintering grounds. The finding that mass losses in larger species are smaller is, probably, caused by mass-specific differences in evaporation rate. According to Dodd (2000), Dunlin on British high-tide roosts loose 1.2% per hour during high tide without being captured. This is near the estimated 1.1% mass loss per hour when captured in the Wadden Sea. There does not seem to be a difference in rates of mass loss when captured or when roosting during high tide.

Masses from older data-sets were re-corrected using the last-mentioned formula when the time interval between catching and measuring was known. Table 5 gives an impression of the difference between the classical correction of 1% per hour and the one obtained with the new formula. Note that the total number of birds per species in Table 5 is a bit smaller than in Table 2 because body masses were not always measured or were obviously wrong. When the body masses of individual birds could not be re-corrected, because the duration of captivity was unknown, we had to work with another, less accurate, method. This method was only applied for the four largest-sized species (Grey Plover, Greenshank, Bar-tailed Godwit, and Eurasian Curlew) and for the three most common situations in the 1970s and the early 1980s: (1) mist-netting on Vlieland, (2) cannon-netting on Vlieland, and (3) mist-netting on Schiermonnikoog (Table 6). Average differences in g between both correction

Table 5. Mass corrections applied for this study. Species-independent corrections of 1% were applied in the older data-sets. We had to use these body masses based on the correction of 1% if the period of captivity was not included in the databases.

Species	Mean mass			Species-dependent (1% per hour[1])		Species-independent	No Corrections
	g	SD	N	Correction %	N	N	N
Ringed Plover	58.8	9.3	297	1.0694	286	11	-
Grey Plover	240.4	35.6	1073	0.6977	783	290	-
Red Knot	148.1	20.1	2203	0.8256	1882	321	-
Sanderling	59.7	10.8	236	1.0654	235	1	-
Curlew Sandpiper	69.0	12.3	333	1.0272	192	141	-
Dunlin	53.4	6.2	17227	1.0949	8274	8943	10
Bar-tailed Godwit	318.2	65.5	2627	0.6237	1410	1033	184
Eurasian Curlew	820.6	123.7	912	0.3736	497	405	10
Spotted Redshank	180.9	43.5	51	0.7727	45	-	6
Redshank	152.8	24.5	3900	0.8173	2483	1411	6
Greenshank	192.1	30.9	265	0.7569	123	142	-
Ruddy Turnstone	117.5	18.1	1012	0.8867	168	844	-

Note: 1 With a maximum of seven hours

methods were calculated. The 1% corrections of Boere (1976) had resulted in overestimated masses for these species in these three situations, being estimated respectively at: 1-2 g too heavy for Greenshanks, 1-3 g for Grey Plovers, 3-5 g for Bar-tailed Godwits, and 13-21 g for Eurasian Curlews. The masses of Greenshanks, Grey Plovers, Bar-tailed Godwits, and Eurasian Curlews on Vlieland and the ones of Bar-tailed Godwits on Schiermonnikoog were adjusted according to the estimates in Table 6.

Table 6. Estimating the average impact of the use of two different estimates to correct the measured masses for the duration of captivity. The percentage difference is defined as: (1 - S) * average time interval. 'S' stands for the species-dependent corrections presented in Table 5. A negative value must thus be interpreted as a systematic under-estimate in the older data-sets and a positive value as a systematic over-correction of the older mass data. The average time-intervals between capture and measurement (sample size indicated) of the three most common situations were calculated and presented in the 3d row.

Species	Boere - mist nets			Boere cannon-nets			Nieboer - mist nets		
	N	%	g	*N*	%	g	*N*	%	g
Average capture to measurement interval (hrs)	2:34 ± 1:34 (478)			2:42 ± 1:12 (253)			4:01 ± 1:54 (4901)		
Ringed Plover	-	-	-	-	-	-	9	-0.3	-0.2
Grey Plover	263	0.8	1.9	16	0.8	2.0	9	1.2	2.9
Red Knot	206	0.5	0.7	113	0.5	0.7	2	0.7	1.0
Sanderling	1	-	-	-	-	-	-	-	-
Curlew Sandpiper	97	-0.1	0.0	11	0.1	0.1	-	-	-
Dunlin	2979	-0.2	-0.1	551	-0.3	-0.1	5366	-0.4	-0.2
Bar-tailed Godwit	476	1.0	3.1	96	1.0	3.3	461	1.5	4.8
Eurasian Curlew	265	1.6	13.2	198	1.7	13.9	2	2.5	20.7
Spotted Redshank	-	-	-	-	-	-	-	-	-
Redshank	770	0.5	0.7	527	0.5	0.8	11	0.7	1.1
Greenshank	17	0.6	1.2	116	0.7	1.3	1	1.0	1.9
Ruddy Turnstone	50	0.3	0.3	702	0.3	0.4	-	-	-

3.2 Methods for analysing body masses in relation to morphology

In morphometrics one is usually not restricting the attention to 'linear' measurements like wing- and culmen lengths as will be done in Chapter 4. Regularly 'angular' measurements and 'mass' are included as well. For angular measurements this is quite natural since, expressed as radians, they also represent 'length'. For mass this is somewhat different.

A transformation of mass is often contemplated, e.g. raising it to some power, the exponent being between 1/3 and 1. This comes close to working with logarithms. Most discussions about 'size and shape' are based on logarithmically transformed measurements. Since the original measurements are always positive, the log-normal distribution is more natural than the normal one. An exception is in this respect De Bruin *et al.* (2001, in prep.), where we start from the original observations and define (the 'best' or 'most natural' characteristic of) size as that linear combination of measurements, in our situation of wing- and culmen length, which minimizes the coefficient of variation (i.e. the ratio standard deviation/ mean) with respect to some reference population, for instance adult males of a specific population. This definition of size may have a statistical appearance, but the underlying idea is 'biological' as it is based on the idea that 'size' expresses 'growth', 'shape' expresses 'development', and 'age' expresses 'maturation'.

Restricting ourselves to wing- and culmen lengths, we note that in the recent past of wader biology both measurements were used as estimates of 'structural size'. Culmen length was used by Davidson (1983), Goede & Nieboer (1983), Davidson *et al.* (1986b), and Piersma &
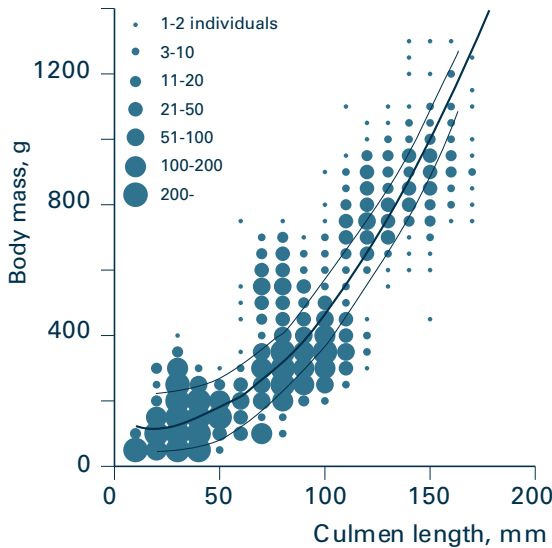
Figure 10: Relationship between body masses and culmen lengths in adult waders captured in the Wadden Sea. The relationship between mass and culmen length is: $y = 24.9991 + 0.7242x + 0.0358x^2$ ($R^2 = 0.825$, SE= 70.9, N= 31.625).
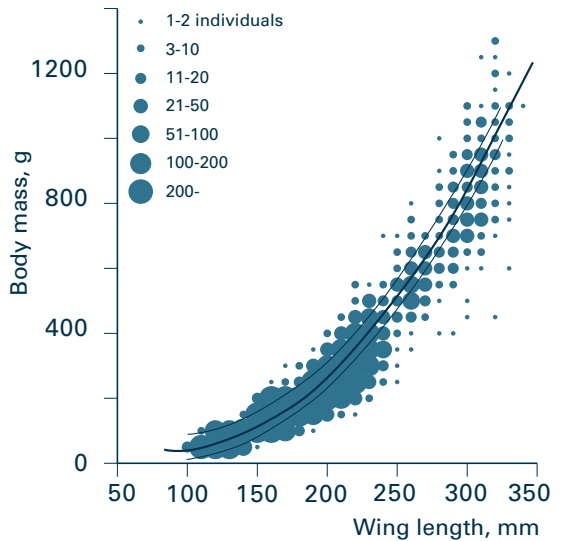
Figure 11: Relationship between body masses and wing lengths in adult waders captured in the Wadden Sea. The relationship between mass and wing length is: $y = 165.1395 - 2.8796x + 0.0164x^2$ ($R^2 = 0.947$, SE= 31.4, N= 27.491).

Van Brederode (1990). Wing length was used by Ens *et al.* (1990b), and Zwarts *et al.* (1990). The theory of De Bruin *et al.* (2001) advocates to use that linear combination of wing- and culmen length, which minimizes the coefficient of variation. Such a combination can be presented as $\sigma_1^{-1} x_1 + \sigma_2^{-1} x_2$, where x_1 stands for wing length, x_2 for culmen length, σ_1 for the standard deviation of wing length and σ_2 for the standard deviation of culmen length. We prefer to restrict the attention to either wing- or culmen length since the specification of covariances and correlations is rather uncertain, depending strongly on the reference population chosen. In this study, wing length appeared to be preferable over culmen length since its coefficient of variation is usually smaller (see Table 10 to be presented as the basis of Chapter 4). Wing length also seems to be more 'relevant' than culmen length, because wing length was more closely related to mass than culmen length especially when all birds captured from all species were combined (Fig. 10 versus Fig. 11). A quadratic relationship between mass depending on, resp. culmen- or wing length suited best, even though one might argue that the best suiting curve should pass through the origin. With wing length as predictor, 95.5% of the variation was explained, whereas 79.3% was explained by culmen length as predictor. The second reason for preferring wing lengths is less unsatisfactory from a statistical point of view and is based upon separate analyses in the various species and age-groups. Then, wing length mostly showed a closer relationship with mass than culmen length, especially in the adults (Table 7).

Table 7. Dependence of the body masses of first winter birds and adults on wing- and culmen lengths. The F-values and their significance levels are indicated as follows: * 0.01 < P < 0.05, ** 0.001 < P < 0.01, *** P < 0.001.

Species	First winter birds		Adults	
	Wing length	Culmen length	Wing length	Culmen length
Ringed Plover	7.509**	0.057	0.398	1.106
Grey Plover	3.529	10.391**	27.355***	7.828**
Red Knot	23.732***	56.266***	35.614***	40.046***
Sanderling	-	-	51.577***	5.277*
Curlew Sandpiper	3.933	16.160***	0.219	9.098**
Dunlin	242.839***	161.169***	1128.294***	1092.184***
Bar-tailed Godwit	34.022***	69.277***	177.795***	85.345***
Eurasian Curlew	74.827***	8.728**	89.846***	55.324***
Redshank	351.303***	22.695***	670.368***	0.801
Greenshank	9.229**	44.849***	1.153	7.388**
Ruddy Turnstone	15.586***	0.964	57.572***	13.874***

Part of the explanation of a somewhat lower coefficient of variation for wing length may be that wing length measurements tend to be more accurate than culmen length measurements. To support this idea, I organised an experiment with repeated measurements: five skins (three Oystercatchers, two Dunlin) from the Zoological Museum in Amsterdam were measured by 50 people during the 1994 Annual Meeting of the International Wader Study Group. The accuracy decreased in the following order (as expressed by the coefficient of variation): wing length, culmen length, tarsus length, middle toe length, bill depth, and finally the length of the first secondary (Table 8). The CV of wing length was 1.2% against 1.9% in culmen lengths.

The biological variation of wing length, as will be studied in Table 10, is larger than the variation in measurement errors but not much larger. It is in the order of 2-3% (5% for culmen length). The experience of people influenced positively and significantly wing lengths (df= 2 and 241; F= 6.433; P= 0.002), but not the other measurements.

Table 8. Accuracy of taking measurements in five individual waders. Fifty practitioners were asked to take five measurements of two Dunlin and three measurements of three Oystercatchers (museum skins) during the annual meeting of the International Wader Study Group of 1994 in Busum. They were asked to grade their own experience: inexperienced (16.3%), moderately experienced (67.3%) and experienced (16.3%)

measurement	Dunlin I	Dunlin II	Oyster-catcher I	Oyster-catcher II	Oyster-catcher III	Mean
Wing length	115.5±1.3(48)	114.7±1.9(49)	252.2±2.9(49)	257.7±2.2(49)	247.5±3.5(49)	-
Culmen length	27.2±0.4(49)	33.0±0.7(48)	71.4±1.6(49)	72.4±1.3(48)	69.0±1.3(48)	-
Tarsus length	23.6±1.3(42)	24.1±1.0(41)	-	-	-	-
Middle toe length	22.0±1.3(39)	21.2±1.4(31)	-	-	-	-
Length first secondary	56.7±6.4(22)	57.4±6.8(23)	-	-	-	-
Bill depth	-	-	9.3±0.6(46)	10.2±0.5(45)	10.1±0.8(45)	-
Coefficients of variation - (s / x) * 100						
CV - wing	1.13	1.65	1.13	0.86	1.40	1.23
CV - culmen	1.53	2.16	2.19	1.80	1.83	1.90
CV - tarsus	5.37	4.26	-	-	-	4.82
CV - middle toe	5.83	6.48	-	-	-	6.16
CV - first secondary	11.28	11.92	-	-	-	11.60
CV - bill depth	-	-	6.17	4.81	8.13	6.37

METHODS FOR ASSESSING BREEDING ORIGIN

4

The main purpose to measure wing- and culmen lengths of waders in the Wadden Sea area is to compare these with distributions of wing- and culmen lengths of breeding populations. This may provide us with estimates of the proportions originating from different breeding areas. To reach this goal, Engelmoer & Roselaar (1998) measured wing- and culmen lengths of museum specimens from various breeding areas, which they corrected for shrinkage. In this chapter attention is paid, firstly, to the comparability of field- and museum-data and, secondly, to the variability of wing- and culmen lengths. The birds measured in the Wadden Sea area have to be corrected such that they can be regarded as observed in the breeding area.

4.1 CORRECTIONS APPLIED TO MUSEUM VALUES OF WING- AND CULMEN LENGTHS

The wings and bills of museum skins are subjected to a process of shrinkage. Therefore museum values need to be corrected for shrinkage in order to make them comparable with the ones of live-trapped birds. Engelmoer & Roselaar (1998) presented such corrections. An additional scrutiny was performed using data from literature. The basic question in this respect was, whether differences between the sample statistics of Engelmoer & Roselaar (1998) and field estimates of breeding populations are statistically significant. If differences are not alarming then estimates can be combined.

Comparison with literature data is only possible if the method of measuring is the same. Wader researchers put a lot of effort in standardising their measuring methodology (e.g. Stroud & Davidson 2003). Focussing on studies with measurements of (maximum) wing- and culmen length of breeding populations with reliable sex- diagnosis, two groups of publications are distinguished. The first group consists of data with measurements of sexed individual birds from the following breeding areas: NE-Canada (Witts 1982), Greenland (Meltofte 1976, Green & Greenwood 1978, Meltofte 1979, De Korte *et al.* 1981), N-Iceland (Summers *et al.* 1987a), Scotland (Etheridge & Taylor 1982, Barrett & Barrett 1986), Central Norway (Innes 1980), and Taimyr (Yesou *et al.* 1992, Spiekman & Groen 1993, Prokosch *et al.* 1993, Van Dijk & Venema pers. comm., Vonk & Duiven pers. comm.). The second group contains statistics based on samples of sexed birds from various breeding regions: Hørring (1939), Lövenskiold (1954), Grosskopf (1963), Heldt (1966), Parmelee *et al.* (1967), Thomas & Dartnall (1970), Maclean & Holmes (1971), Morrison & Wilson (1972), Soikkeli (1974), Morrison (1975), Hilden (1975), Pienkowski & Dick (1975), Dick *et al.* (1976), Elliott *et al.* (1976), Barter (1985), Tomkovich (1985), Holz (1987), Jönsson (1987), Summers *et al.* (1988a & 1988b), Nicoll *et al.* (1991), Underhill *et al.* (1993), and Tomkovich & Soloviev

(1996). Information from this second group is used for comparison with the sample statistics presented in Engelmoer & Roselaar (1998). Samples with sizes less than five were ignored. When, for example, 4 authors had sample statistics of Ringed Plovers, theoretically 8 mean wing lengths (males and females) can be compared with the mean wing lengths of Engelmoer & Roselaar (1998) for that specific breeding region and sex. (In this specific situation only 7 means were available due to one female sample lacking.) It was then tested with a 2-sided paired sample t-test (Norušis 1992a), where the difference between the 8 pairs is calculated and where it is tested whether the average difference differs from 0. The statistical method used is crude and the assumptions are questionable. A more sophisticated analysis was not carried out, because the results were expected to be not much different.

Mean wing length of live-captured Sanderling, Purple Sandpiper, and Dunlin differed from the lengths, corrected and presented by Engelmoer & Roselaar (1998), with ± 1.1 mm (Table 9). Also the culmen lengths of live-captured Ringed Plover, Dunlin, and Ruddy Turnstone differed significantly from the values, corrected and presented by Engelmoer & Roselaar (1998), with resp. +0.55, +0.7, and +1.0 mm. Strikingly, their corrections for Ringed Plover-

Table 9. Differences between sample means of live-trapped breeding birds and the ones of museum specimens, corrected for shrinkage by Engelmoer & Roselaar (1998). The differences were tested with a 2-sided t-test. Positive values indicate longer museum measurements and negative values smaller ones. For every species and measurement the mean difference ($\bar{x}$ in mm), standard deviation (SD), Student's t-value (t), the degrees of freedom (df) and the significance (s) are presented. Significant differences are printed bold-type: [1] $0.01 < P < 0.05$, [2] $0.001 < P < 0.01$, [3] $P < 0.001$.

	Wing length					Culmen length					Tarsus length				
Species	$\bar{x}$	SD	t	df	s	$\bar{x}$	SD	t	df	s	$\bar{x}$	SD	t	df	s
Ringed Plover	0.691	1.462	1.25	6	0.257	**0.550**	**0.298**	**4.88**	**6**	**0.003**[2]	-1.128	1.842	-1.50	5	0.194
Grey Plover	1.275	2.177	1.17	3	0.326	-0.208	0.744	-0.56	3	0.616	-1.050	1.148	-1.83	3	0.165
Red Knot	1.478	1.882	1.57	3	0.214	-1.255	1.248	-2.46	5	0.057					
Sanderling	**-0.883**	**0.814**	**-2.66**	**5**	**0.045**[1]	-0.133	0.343	-0.95	5	0.385	0.000	0.990	0.00	1	1.000
Little Stint	-0.236	0.627	-0.84	4	0.447	0.340	0.461	1.65	4	0.175	-1.565	0.375	-5.91	1	0.107
Temminck's Stint	2.050	0.778	3.73	1	0.167	0.600	0.141	6.00	1	0.105					
Curlew Sandpiper	1.860	0.995	3.24	2	0.084	0.276	0.827	1.00	8	0.347	0.120	0.817	0.33	4	0.759
Purple Sandpiper	**-1.286**	**1.113**	**-3.06**	**6**	**0.022**[1]	0.254	0.646	1.42	12	0.182	-0.250	0.212	-1.67	1	0.344
Dunlin	**1.075**	**1.477**	**3.25**	**19**	**0.004**[2]	**0.725**	**0.727**	**5.46**	**29**	**0.000**[3]	-0.413	1.189	-0.92	6	0.394
Bar-tailed Godwit	0.735	4.151	0.25	1	0.844	-0.500	0.071	-10.00	1	0.063	**-2.425**	**0.035**	**-97.00**	**1**	**0.007**[2]
Redshank	0.675	3.145	0.43	3	0.697	1.500	1.230	2.44	3	0.093	**-4.950**	**0.212**	**-33.00**	**1**	**0.019**[1]
Ruddy Turnstone	-0.800	1.873	-1.60	13	0.134	**0.996**	**0.740**	**5.04**	**13**	**0.000**[3]	1.510	3.664	0.82	3	0.470

and Ruddy Turnstone bills were exceptionally large (their Table 6). After adjustment, bills of museum skins seem to shrink about 2% irrespective of the species. For these five species, the wing- and culmen lengths, presented in Engelmoer & Roselaar (1998), were re-corrected in order to reach the best comparative basis with the measurements of living breeding birds on the breeding grounds during the breeding season. The corrections are such, that the wing- and culmen lengths of live breeding birds are taken as the standard.

After these re-corrections, the data of the reliably measured, live-captured breeding adults were incorporated in the breeding samples in order to increase sample sizes. This was especially attractive for the N-Taimyr Red Knots, since there is a considerable discrepancy between the relatively short culmen lengths of museum skins (Tomkovich 1992, Engelmoer & Roselaar 1998) and the longer culmen lengths obtained with recent field work (Prokosch *et al.* 1993, Tomkovich & Soloviev 1996). The resulting sample statistics of wing- and culmen lengths of the various breeding populations are presented in Table 10. These are the breeding samples used in the morphometric analyses against which the Wadden Sea data are compared.

4.2 CORRECTING WING- AND CULMEN LENGTHS WITH RESPECT TO ANNUAL AND SEASONAL VARIATION

Since a major aim of this study is to estimate the population composition of wader-populations in the Wadden Sea in terms of their breeding origin by using morphometrics, it is important to investigate the variability of wing- and culmen lengths due to annual and seasonal variation. Different feeding habits between breeding and staging grounds might result in changes of culmen lengths. Also, wear of primaries might result in decreasing wing lengths within one moulting cycle. To derive the appropriate correction formulas incorporating the time of the year and age-category of the bird, measurements of 623 recaptured birds from ten species were considered: Ringed Plover (*N*= 1), Grey Plover (*N*= 19), Red Knot (*N*= 19), Sanderling (*N*= 3), Curlew Sandpiper (*N*= 2), Dunlin (*N*= 326), Bar-tailed Godwit (*N*= 8), Eurasian Curlew (*N*= 13), Redshank (*N*= 86), and Ruddy Turnstone (*N*= 146). Using scores at the moments of capture and re-capture, proportional differences (in %) can be calculated for a variety of contexts.

Within one moulting cycle, wing length appears to shorten due to the abrasion of the outer primaries (Fig. 12). The estimated wear is 0.09% per month in adults and 0.21% per month in first winter birds. In Red Knot and Dunlin, the negative regression is statistically significant
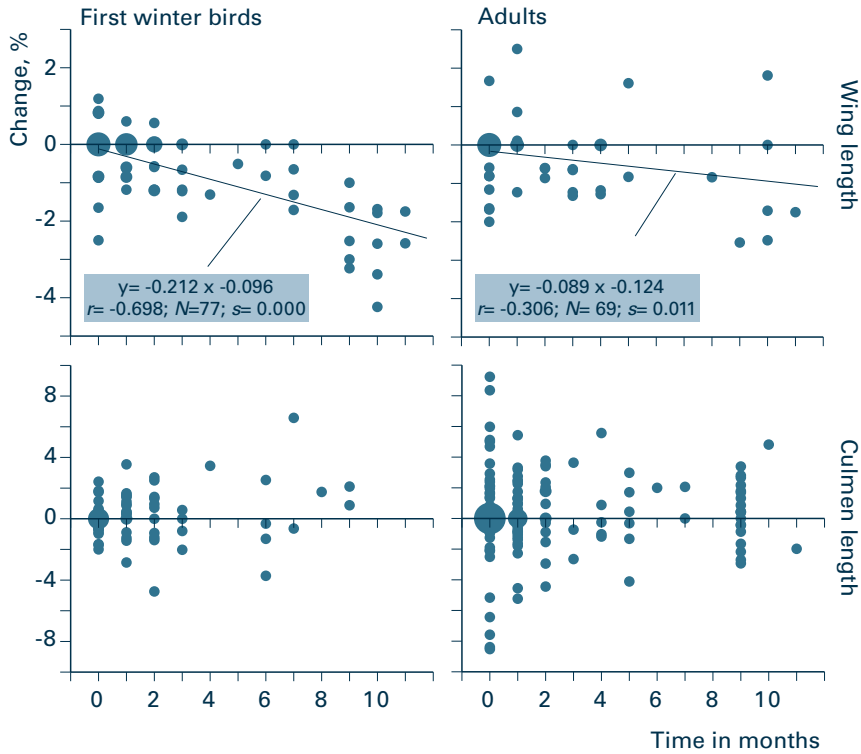
Figure 12: The percentage change in wing- and culmen lengths in the course of a winter season as based upon the initial measurements of recaptured individuals. A 'season' is defined as the non-breeding period between July and June in case of the culmen length. However, a 'wing length's season concerns a complete period between two moult cycles ranging from a set of fresh, full-grown primaries to worn ones.

at the 1% level and in Redshank and Ruddy Turnstone at the 5% level. Sample sizes are too small to establish species-dependency. Primaries of 'juveniles' appear to grow somewhat larger every next moulting cycle during the first three years (Fig. 13). The increase is estimated at 0.7% per year. It looks as if ultimate wing length is reached in about four years. The wings of adults also continue to grow for another one or two years with an increase of about 0.3% every next moulting cycle. Note that some selection may be involved, due to better survival of longer-winged birds. It was impossible to study species-dependency in the growth of the outer primaries every new moulting cycle, since in most species too few first winter birds were recaptured in later seasons. Culmen length does not seem to change markedly during either the non-breeding season (Fig. 12) or during a bird's life (Fig. 13). These findings resulted in the following correction of the measurements of living birds:
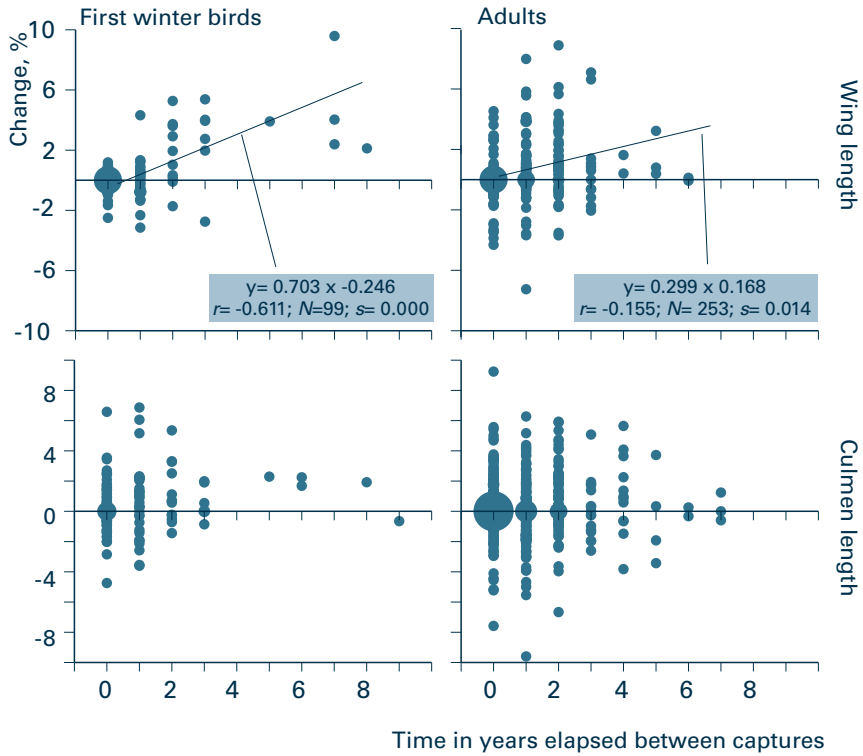
Figure 13: The percentage change in wing- and culmen lengths over the years as based upon the initial measurements of recaptured individuals. The X-axis represents the number of years passed between trap and retrap.

1. *Culmen lengths.* Measured culmen lengths are not corrected.
2. *Wear of primaries within a moulting cycle.* Within a moulting cycle measured wing lengths of adults are corrected with 0.09% wear per month to the moment of breeding (June). The wear in the wing lengths of first winter birds is corrected with 0.21% per month in order to obtain the original length.
3. *Age corrections in wing lengths.* Wing lengths of adults are not corrected for annual increase every new moulting cycle, since age composition of adult populations in the Wadden Sea is unknown, but wing lengths of first winter birds are corrected by adding 2% to the measured length. Since the adult populations consist of second winter birds as well as older ones, the correction of 2% from first- to second winter birds ought to be considered as a minimal value.

The analyses concerning population composition estimates are restricted to the adults. This implies that only a correction because of wear is made for wing length.

Table 10. Mean measurements of the breeding samples of wader populations of known breeding origin used in this study. Measurements were corrected for shrinkage (see text), such that statistics refer to live animals. The sample sizes of respectively males and females are shown. The mean values of the various measurements are presented together with the standard deviations. Since sexes in the Grey Plover did not show morphometric differentiation (Engelmoer & Roselaar 1998), both are combined and presented under the columns of the male-samples.

Species	Breeding area	Subspecies	N	Males		Females	
			♂ / ♀	wing	culmen	wing	culmen
Ringed Plover	NE-Can./Greenl./Icel.	*psammodroma*	125/73	133.3±3.2	13.8±0.8	133.5±3.2	13.8±0.7
	W-Europe	*hiaticula*	36/20	136.3±3.7	14.7±0.7	139.8±4.2	14.9±1.0
	N-Europe & Siberia	*tundrae*	164/87	131.5±2.8	13.4±0.7	132.1±2.8	13.2±0.7
Grey Plover (sexes combined)	N-Europe	*squatarola*	8	201.2±2.2	29.8±1.8		
	Yamal & Taimyr	*squatarola*	78	205.3±4.8	29.1±1.4		
	E-Siberia & Alaska	*squatarola*	45	206.1±5.7	30.8±1.4		
	Vrangelya	*tomkovichi*	29	210.4±5.0	29.3±1.7		
	N-Canada	*cynosuræ*	79	196.9±4.4	30.2±1.5		
Red Knot	NE-Can./Greenl./Icel.	*islandica*	78/57	169.7±4.5	31.6±1.3	173.8±4.0	34.0±1.3
	Taymyr	*canutus*	16/18	168.9±2.3	32.0±2.4	172.2±5.2	34.6±1.5
	Novosib. Islands	*piersmai*	8/5	161.9±4.5	30.0±0.9	169.4±3.2	33.3±0.6
	Vrangelya	*roselaari*	17/13	173.6±2.5	35.1±1.4	178.2±4.0	36.7±1.6
	N-Canada	*rufa*	15/23	170.3±3.0	34.8±0.9	174.2±3.7	36.6±1.4
Sanderling	Alaska & N-Canada	*rubidus*	52/45	126.7±2.7	24.8±0.9	129.9±2.8	26.7±1.1
	Siberia/Greenland	*alba*	96/60	125.3±3.0	23.8±1.3	128.8±2.7	25.6±1.1
Curlew Sandpiper	combined		42/47	132.5±2.9	36.4±1.8	134.5±3.3	40.1±1.6
Dunlin	Greenland	*arctica*	87/58	112.5±2.5	26.1±1.2	116.3±2.5	29.1±1.2
	W-Europe	*schinzii*	177/134	112.5±2.4	27.8±1.5	116.5±2.7	31.9±1.6
	N-Fennoscandia	*alpina*	49/53	116.2±2.5	30.6±1.6	118.6±2.9	32.9±2.4
	W-& Central Siberia	*alpina* & *centralis*	55/30	117.8±2.9	31.7±1.8	120.2±2.3	35.0±1.8
	E-Siberia & N-Alaska	*sakhalina*	89/56	121.2±3.0	33.2±2.0	123.4±2.8	36.9±2.4
	W-Alaska	*pacifica*	6/5	123.9±3.0	36.6±2.5	127.1±3.4	39.9±2.6
	N-Canada	*hudsonia*	61/45	120.4±2.9	36.1±1.3	121.6±2.9	38.5±1.8
Bar-tailed Godwit	N-Fennoscandia	*lapponica*	32/22	218.3±6.0	81.5±4.2	231.6±5.5	101.6±5.4
	Yamal & Taimyr	*taymyrensis*	46/35	214.5±4.9	78.8±3.9	226.6±4.7	95.8±4.7
	Lena-Chaunsk	*menzbieri*	12/16	220.3±4.4	85.3±3.8	231.5±5.1	108.6±4.2
	Anadyr & S-Chukotsk	*anadyrensis*	13/11	228.3±5.8	84.6±3.4	240.7±8.0	106.1±9.3
	Alaska	*baueri*	37/24	232.4±5.4	87.8±9.2	248.4±5.4	110.4±6.4
Eurasian Curlew	N-& W-Europe	*arquata*	50/39	298.6±7.1	121.3±7.7	315.5±11.1	144.6±11.3
	S-Ural & Kazakhstan	*sushkini*	5/7	300.3±6.2	124.6±6.7	303.7±3.9	137.7±3.3
	Central Siberia	*orientalis*	16/10	303.6±8.9	137.6±7.7	319.1±4.9	176.0±8.4

Spotted Redshank	combined		47/20	168.3±3.8	57.4±2.6	172.7±4.8	58.8±3.7
Redshank	Iceland	*robusta*	57/46	168.9±4.0	40.0±2.0	171.9±4.0	42.5±1.4
	North Sea	*brittannica*	52/24	160.8±4.3	42.9±1.6	164.5±3.0	45.4±1.7
	Fennoscandia	*totanus*	41/29	157.9±3.3	40.9±1.9	161.0±3.5	41.8±1.6
Greenshank	combined		81/60	192.6±4.9	54.2±2.5	196.0±4.7	54.4±2.8
Ruddy Turnstone	low arctic Canada	*morinella*	68/40	152.3±3.4	22.4±1.2	154.4±4.2	23.1±1.1
	other	*interpres*	253/167	155.2±4.2	21.6±1.1	157.9±4.3	22.3±1.1

4.3 THE STATISTICAL APPROACH FOR ESTIMATING POPULATION COMPOSITION WITH RESPECT TO BREEDING ORIGIN

How to compare the measurements of waders captured in the Wadden Sea with the ones of breeding populations in order to estimate the composition of these wader populations with respect to their breeding origin? That is the question we shall consider. The information on breeding samples, presented in Table 10, is used for several purposes:

1. To ascertain the population of origin on the basis of wing- and culmen length of any individual caught in the Wadden Sea.
2. As this may be too ambitious, to discuss group membership of individual birds by using probabilities.
3. As the second point does not respect the idea that the real interest is not in individual birds separately but in a group present in the Wadden Sea, to estimate the proportions of this group originating from different breeding areas.
4. If the assumption can be made that the entire group is from only one breeding area, to make statements about the probabilities or likelihoods of various candidate breeding areas.

To resolve the issues involved is hazardous, since statistical assumptions have to be made, especially about the randomness of samples. If a group of adult birds in breeding plumage is considered, immediately after their arrival in the Wadden Sea then one will have no difficulty in assuming that each of these birds can be regarded as taken at random from its breeding population. The fourth approach might then be of interest. However, the composition of the flocks, from which the birds are captured, may fluctuate from day to day. Through the years a variety of statistical techniques were employed. These will now be discussed.

POSCON-analysis
Engelmoer & Roselaar (1998) discussed group membership in individual waders by applying the methods implemented in the POSCON-program under the heading typicality probability.

The title of the program refers to CONfidence intervals of POSterior probabilities. The definition of such posterior probabilities $\alpha(1|x),...,\alpha(k|x)$ (x denoting the vector of scores of some individual) requires knowledge of prior probabilities $\alpha(1),...,\alpha(k)$ which, in our research, does not exist. In fact, it was a major aim of this study to obtain knowledge of these 'proportions' or 'prevalences' in the group considered. Waders in the Wadden Sea are either from Canada, Greenland, or Siberia, etc. but the proportions stemming from these breeding areas are not known. We conjecture that these proportions vary considerably throughout the area and in the course of time and are interested in their estimation. For that purpose, we cannot use the perspective of the POSCON program at large. In this computer package, however, an option is implemented to compute 'typicality probabilities'.

The typicality probability is a criterion of how 'typical' an individual with a given wing- and culmen length is for a population of interest, e.g. Red Knots breeding at the Taimyr peninsula. One minus the typicality probability characterizes how 'atypical' it is (given its wing- and culmen length). In fact there are at least two different concepts of typicality probability, both having their origin in the following. Suppose that the density f of the distribution of wing- and culmen length in some population, e.g. Taimyr-breeding Red Knot, is known and that $x = (x_1, x_2)$ is the vector of scores, here wing- and culmen length, of some Red Knot. This individual is very typical for the Taimyr-population if x is close to the vector $\mu = (\mu_1, \mu_2)$ of mean values of wing- and culmen length in this population or, almost equivalently, if the density $f(x)$ is not much smaller than the maximum $\max_z f(z)$ of this density. This concept $f(x)$ for the typicality can be standardized by computing $f(x)/\max_z f(z)$ such that it assumes the value 1 if $f(x)$ is maximum. The basic concept of typicality, however, is defined somewhat differently, in probabilistic terms, as the probability

$$P = P(f(X) \leq f(x)) = \int\limits_{\{z; f(z) \leq f(x)\}} f(z)dz_1 dz_2$$

to 'observe' a value $f(X)$ of the density f less than the value $f(x)$ actually observed if (in a construction of the mind) X is the vector of scores of an individual taken at random from the population. Fisher established that this value P is the outcome of a random variable with the uniform distribution on [0, 1] if x is, indeed, the vector of scores of an individual taken at random from the population. If f is the density

$$f(x_1, x_2) = \frac{1}{2\pi\sigma_x\sigma_y(1-\varphi^2)^{1/2}} \exp\left(-\frac{1}{2(1-\varphi^2)}\left\{\left(\frac{x_1 - \mu_1}{\sigma_1}\right)^2 - 2\varphi\frac{(x_1\mu_1)(x_2\mu_2)}{\sigma_1\sigma_2} + \left(\frac{x_2 - \mu_2}{\sigma_2}\right)^2\right\}\right)$$

of the bivariate normal distribution, as may be assumed in our case of wing length (x_1) and culmen length (x_2), we, somewhat surprisingly, have that the probability P is equal to $f(x)/\max_z f(z)$ (see Albers *et al.*, in prep.). This does not hold if more than 2 variables are

considered. In that case the significance probability should be used because of its statistical interpretation. In practice the density f is not exactly known and that is why, even in this bivariate case, at least two different types of typicality probability exist. The first one is that where the actual definition of P is used and next the dependence on the unknown density f is acknowledged; regarded this way, P appears as an unknown value which can be estimated from a sample, preferably by means of a confidence interval or, almost equivalently, a distributional inference. Theory has been presented in literature around POSCON. The results, however, are rather complicated, unless one contents oneself with the determination of one specific value, e.g. that where the (unknown) significance probability P is simply replaced by a point estimate, e.g. that based on the replacement of $(\mu_1, \mu_2, \sigma_1, \sigma_2, \varphi)$ by corresponding (conventional) estimates. As the involved statistical uncertainties may be considerable, Kardaun *et al.* (2003) and Albers *et al.* (in prep.) concentrate the attention on the construction of a confidence interval or distributional inference for P. As this is somewhat complicated another approach was used in Engelmoer & Roselaar (1998) and in the present book. It is implemented in POSCON as well and is also based on the idea that statistical uncertainties should not be ignored. Concentrating the attention on the idea that the value P defined earlier is a significance probability (in a theoretical context such that it is not exactly known), this second type of typicality probability is defined as the P-value if the null hypothesis is tested that the sample (of only one element) representing the specific individual and the sample from the reference population (of Red Knots of the Taimyr peninsula) are from the same population. As we assume that f is the density of a bivariate normal distribution with, both, the population mean $\mu = (\mu_1, \mu_2)$ and covariance matrix $\Sigma = (\sigma_{gh})$ unknown, we use Hotelling's generalized T^2 statistic and regard the corresponding 'p-value' or 'significance probability' as the typicality probability to be used.

Implementation

Each individual bird captured and measured in the Wadden Sea can be confronted with each of, say $k = 8$, samples of breeders such that eight typicality probabilities arise. This may be useful in making a 'differential' diagnosis for the individual bird of interest.
In Engelmoer (1995) and Engelmoer & Roselaar (1998) it was decided to use this second concept of typicality probability, i.e. that based on Hotelling's test, under the additional assumption of homogeneity of the covariance matrices. As the interest was not in making a differential diagnosis for one or more particular birds, but to estimate proportions $\alpha(1),...,\alpha(k)$ in a group of birds, we manipulated the results obtained by selecting the population with the largest typicality probability. We knew that the assignments thus obtained could be erroneous. In fact, the second largest typicality probability provides very useful information in this respect. The purpose of these computations, however, was to estimate the proportions $\alpha(1),...,\alpha(k)$ in a group of birds, present somewhere and some time in the

Wadden Sea, and captured such that scores were available, $\alpha_{(h)}$ denoting the proportion stemming from breeding region h. By making these assignments to the populations with the largest typicality probability we, at least, obtained frequencies from which $\alpha(1),...,\alpha(k)$ could be estimated. It was very clear, e.g. on the basis of second largest typicality probabilities, that a considerable number of misclassifications may be involved and, hence, the estimates of $\alpha(1),...,\alpha(k)$ are considerably uncertain.

NAG-optimizations

Feeling unhappy about the manipulation just discussed, a more direct method of estimating these 'proportions' or 'prior probabilities' $\alpha(1),...,\alpha(k)$ was developed and implemented in close co-operation with Dr. R. De Bruin (Rekencentrum RUG). In fact the method is fairly standard: it is based on the idea that some 'likelihood function' has to be maximized. NAG-optimization technique E04 was used to provide population composition estimates for the mixed wader populations in the Wadden Sea (NAG 2004). Both the group of adult migrants (a 'sample' from some mixed Wadden Sea 'population') and the breeding samples are characterized by their wing- and culmen lengths. With the routine E04 the measurements of a mixed Wadden Sea sample are compared with a set of samples each consisting of the measurements of morphometrically distinct breeding populations. The samples of these distinct breeding populations are referred to as 'breeding samples' and the sample of the mixed Wadden Sea population as the 'mixed sample'. The breeding samples as well as the mixed sample consist of individuals characterized by measurements of wing- and culmen lengths. The aim is then to provide estimates of the population composition of the mixed 'populations' in the Wadden Sea throughout the non-breeding season and to discuss the reliability of such estimates. In order to reach this goal four steps have to be taken.

In **step 1** the breeding samples are characterized. Each breeding sample consists of a number of individuals with known wing- and culmen lengths. A given breeding population h is characterized by the (not exactly known) mean vector μ_h and the covariance matrix Σ_h. If the distribution of wing- and culmen length is supposed to be normal, then the density is determined by the formula $f(x_1,x_2)$ discussed before. Henceforth the dependence of this formula on $(\mu_1, \mu_2, \sigma_1, \sigma_2, \varphi)$ is expressed by using the notation $P_{\mu,\Sigma}(x_1,x_2)$ in stead of $f(x_1,x_2)$. The unknown values $\mu_1, \mu_2, \sigma_1, \sigma_2$ and φ can, of course, be estimated from the breeding samples. The notation μ_h, Σ_h will be used to denote dependence on breeding sample h ($h= 1,..., k$).

In **step 2** the mixing of breeding populations during non-breeding in the Wadden Sea is defined. A group of n birds captured in the Wadden Sea is considered to originate from k breeding populations. Then the proportion α_h of breeding population h in the group of captured birds

must be estimated for $h = 1, \ldots, k$. If wing length x and culmen length y concern an individual taken at random from a Wadden Sea population with proportions $\alpha(1),\ldots,\alpha(k)$, then (x, y) is the outcome of a random vector (X, Y) with density $\sum_{h=1}^{k} \alpha_h p_{\mu_h, \Sigma_h}(x,y)$, where $p_{\mu_h, \Sigma_h}(x,y)$ is the above defined density. As we assume, that the n captured birds originate from the k breeding areas, we have $\sum_{h=1}^{k} \alpha_h = 1$. Working with $(\mu_h, \Sigma_h)(h = 1, \ldots, k)$ as estimated by updating the estimates in Engelmoer & Roselaar (1998), and considering these estimates as the true values, the vectors of scores (x_i, y_i) (i = 1, \ldots , n) of the group of non-breeding birds captured in the Wadden Sea are regarded as the outcome of an independent random sample from the distribution just defined. Hence the joint density of $(X_1Y_1,\ldots,X_nY_n)$ is given by $p_{\alpha_1,\ldots,\alpha_k}(x_1,\ldots,y_n) = \prod_{i=1}^{n} (\sum_{h=1}^{k} \alpha_h p_{\mu_h, \Sigma_h}(x_i,y_i))$ in an arbitrary outcome $(x_1, \ldots ,y_n)$ of $(X_1, \ldots , Y_n)$. We are however interested in estimating $(\alpha(1),\ldots,\alpha(k))$ on the basis of the given outcome $(x_1, \ldots ,y_n)$. This task can be performed by considering the likelihood function $l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_k)$, which is obtained from the joint density $p_{\alpha_1,\ldots,\alpha_k}(x_1,\ldots,y_n)$, by regarding it as a function of $\alpha_1,\ldots,\alpha_k$, $x_1,\ldots,y_n$ and, next, taking $(x_1,\ldots,y_n)$ equal to the fixed values factually observed. This likelihood function is not a probability density in a formal way, but it can be transformed into a probability density by applying some normalization, respecting the relations $\alpha_h \geq 0$, $\sum_{h=1}^{k} \alpha_h = 1$. In practice one is usually concentrating the attention on the maximum likelihood estimates $\hat{\alpha}(1),\ldots,\hat{\alpha}(k)$ which are obtained by maximizing the likelihood function under these restrictions.

Step 3 concerns *the optimization process* itself. Usually the logarithm of $l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_k)$ is maximized as a function of $(\alpha_1,\ldots,\alpha_k)$ instead of the likelihood function itself. Maximizing the likelihood function is equivalent to minimizing the negative of its logarithm. This minimization is a standard non-linear constrained optimization technique in NAG-subroutine E04 (NAG 2004).

Step 4 concentrates on *the reliability of the optimal solution*, which is complicated. Firstly, by writing $l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_{k-1}) = \prod_{i=1}^{n} (\sum_{h=1}^{k-1} \alpha_h p_{\mu_h, \Sigma_h}(x_i,y_i) + (1 - \alpha_1 - \ldots - \alpha_{k_k}) p_{\mu_k, \Sigma_k}(x_i,y_i)$ the restriction $\sum_{h=1}^{k} \alpha_h = 1$ is taken into account by substituting $\alpha_k = 1 - \alpha_1 - \ldots - \alpha_{k-1}$. The likelihood function thus obtained can be maximized as a function of $(\alpha_1,\ldots,\alpha_{k-1})$, where $(\alpha_1,\ldots,\alpha_{k-1})$ is restricted by $\alpha_h \geq 0, \sum_{h=1}^{k} \alpha_h \leq 1$. Next one may consider the probability density

$$l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_{k-1}) / \int_{\{\alpha_h \geq 0, \sum_{h=1}^{k} \alpha_h \leq 1\}} l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_{k-1}) d\alpha_1,\ldots,d\alpha_{k-1}$$

as a 'posterior density' defining the 'opinion' one 'should' have about $(\alpha_1,\ldots,\alpha_{k-1})$ in the form of a distributional inference (see Kardaun & Schaafsma 2003 for further references). Then, $-log(l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_{k-1}))$ can be expanded around the maximum likelihood estimates $\hat{\alpha}_1,\ldots,\hat{\alpha}_{k-1}$ provided by NAG (2004). As the first order differences are 0 in $\hat{\alpha}_1,\ldots,\hat{\alpha}_{k-1}$, at least if the optimum is not achieved at the boundary of the region defined by $\alpha_h \geq 0, \sum_{h=1}^{k} \alpha_h = 1$,

we have $\log l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_{k-1}) = \log l_{x_1,\ldots,y_n}(\hat{\alpha}_1,\ldots,\hat{\alpha}_{k-1}) - \frac{1}{2} l_{x_1,\ldots,y_n}(\alpha-\hat{\alpha})H(\alpha-\hat{\alpha})^T + \ldots$

where H is the matrix of second order derivatives

$$-\frac{\partial^2}{\partial\alpha_h\partial\alpha_i}\ \log l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_{k-1})\bigg|_{\hat{\alpha}_1,\ldots,\hat{\alpha}_{k-1}}$$

evaluated at the maximum likelihood estimate, and $(\alpha - \hat{\alpha}) = (\alpha_1 - \hat{\alpha}_1,\ldots,\alpha_{k-1} - \hat{\alpha}_{k-1})$. By ignoring higher order derivatives, we obtain

$$\log l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_{k-1}) = c - \frac{1}{2}(\alpha-\hat{\alpha})H(\alpha-\hat{\alpha})^T$$

and hence $l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_{k-1}) = c'\, e^{-\frac{1}{2}(\alpha-\hat{\alpha})H(\alpha-\hat{\alpha})^T}$, which is the density of the normal distribution $N(\hat{\alpha},H^{-1})$. This application of 'classical likelihood inference' provides estimates $\hat{\alpha}_1,\ldots,\hat{\alpha}_{k-1}$ equipped with standard errors. These standard errors are obtained by inverting the Hessian H and taking the square root of diagonal elements. A standard error of the estimate $1 - \hat{\alpha}_1 - \ldots - \hat{\alpha}_{k-1}$ of α_k can then be derived.

Remark 1

Actually the computations performed were somewhat different. We (RdB and I) had concluded from the typicality approach that the existence of one (or more) additional populations (in addition to the k breeding samples included) cannot be excluded and that, hence, $\sum_{h=1}^{k}\alpha_h$ should be allowed to be smaller than 1. Moreover we worried about the statistical uncertainties in $\mu_1,\ldots,\mu_k$, Σ, which are visible in Table 10. That is why we extended the methodology just described by regarding $\mu_1,\ldots,\mu_k$ as parameters to be estimated from the combined samples from the mixed population as well as the breeding populations. (The off-line estimate of Σ was treated as true value because otherwise everything would become too complicated). The likelihood function involved is more complicated than that discussed earlier because $(\mu_1,\ldots,\mu_k$, $\alpha_1,\ldots,\alpha_k)$ is regarded as the unknown value about which an inference is required. The dependence on $(\alpha_1,\ldots,\alpha_k)$, however, appears only in the form of a factor, which is equal to the likelihood function $l_{x_1,\ldots,y_n}(\alpha_1,\ldots,\alpha_k)$ discussed before. That is why the estimates $\hat{\alpha}_1,\ldots,\hat{\alpha}_k$ obtained are (almost) the same (slight differences are caused by adapting the original estimates of $\mu_1,\ldots,\mu_k$). The standard errors computed with this generalized perspective were useless, partly because of the additional uncertainty included in the generalized model $(\mu_1,\ldots,\mu_k)$ were not postulated and $\sum_{h=1}^{k}\alpha_h = 1$ was not postulated either) and partly because of a misinterpretation. That is why only point estimates are presented in the tables.

Remark 2

It is not in line with the POSCON philosophy, nor with statistics at large, not to express statistical uncertainties if these are large. That is why we like to emphasize that the statistical uncertainties in the estimates $\hat{\alpha}_1, ..., \hat{\alpha}_k$ will be considerable. If an estimate is equal to .33, say, then we would not be surprised if the true proportion in the group is .50 or .20. That the uncertainties are considerable is illustrated with an example concerning Redshank. Six breeding samples of Redshank with only wing- and culmen lengths were used in this study: males and females of nominate *totanus*, *britannica*, and *robusta*. In total, 4280 birds could be analysed. The measurements of the breeding samples and the mixed sample are shown in Fig. 14. With POSCON-analysis only 445 birds (10.4%) were assigned to just one breeding sample: the Hotelling test indicated that they were not a-typical for one sample, while they were a-typical for all other five samples. The other 89.6% was divided as follows: 16.6% resembled 2 samples, 23.9% 3 samples, 22.7% 4 samples, 16.9% 5 samples, 7.0% 6 samples, and 2.4% did not resemble any breeding sample. We have chosen this example because Table 10 shows that the separation between Redshank populations is more distinct than those between, e.g., Dunlin, Red Knot or Grey Plover populations. There the uncertainties in the estimates $\hat{\alpha}_1, ..., \hat{\alpha}_k$ of proportions will be even larger.
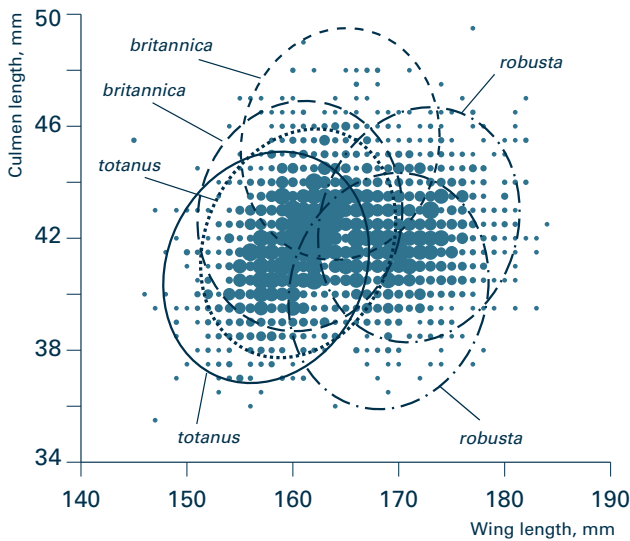
Figure 14: Relationship between culmen- and wing length in the Redshank. The measurements obtained in the Wadden Sea are presented as circles ranging from one (smallest circles) to 21 observations (largest-sized circles). The ellipses represent the means and variances of the breeding samples of Redshank presented in Table 10: 95% of the wing- and culmen lengths per breeding population and sex are estimated to occur within this range.

NUMBERS

5
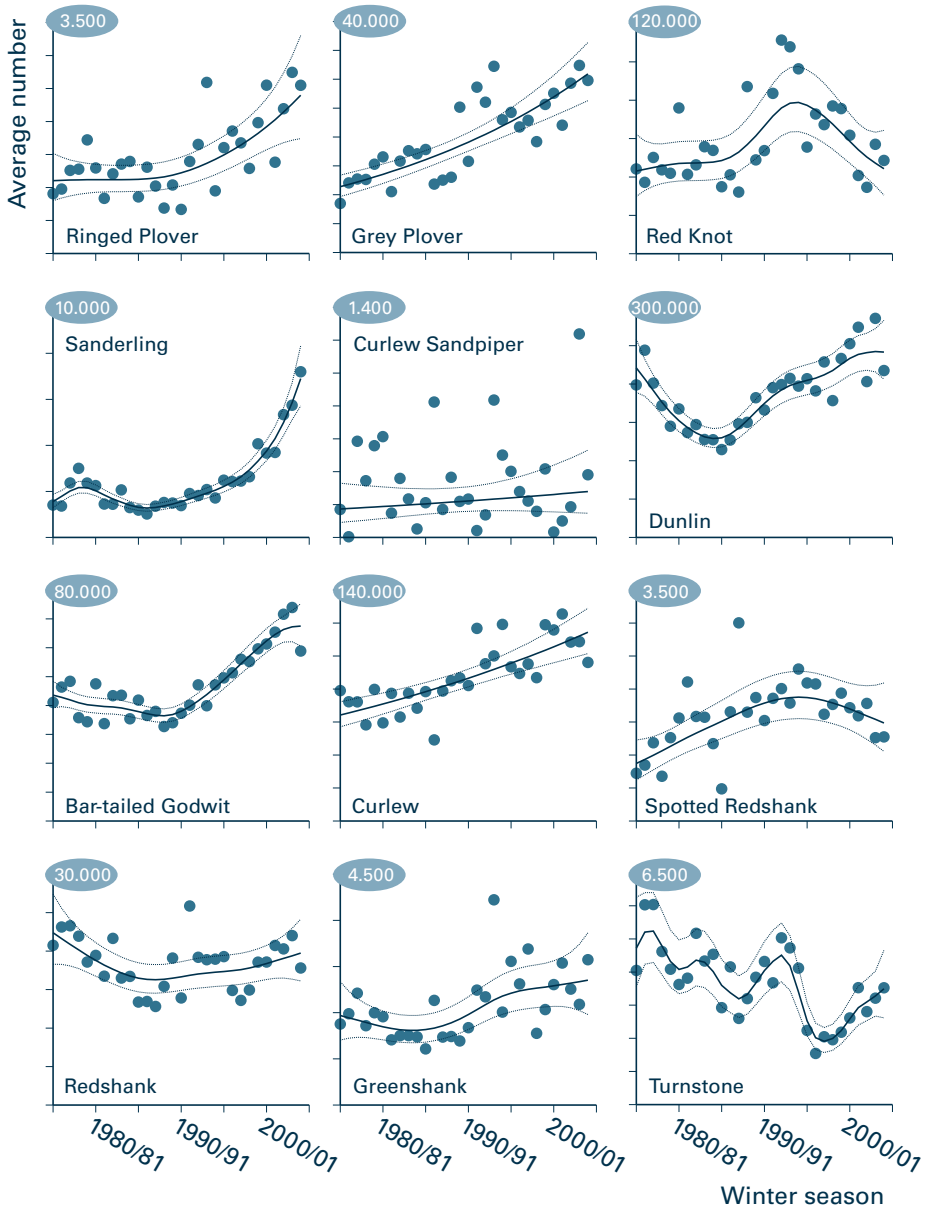
Figure 15: Changes in the abundance of the various wader species in the Wadden Sea since 1975/76 after Van Roomen et al. *(2007). The drawn line concerns the line computed with TrendSpotter (Visser 2002, 2004). The confidence intervals are shown with the interrupted lines. The Y-axes are differently scaled per species. The maximum values are printed in grey in the top-left corner of each graph.*

Most of the wader species, studied in this thesis, show increasing numbers in the Dutch Wadden Sea. In Fig. 15 estimates of the average numbers per 'winter' season present in the Wadden Sea are given. These estimates were produced with the computer program TrendSpotter by SOVON Vogelonderzoek Nederland (described in Section 2.3). The dotted lines provide an indication of statistical uncertainties. The increases displayed in Fig. 15 are not in line with the trend figures in the international Wadden Sea or in other parts of the East Atlantic Flyway, where most populations are declining (Table 11). The increases in numbers are possibly caused by the occurrence of milder winters in recent years, since the numbers present in the Wadden Sea during January are positively related to mean temperatures in the area (Fig. 16). In the past, severe winters often caused an exodus of waders to wintering grounds elsewhere in S- and W-Europe with milder wintering circumstances (Elkins 1983, Hulscher 1989, Camphuysen *et al.* 1996, Hulscher 2000).

Table 11. The trends in wader numbers of the Dutch Wadden Sea compared with the ones known from the international Wadden Sea and from the European, Mediterranean and/or African parts of the East Atlantic flyway populations.

		Europe/ Africa	International Wadden Sea (overall)	International Wadden Sea (January counts 1980-2000)	Dutch Wadden Sea
Species	**period/ population**	**Wetlands International (2006)**	**Blew *et al.* (2005), Koffijberg *et al.* (2005)**	**Blew *et al.* (2005)**	**SOVON & CBS (2005)**
Ringed Plover	winter W Europe & W-Mediterranean 1992-2001 passage	Decrease NW Europe 1989-2002 1992-2000 Decrease W Africa since 1990s	Increase 1980-2000; increase? 1994-2004	increase	Increase 1980-2004;
Grey Plover	winter passage	Decrease NW-Europe 1995-2002 Decrease W-Africa since 1990s	Stable 1980-2000; substantial decrease 1992-2000 1994-2004	Substantial increase increase	increase 1980-2004;
Red Knot	winter (*islandica*) passage (*canutus*)	Decrease since 1992 ?	Decrease 1980-2000; substantial decrease 1992-2000	Substantial increase?	Stable 1980-2004; decrease 1994-2004

Sanderling	winter	Increase NW-Europe 1989-2002	Increase 1980-2000; decrease? 1992-2000	Substantial increase?	Increase 1980-2004; substantial increase 1994-2004
	passage	?			
Curlew Sandpiper	passage	Increase	Increase? 1980-2000; substantial decrease 1992-2000		
Dunlin	*alpina*	Stable NW-Europe 1989-2002	Stable 1980-2000; substantial decrease 1992-2000	Substantial increase?	Increase 1980-2004; increase 1994-2004
	schinzii (Iceland)	Stable			
	schinzii (Baltic)	Decrease			
	arctica	Stable?			
Bar-tailed Godwit	winter	Stable	Stable 1980-2000; decrease 1992-2000	Substantial increase?	Increase 1980-2004; increase 1994-2004
	winter passage	Stable Decrease			
Eurasian Curlew	winter & passage breeding	Decrease since 1995 Decrease	Stable 1980-2000; decrease 1992-2000	Substantial increase?	Increase 1980-2004; increase 1994-2004
Spotted Redshank	passage	Stable?	Stable 1980-2000; decrease 1992-2000		Stable 1980-2004 ? 1994-2004
Redshank	*robusta* *totanus* *britannica*	Stable/ increasing? Stable/decrease? Decrease	Stable 1980-2000; substantial decrease 1992-2000	Fluctuating	Stable 1980-2004 increase 1994-2004
Greenshank	passage	Stable	Stable 1980-2000; decrease 1992-2000		Increase 1980-2004; ? 1994-2004
Ruddy Turnstone	winter (Nearctic) passage (N-Europe)	Decrease NW-Europe 1989-2002 Decrease W-Africa since 1990s	Stable 1980-2000; substantial decrease 1992-2000	Increase?	Stable 1980-2004; stable 1994-2004

The numbers in the Wadden Sea fluctuated during the past 30 years and these fluctuations differed per species. Curlew Sandpiper, Spotted Redshank, and Ruddy Turnstone had varying population levels. Ringed Plover, Grey Plover, Sanderling, Dunlin, Bar-tailed Godwit, and Redshank occurred in increasing numbers. The early 1980s were characterized by relatively low numbers of Ringed Plover, Grey Plover, Red Knot, Sanderling, Dunlin,

Bar-tailed Godwit, Eurasian Curlew, Spotted Redshank, and Greenshank. In the second half of the 1980s numbers started to recover with Grey Plover, Red Knot, Dunlin, and Spotted Red-shank earlier than Ringed Plover, Sanderling, and Bar-tailed Godwit. Numbers of Red Knot and Spotted Redshank peaked in the first half of the nineties and declined since then. Ruddy Turnstone numbers also showed this peak and decline during the mid-1990s, but in this species the numbers started to increase from the end of the 1990s up to now.

The numbers of waders are also counted in other parts of the East Atlantic Flyway. In some situations, a fairly reliable set of data was available from the past 10-30 years. The degree of similarity in trends might teach us more about the relatedness between these populations. Pictures similar to Fig. 16 can be drawn for other parts of the East Atlantic Flyway. We can compute the correlation coefficient between the annual abundance of, e.g. Ringed Plover in the Wadden Sea, and the annual abundance of the Ringed Plover on Falsterbo or on the British isles. However, it is only a data-analytic concept, and one has to keep in mind that significancy must be expected in 5% of the correlations due to chance. The correlations are presented in Table 12.
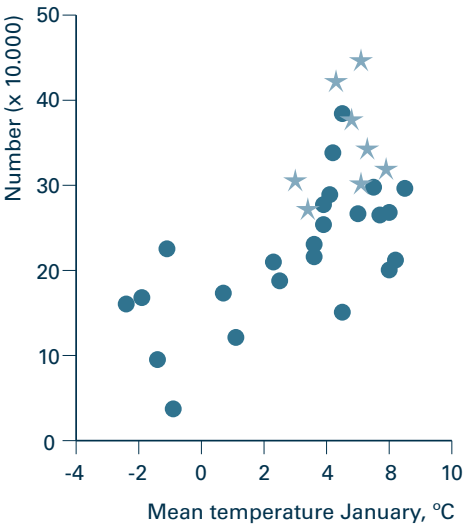
The Wadden Sea series of data (nearly) never correlated with the Falsterbo time-series, the W-European totals and the figures from Langebaan Lagoon. They correlate badly with the trends in the Dutch Delta area: only the trends of Sander-ling and Greenshank numbers are significantly (and positively) correlated. The Sanderling appears to increase everywhere in NW-Europe. The similarity between Wadden Sea trends and the ones from France and the British isles is

Figure 16: . The total wintering numbers of the 12 wader species under study in the Wadden Sea related to the mean temperature (°C) during January. The total numbers are based on the yearly January counts performed since 1974 (Boere & Zegers 1974, 1975, 1977, Zegers 1985, Zegers & Kwint 1992, Meltofte et al. 1994, Smit & Zegers 1994, Koffijberg et al. 1999, De Boer et al. 2001, Van Roomen et al. 2002, 2003, 2004, 2006a, 2006b). The mean January temperatures are gathered at airport De Kooy (near Den Helder 52.58N 4.46E) in the west part of the Wadden Sea (http://www.knmi.nl/klimatologie/maandgegevens/index.html) . The black circles represent counts performed before 1998 and the grey squares the ones from 1998 until and including January 2005.

Table 12. The (lack of) correlation between the wader abundances of the Wadden Sea with respectively the numbers counted on Falsterbo, S-Sweden(Falsterbo Bird Observatory, unpubl.), in the Dutch Delta area (Van Roomen et al., 2007 - also Wadden Sea index) , in France (LPO - BirdLife France, 2007), on the British isles (Pollitt et al., 2003), in NW-Europe (Wetlands International, 2006) as a total and on the S-African Langebaan Lagoon (Underhill, unpubl.) since 1969/70 (when possible).

Species	Falsterbo	Delta area total	France Lagoon	British isles	NW Europe	Langebaan
N of cases	29	27	30	28	14	26
Ringed Plover	-0.058	-0.153	0.351	-0.440*	-0.418	-0.359
Grey Plover	0.054	0.282	0.562***	0.693***	-0.016	-0.193
Red Knot	-0.066	0.021	0.258	0.138	0.243	-0.535***
Sanderling	-0.082	0.807***	0.785***	0.550**	-	0.297
Curlew Sandpiper	-0.157	-0.071	-	-	-	0.150
Dunlin	-0.059	0.211	0.569***	0.344	-0.136	-
Bar-tailed Godwit	-0.043	0.026	0.443*	-0.108	0.398	0.038
Eurasian Curlew	0.194	0.223	-0.071	0.773***	0.183	0.055
Spotted Redshank	-0.132	0.137	-	-	-	-
Redshank	0.205	0.294	-0.190	-0.092	0.042	-
Greenshank	-0.090	0.421*	-	-	-	0.272
Ruddy Turnstone	-0.351	-0.093	-0.508**	0.144	0.231	0.051

better, since correlations were significant in half of the species with Grey Plover, Sanderling, Dunlin (France), Bar-tailed Godwit (France) and Eurasian Curlew (British isles) being positively correlated and Ringed Plover (British isles) and Ruddy Turnstone (France) negatively. The positive correlations reveal the exchange between the Dutch, French and British wader populations. These results pose the question where in NW Europe the numbers of Grey Plovers are so quickly decreasing, that it is not compensated by the increases in the Dutch Wadden Sea, France and the British isles. That is why a more detailed approach is required.

In order to get a better understanding of the seasonal patterns in combination with the population changes in the Wadden Sea since the early 1970s, the monthly averages during the past three decades are presented in Fig. 17. Ringed Plover, Curlew Sandpiper, Spotted Redshank, and Greenshank are (nearly) not wintering in the Wadden Sea. Others like Red Knot, Sanderling, Dunlin, Eurasian Curlew, and Ruddy Turnstone winter in good numbers in the area. Ringed Plover, Curlew Sandpiper, Spotted Redshank, Redshank, and Greenshank are more abundant during the period of post-breeding migration than during spring migration, while spring peaks are higher in Grey Plover and Bar-tailed Godwit.
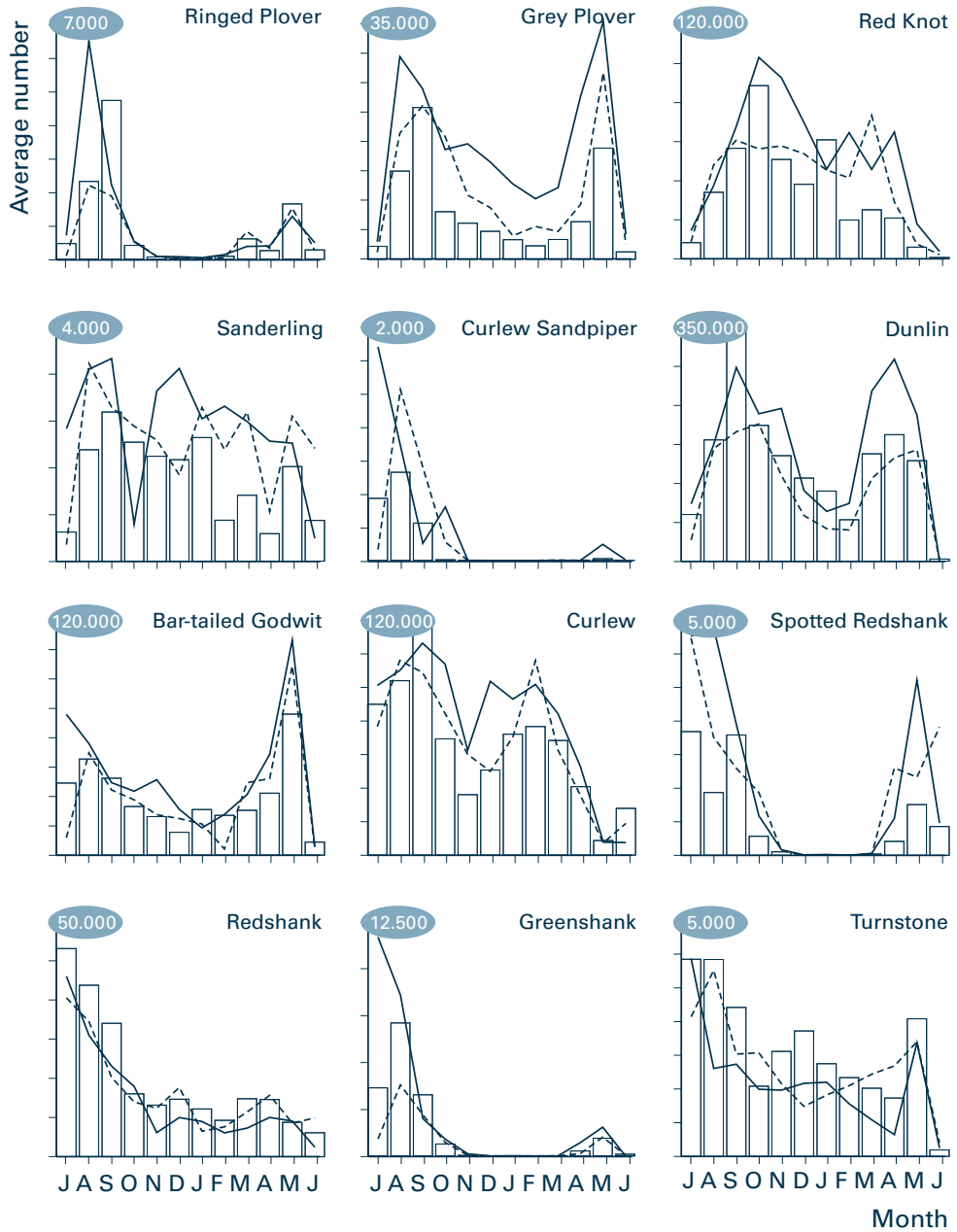
Figure 17: The monthly abundance of the various wader species in the Wadden Sea since the 1970s. Three decades are distinguished: 1970s (bars), 1980s (broken lines) and 1990s (straight lines). The Y-axes are differently scaled per species. The maximum values are printed in grey in the top-left corner of each graph.

Increased numbers during the 1980s were observed in Grey Plover (+51%), Red Knot (+18%), Sanderling (+42%), Curlew Sandpiper (+54%), and Spotted Redshanks (+85%) (Fig. 17). The numbers of Grey Plover and Sanderling were higher throughout the non-breeding season and the ones of Spotted Redshank during the post- and pre-breeding periods. The higher numbers of Red Knot were limited to the period from February onwards and the ones in the Curlew Sandpiper to the post-breeding period. In Ringed Plover (mean change -28%), Red Knot (+18%), Dunlin (-24%), Eurasian Curlew (+3%), Redshank (-17%), Greenshank (-45%), and Ruddy Turnstone (-15%) the post-breeding numbers dropped during the 1980s. The declines in the numbers of Ringed Plovers, Red Knots, Dunlins, and Eurasian Curlews occurred in the months September or October when many juveniles are present. However, in the other three species the decline was evident during the whole post-breeding period (Redshank, Greenshank) or throughout the non-breeding season (Ruddy Turnstone).

The mean numbers of 10 of the 12 species increased from the 1980s to the 1990s. Exceptions are Redshank (-10%) and Ruddy Turnstone (-18%). In Grey Plover, Sanderling, Dunlin, Bar-tailed Godwit, and Eurasian Curlew the increase is evident from all months. In the Ringed Plover the August numbers doubled. In Curlew Sandpiper and Greenshank especially the July numbers were much higher. During this month only adults are present. The increase in Red Knot-numbers is mainly restricted to the period October - December. In Spotted Redshank the August and May numbers were considerably higher. The declines in Redshank and Ruddy Turnstone were evident throughout the year.

The spatial use of the Wadden Sea by waders strongly differs between species (Table 13). A species like Sanderling strongly prefers the sandy coasts of the barrier islands, while others like Curlew Sandpiper and Spotted Redshank have a strong preference for the muddy areas along the mainland coast. Red Knot and Bar-tailed Godwit also prefer the sandy areas, but not as absolute as the Sanderling. Ringed Plover and Redshank show preference for the muddy coastal areas but less pronounced than Curlew Sandpiper and Spotted Redshank. The other species studied are distributed equally between the sandy barrier islands and the muddy coast. This preference is also shifting in the course of the non-breeding season. For instance, the barrier islands become relatively more important for Grey Plover, Bar-tailed Godwit, Redshank, and Ruddy Turnstone during winter, while the relative importance of the mainland coast is increasing in nearly all species during spring.

Some areas appear to be real strongholds, like Ringed Plovers and Greenshank along the Groningen coast (spring), Red Knots on Griend, Sanderlings and Bar-tailed Godwits on Terschelling, Curlew Sandpipers along the Frisian mainland and the N-Holland coast, and Eurasian Curlews and Redshank along the Frisian and Groningen coast.

Table 13. The proportional distribution of wader numbers over the various counting sites and split per species and monthly period.

Proportional distribution

Period	n of counts	average number	Noorderhaaks	Texel	Vlieland	Richel	Griend	Terschelling	Ameland	Engelsmanplaat	Schiermonnikoog	Simonszand	Rottumerplaat	Rottumeroog	Eems	Dollard	Groningen coast	Frisian coast	Harlingen - Afsluitdijk	Afsluitdijk	Noord-Holland
Ringed Plover																					
July - August	7	2258	0	5	3	0	1	15	9	0	13	0	4	5	1	5	14	21	0	0	4
September - November	21	1261	0	9	2	0	2	11	4	0	12	0	8	4	2	8	12	17	0	0	9
December - February	33	44	0	18	3	1	0	3	1	0	1	0	1	3	10	0	12	11	0	0	36
March - April	11	556	0	7	1	0	0	4	6	3	5	0	4	1	1	4	43	11	0	0	10
May	12	1215	0	4	1	0	0	2	2	0	4	0	3	2	0	5	44	22	0	0	10
June	2	585	0	11	1	0	0	12	6	0	6	0	9	4	4	1	15	16	0	0	15
Grey Plover																					
July - August	7	13760	0	4	7	0	1	9	7	2	10	3	2	8	0	4	17	20	0	0	4
September - November	21	18363	0	3	5	0	1	15	9	2	11	5	5	8	0	2	14	17	0	0	3
December - February	33	7543	0	3	5	1	3	19	15	2	10	8	3	3	0	0	11	11	0	0	4
March - April	11	7264	0	1	9	3	3	8	13	1	12	4	2	1	0	1	28	9	0	0	5
May	12	28457	0	3	4	0	3	7	6	2	9	4	4	3	0	5	21	25	0	0	4
June	2	2510	0	3	4	0	3	6	1	2	3	1	7	1	0	5	35	22	0	0	8
Red Knot																					
July - August	6	44114	0	0	23	3	20	5	1	6	21	7	4	7	0	0	0	2	0	0	0
September - November	22	65481	0	3	22	4	13	11	1	1	15	1	4	2	0	0	0	2	0	0	20
December - February	33	53983	0	6	9	10	37	10	2	0	1	0	0	1	0	0	0	1	0	0	23
March - April	11	38591	0	4	4	21	33	4	1	0	1	0	0	0	0	0	0	1	0	0	30
May	12	9963	0	4	4	6	54	8	4	1	2	0	0	0	0	0	5	9	0	0	2
June	2	2717	0	9	0	0	76	1	2	0	2	0	1	0	0	0	2	2	2	0	2
Sanderling																					
July - August	6	2787	11	1	17	0	2	28	4	3	10	6	7	12	0	0	0	0	0	0	0
September - November	22	2995	7	7	7	4	1	26	9	6	8	2	9	7	0	0	0	0	5	0	0
December - February	33	2814	6	11	11	1	0	34	11	1	8	4	5	6	0	0	0	0	0	0	0
March - April	11	1735	15	13	8	4	0	26	6	7	5	2	8	6	0	0	0	0	0	0	0
May	12	2312	9	3	1	8	1	20	4	30	6	3	7	9	0	0	0	0	0	0	0
June	2	417	0	1	1	0	20	0	8	19	14	7	6	23	0	0	0	0	0	0	0
Curlew Sandpiper																					
July - August	7	968	0	6	10	0	2	3	3	0	7	0	0	0	0	3	1	39	0	0	24
September - November	21	250	0	1	10	0	0	2	0	0	1	0	0	0	0	3	0	29	0	0	53

	n of counts	average number	Noorderhaaks	Texel	Vlieland	Richel	Griend	Terschelling	Ameland	Engelsmanplaat	Schiermonnikoog	Simonszand	Rottumerplaat	Rottumeroog	Eems	Dollard	Groningen coast	Frisian coast	Harlingen - Afsluitdijk	Afsluitdijk	Noord-Holland
December - February	33	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
March - April	11	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	0	0	42
May	12	38	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	11	0	0	84
June	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27	73	0	0	0
Dunlin																					
July - August	7	152078	0	2	9	0	7	15	12	4	16	2	5	9	0	5	2	9	0	0	3
September - November	21	216716	0	1	7	2	6	9	7	3	9	2	12	9	0	8	6	16	0	0	5
December - February	33	79571	0	1	5	2	10	9	10	3	6	2	4	5	0	8	6	17	0	0	13
March - April	11	173511	0	1	4	3	8	4	7	4	10	1	2	2	0	13	14	20	0	0	6
May	12	179444	0	2	5	0	8	3	6	3	10	2	5	4	0	12	12	23	0	0	6
June	2	555	0	2	1	0	2	15	1	3	2	11	5	4	0	5	12	26	0	0	11
Bar-tailed Godwit																					
July - August	7	49006	0	10	16	0	4	19	12	2	11	1	1	2	0	3	5	6	0	0	6
September - November	21	31487	0	6	18	5	10	36	2	0	10	1	1	2	0	1	1	3	0	0	4
December - February	33	18139	0	7	29	7	14	27	2	0	4	4	0	0	0	0	0	0	0	0	4
March - April	11	32863	0	7	11	6	28	12	9	0	10	1	0	0	0	3	3	3	0	0	6
May	12	94856	0	12	2	2	11	9	12	2	4	1	1	1	0	11	9	16	0	0	7
June	2	4430	0	15	1	3	27	8	13	0	1	1	1	0	0	5	9	7	0	0	8
Eurasian Curlew																					
July - August	7	83389	0	7	5	0	2	13	7	3	9	2	5	4	0	2	7	29	0	0	6
September - November	21	81483	0	5	5	2	2	9	10	2	8	4	3	6	1	2	13	24	0	0	5
December - February	33	75632	0	7	3	1	3	11	10	1	7	8	2	5	1	1	13	21	1	0	5
March - April	11	50056	0	4	5	1	3	9	10	2	9	4	5	1	1	3	16	20	1	0	7
May	12	6270	0	6	6	0	6	12	8	2	6	1	4	9	1	2	8	19	0	0	11
June	2	9236	0	4	5	1	8	9	6	2	9	1	6	5	0	2	19	15	0	0	10
Spotted Redshank																					
July - August	7	2416	0	5	2	0	0	1	2	0	1	0	0	0	0	37	6	20	0	0	27
September - November	21	1197	0	2	0	0	0	2	4	0	6	0	0	0	1	23	10	19	0	0	32
December - February	33	9	0	4	3	0	1	4	13	0	1	0	0	0	1	20	4	13	2	0	34
March - April	11	220	0	1	2	0	0	1	0	0	2	0	0	0	1	38	28	18	0	0	9
May	12	2179	0	1	0	0	0	0	1	0	2	0	0	0	0	54	10	18	0	0	13
June	2	1140	0	1	0	0	0	0	0	0	0	0	0	0	0	35	12	2	0	0	49
Redshank																					
July - August	7	27942	0	8	5	0	0	7	8	0	3	0	0	0	0	3	15	39	0	0	10

	n of counts	average number	Noorderhaaks	Texel	Vlieland	Richel	Griend	Terschelling	Ameland	Engelsmanplaat	Schiermonnikoog	Simonszand	Rottumerplaat	Rottumeroog	Eems	Dollard	Groningen coast	Frisian coast	Harlingen - Afsluitdijk	Afsluitdijk	Noord-Holland
September - November	21	14314	0	5	7	0	1	11	8	0	4	0	1	1	1	1	17	32	0	0	10
December - February	33	7225	0	7	7	0	2	16	9	0	4	0	0	1	3	1	14	21	0	0	15
March - April	11	11248	0	3	5	0	1	9	8	0	4	0	0	0	1	6	22	28	0	0	12
May	12	7538	0	4	2	0	0	8	3	0	3	0	0	0	2	7	25	38	0	0	9
June	2	3964	0	7	1	0	0	10	5	0	2	0	0	0	3	12	9	30	2	0	20
Greenshank																					
July - August	7	5814	0	14	10	0	1	16	12	1	16	0	2	2	0	2	11	5	0	0	9
September - November	21	1215	0	7	6	0	1	14	13	0	13	0	3	3	2	2	13	9	0	0	14
December - February	33	3	0	2	0	0	0	17	47	0	0	0	15	15	0	0	3	1	0	0	1
March - April	11	177	0	1	2	0	0	9	4	1	7	0	0	0	0	0	59	10	0	0	6
May	12	1151	0	4	6	0	0	10	12	1	8	0	1	4	2	2	29	10	0	0	11
June	2	37	0	12	8	0	0	11	1	3	3	0	1	0	3	0	26	4	0	0	28
Ruddy Turnstone																					
July - August	7	3335	0	12	13	0	3	11	13	3	9	0	2	4	0	0	3	6	4	0	16
September - November	21	2351	0	10	10	0	10	7	8	0	4	0	4	2	3	0	5	7	11	0	19
December - February	33	1908	4	11	9	0	12	7	9	0	3	1	1	2	7	0	4	2	11	0	16
March - April	11	1487	0	9	12	0	14	9	8	0	3	0	2	1	1	0	3	3	5	0	29
May	12	2802	0	13	7	3	5	7	7	0	4	0	2	0	6	0	6	11	5	0	23
June	2	201	0	10	2	2	3	4	16	0	4	0	4	0	0	0	4	3	29	0	17

The causation of these changes is complex, since many potential factors can influence these estimates. For instance, the increase in Curlew numbers since the early 1990s is explained by a decrease in hunting pressure during passage through Denmark (Laursen 2005) while the increase in Sanderling numbers is explained by better feeding conditions in the Wadden Sea (Reneerkens *et al.* 2005). The potential factors also include productivity of the various populations. Reneerkens *et al.* (2005) produced a detailed overview of the complexity, when explaining the trends.
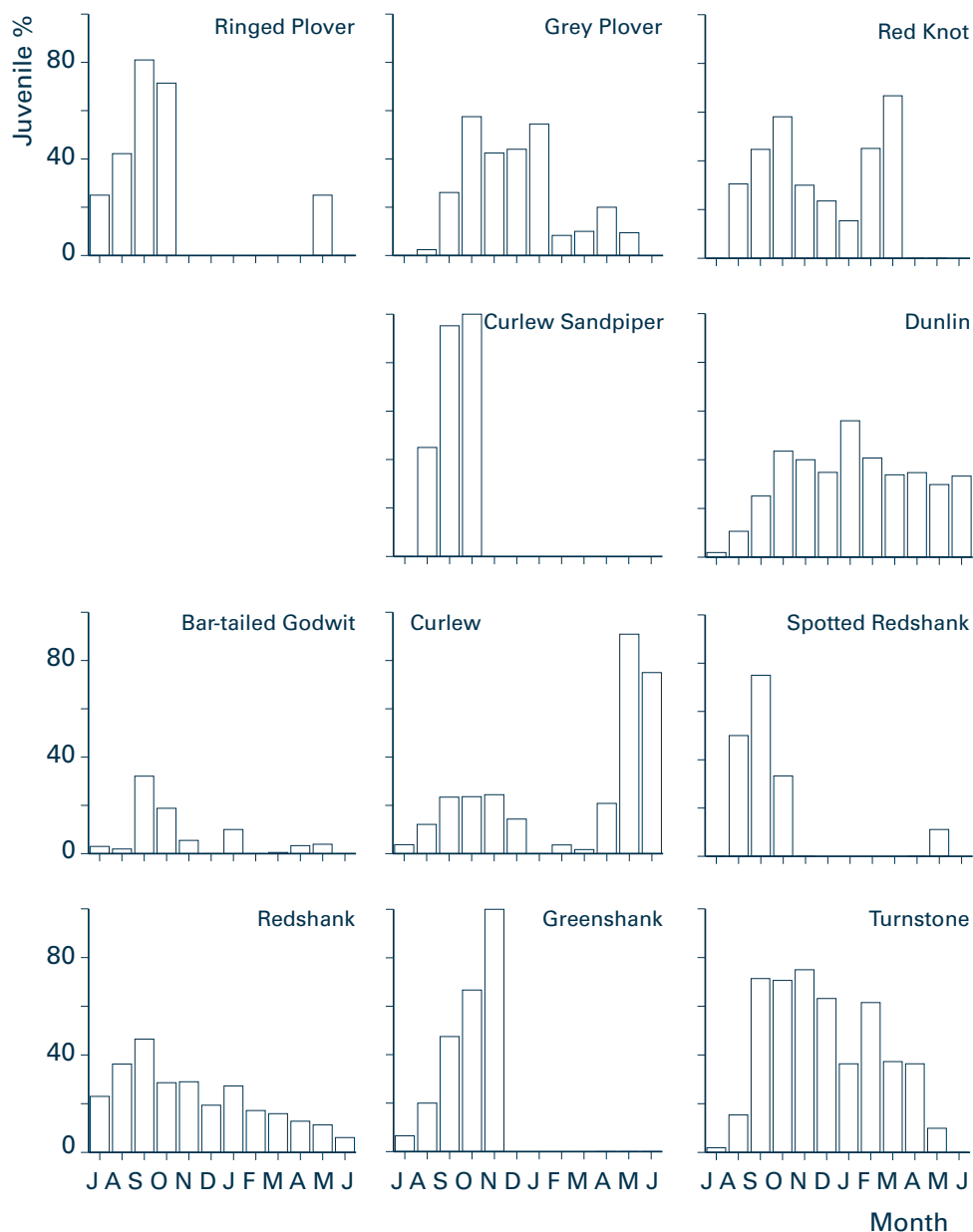
AGE COMPOSITION

6

Figure 18: Mean monthly juvenile percentages in the wader populations of the Wadden Sea during post-breeding. No graph for Sanderling is presented, since there were too few data.

The overall percentages first winter birds in the Wadden Sea ranged from less than 10% in Sanderling and Bar-tailed Godwit to more than 50% in Curlew Sandpiper and Ringed Plover (Table 2) with important fluctuations throughout the non-breeding season. Since adults depart earlier from the breeding grounds than juveniles, percentages first winter birds increase in all species from July onwards (Fig. 18). In species like Curlew Sandpiper and Greenshank, most adults only stay for a few weeks in the Wadden Sea, leaving the area before the juveniles. Once the juveniles have left the area as well, the species is no longer present. On the other hand, adult Dunlin or Redshank stay much longer, resulting in both adults and juveniles trapped during autumn, winter, and spring.

We hoped that by catching so many waders, the reproduction rates of the species can be studied. Since these data are hard to get from the breeding grounds, this information might teach us more about the factors influencing the reproductive output of waders in the past 30 years. The 'average' picture presented in Fig. 18, hides a lot of variability. It could happen in juvenile-rich months like September and October, that in one species all individuals, caught during a night's catch, were juveniles, whereas in another species all were adults. I therefore ran a series of univariate GLM-analyses (general linear models) on the samples collected between July and December even though the underlying assumptions for such a statistical procedure are not satisfied. For instance, the juvenile percentages are not normally distributed as is requested from the procedure.

Therefore, no formulae were derived from the procedures. Juvenile percentage was considered to be the dependent variable, day number and sample size the co-variates and location the

Table 14. Results of GLM-analysis with respect to the juvenile percentages of waders in the Wadden Sea during post-breeding. Only samples with at least four birds were included. Significance levels: * 0.01 < P < 0.05; ** 0.001 < P < 0.01; *** P < 0.001.

Species	df	F corrected model	R^2	sign. F day number	sign. F sample size	sign. F catching site
Ringed Plover	28/ 4	7.455***	0.516	***		
Grey Plover	135/ 4	23.680***	0.412	***		***
Red Knot	103/ 4	13.689***	0.347	***	***	
Curlew Sandpiper	39/ 4	18.876***	0.690	***	*	
Dunlin	577/ 4	149.309***	0.509	***	*	***
Bar-tailed Godwit	120/ 4	2.852*	0.087	**		
Eurasian Curlew	64/ 4	0.830	0.049			
Redshank	252/ 4	12.870***	0.170	*	*	***
Greenshank	25/ 3	3.666*	0.305		*	*
Ruddy Turnstone	28/ 4	4.009*	0.364		*	

only fixed factor (tables 14 & 15). The variability in percentages first winter birds is often significantly related to the day number, but also sample size and catching site appear to be important. In Red Knot, Dunlin, Redshank, Greenshank, and Ruddy Turnstone larger samples result in catches with lower percentages first winter birds, as was found earlier by Van der Have *et al.* (1984) in Dunlin and by Swennen (1984) in Oystercatcher. They interpreted this outcome by arguing that large catches are linked to large flocks. These large flocks contain relatively few juveniles due to a high degree of competition within the flocks: juveniles are pushed aside to the edges of these flocks or to smaller flocks in less-preferred roosting areas. Curlew Sandpiper is the exception: larger sample sizes coincide with higher juvenile percentages. The ecological explanation of this exception might be, that in good production years many birds can be caught since many are present, being mostly juveniles and thus having high percentages first winter birds. When few birds are trapped, few are present with hardly any juveniles among them and thus low percentages first winter birds. It also appears, that both age-groups use the Wadden Sea somewhat differently. On Vlieland and the Frisian coast 15-35% more juvenile Grey Plovers, Dunlin, and Greenshank and 18 - 24% less juvenile Redshank are caught in comparison with Schiermonnikoog (Table 15).

Unstandardized residuals were calculated with the above presented GLM-analyses. Residuals are the part of observations left unexplained after correction for day number, sample size and/ or catching site and correspond to the actual observation minus the predicted value. They are presented in Fig. 19. Both the residuals and the uncorrected juvenile percentages were correlated with the data sets mentioned in Section 2.4 under 'age':

Table 15. Parameter estimates of the GLM-analyses presented in Table 14. Day-number is used with July 1st being day number 1, August 1st day number 32, etc.

	Parameter estimates				
Species	day number	sample size	Vlieland	Frisian coast	Schiermonnikoog
Ringed Plover	1.597	-	-	-	-
Grey Plover	0.668	-	14.627	25.911	0
Red Knot	0.866	-0.477	-	-	-
Curlew Sandpiper	1.795	2.248	-	-	-
Dunlin	0.440	-0.055	30.990	28.629	0
Bar-tailed Godwit	0.160	-	-	-	-
Eurasian Curlew	-	-	-	-	-
Redshank	-0.094	-0.242	-18.028	-24.009	0
Greenshank	-	-1.636	34.423	-	0
Ruddy Turnstone	-	-0.361	-	-	-

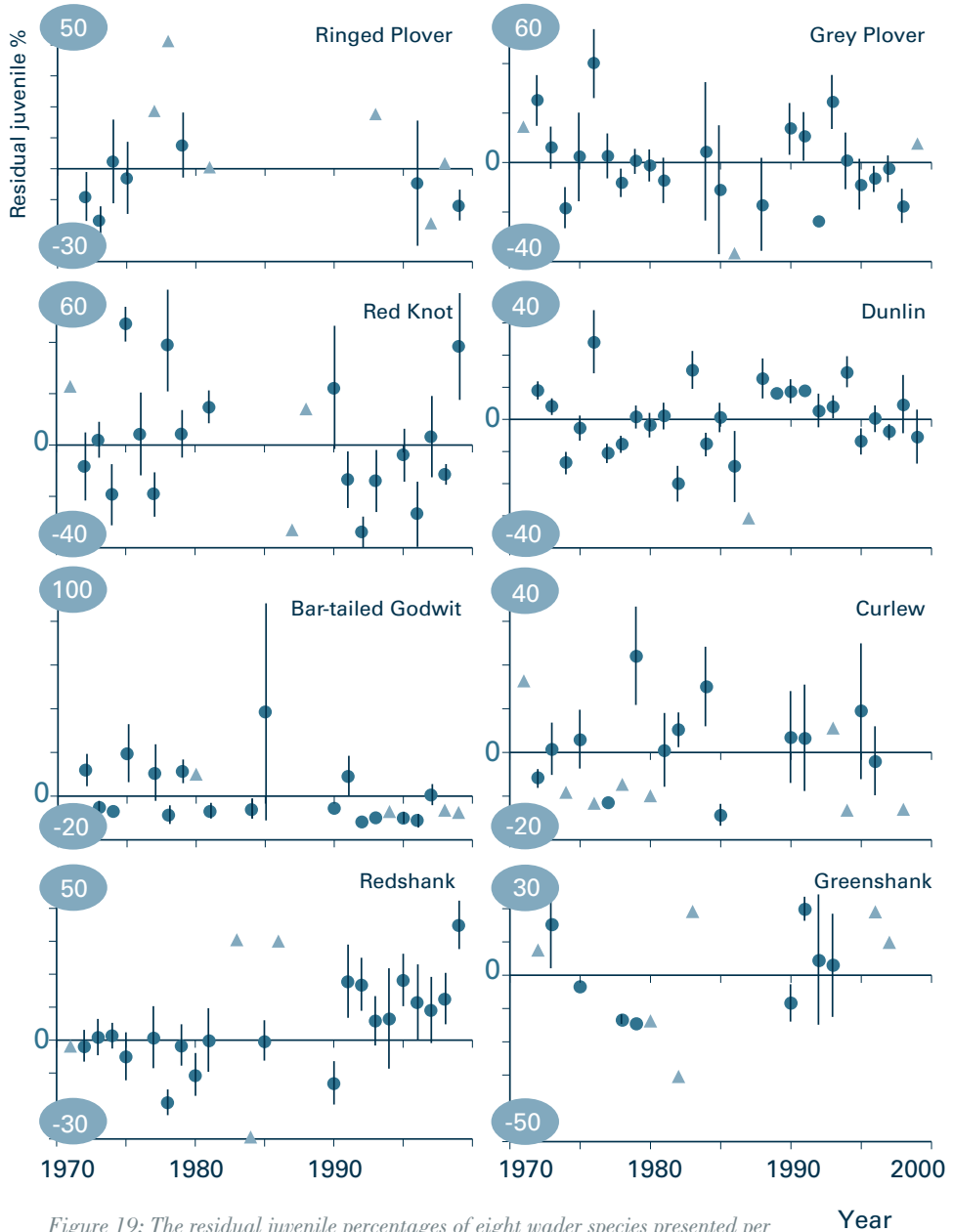*Figure 19: The residual juvenile percentages of eight wader species presented per breeding season on the X-axis. The residuals were obtained after correction for day number, sample size and/ or catching site in accordance with the findings presented in Table 13. The average values per year are given plus or minus the standard errors. A triangle indicates the data-points based on a single sample.*

Productivity

The Bar-tailed Godwit is the only species out of the 10 tested, of which the productivity shows high juvenile percentages in good breeding years of the Dark-bellied Brent Geese (Table 16). It is striking, that no similarity between the Brent Geese cycle and the productivity patterns was found in other Siberian species like Ringed Plover, Grey Plover, Red Knot, Curlew Sandpiper, Dunlin and Ruddy Turnstone. It forces the question, 'why these wader species are not subjected to the lemming cycle?' or additionally 'why we cannot retrace the lemming cycle pattern in the data of our Wadden Sea populations?'. Even in non-breeding years for Brent Geese these wader species returned with juveniles to the Wadden Sea. When Brent Geese were very productive, this was nearly never so in the wader species. The latter species had a higher mean productivity, when Brent Geese reached 16-30% juveniles. The most obvious significant correlations were the ones between the residual juvenile percentages of Dunlin in the Wadden Sea with the juvenile proportions of Dunlin on the British isles (Pearson's r= 0.758; N= 8; s= 0.029) and between the residuals of Dunlin and the number of juveniles caught at Ottenby - Sweden (Ottenby Bird Observatory unpubl. data): Pearson's r= 0.530; N= 28; s= 0.004. This indicates, that the Swedish juveniles on passage are the same population as the one staging in the Dutch Wadden Sea and wintering on the British isles.

Numerical changes and abundance

Increases in wader abundance might be caused by both increased productivity or decreased mortality and oppositely decreasing abundances might indicate low productivity or high mortality. In 10 of the 12 species, virtually no significant correlations (1 on 100) were found between juvenile percentages or the residuals in the Wadden Sea wader populations on the one side and changes in wader abundance in the following time-series: Falsterbo - Sweden (Kjellén pers. comm.), Wadden Sea (Van Roomen *et al.* 2006b), Dutch Delta area (Van Roomen *et al.* 2006b), British isles (Pollitt *et al.* 2003) and France (LPO unpubl. data). Correlations with the abundances themselves showed again few significant correlations (3 on 92). Boyd & Piersma (2001a) showed for the Red Knot that density dependency on the breeding grounds caused negative correlations on the W-European wintering grounds with low productivity estimates at high population levels and high ones at low levels. This is also evident from our data: large residuals in the Wadden Sea correlate negatively with the UK index for Red Knot (Pearson's r= -0.460; N= 21; s= 0.036).

Climate Wadden Sea

The attention was focussed on the climate conditions prior to the breeding season both during winter and during spring. Only 2 out of 80 correlations were significant, which is less than the 5% expected at minimum. Therefore, there is no indication from this material that winter- or spring-climate conditions influence the yearly wader productivity.

Table 16. Juvenile percentages of 10 wader species in the Wadden Sea related to the productivity cycle of the Siberian Dark-bellied Brent Geese. Presented are means ± standard deviations with the sample sizes between brackets. For explanation on residuals see text.

Species	Juvenile percentage Siberian Brent Geese				F-value	df	s
	0	1-15	16-30	>30			
Mean juvenile percentages waders per winter season without corrections							
Ringed Plover	40. 0 (1)	73.1±19.5(5)	72.8±23.8 (3)	58.7±17.7(7)	n.s.		
Grey Plover	5.0±6.9(4)	29.9±34.7(7)	37.7±20.8(4)	32.8±16.7(8)	n.s.		
Red Knot	23.8±19.3(3)	26.9±25.0(7)	58.6±16.7(4)	55.7±26.9(8)	n.s.		
Curlew Sandpiper	2.4 (1)	65.3±33.4(3)	100.0±0.0(2)	62.8±30.2(7)	n.s.		
Dunlin	15.8±8.4(5)	24.1±13.1(9)	21.8±5.6(4)	25.4±5.4(9)	n.s.		
Bar-tailed Godwit	0.7±1.2(3)	7.3±8.6(6)	1.2±1.5(4)	20.7±16.1(7)	3.907	3/16	0.029
Eurasian Curlew	12.8±18.2(2)	7.9±13.4(6)	15.2±4.3(3)	10.3±10.0(10)	n.s.		
Redshank	51.3±12.2(4)	40.6±20.7(7)	47.2±14.2(4)	42.9±14.5(9)	n.s.		
Greenshank	25.0 (1)	35.0±7.1(2)	22.4±16.5(3)	21.8±15.1(7)	n.s.		
Ruddy Turnstone	42.1±6.6(2)	100.0 (1)	86.1±24.1(3)	42.9±37.8(5)	n.s.		
Residual mean juvenile percentages							
Ringed Plover	2.3 (1)	7.1±19.0(5)	0.3±15.5(3)	4.6±18.6(7)	n.s.		
Grey Plover	-22.3±11.5(4)	2.9±18.1(7)	9.9±13.0(4)	1.1±13.5(8)	3.654	3/19	0.031
Red Knot	-18.9±15.0(3)	-6.9±17.6(6)	5.0±30.4(4)	4.6±30.1(8)	n.s.		
Curlew Sandpiper	-23.3 (1)	-10.3±11.9(3)	23.4±25.4(2)	3.3±17.5(7)	n.s.		
Dunlin	-4.8±9.9(5)	0.8±16.4(9)	1.8±5.9(4)	0.6±10.0(9)	n.s.		
Bar-tailed Godwit	-9.6±2.4(3)	-2.9±7.0(6)	-8.5±2.5(4)	10.9±15.7(7)	4.373	3/16	0.020
Eurasian Curlew	0.2±13.1(2)	-5.7±11.4(6)	2.3±4.0(3)	-0.4±10.1(10)	n.s.		
Redshank	16.6±11.8(4)	4.2±18.0(7)	9.7±19.8(4)	-0.5±14.1(9)	n.s.		
Greenshank	4.4 (1)	14.5±6.6(2)	4.6±13.8(3)	-2.8±18.1(7)	n.s.		
Ruddy Turnstone	-12.2±36.6(2)	33.3 (1)	18.4±25.0(3)	-8.2±29.4(5)	n.s.		

The North Atlantic Oscillation

Only 2 out of 80 correlations were significant, which is less than the 5% expected at minimum. Therefore, there is no indication from this material that the North Atlantic Oscillation is of influence on the yearly wader productivity, whether it is during the winter and spring preceding a breeding season or during the breeding season or during the period that the fledged juveniles head for W-Europe. When Boyd & Petersen (2006) analysed the degree of relatedness between the arrival dates of waders breeding in Iceland on the one side with the winter and spring values of the North Atlantic Oscillation, they also found relatively few significant correlations (7 on 36). Most of their significant outcomes (5 out of 7) concerned later arrival following a positive spring-index, representing warm and wet spring circumstances.

The analyses concerned both GLM-analyses and bivariate correlations. The results of the bivariate correlations were mostly not supporting the expectations: with many tests at least 5% can be expected to be statistically significant. More sophisticated analyses, including non-linear relationships and density-dependency, might produce better results. Moreover the data-gathering is slow, since only one data-point per year and per species can be obtained, while the temporal and spatial variation of juvenile percentages in flocks on migration or wintering is large.

PRIMARY MOULT

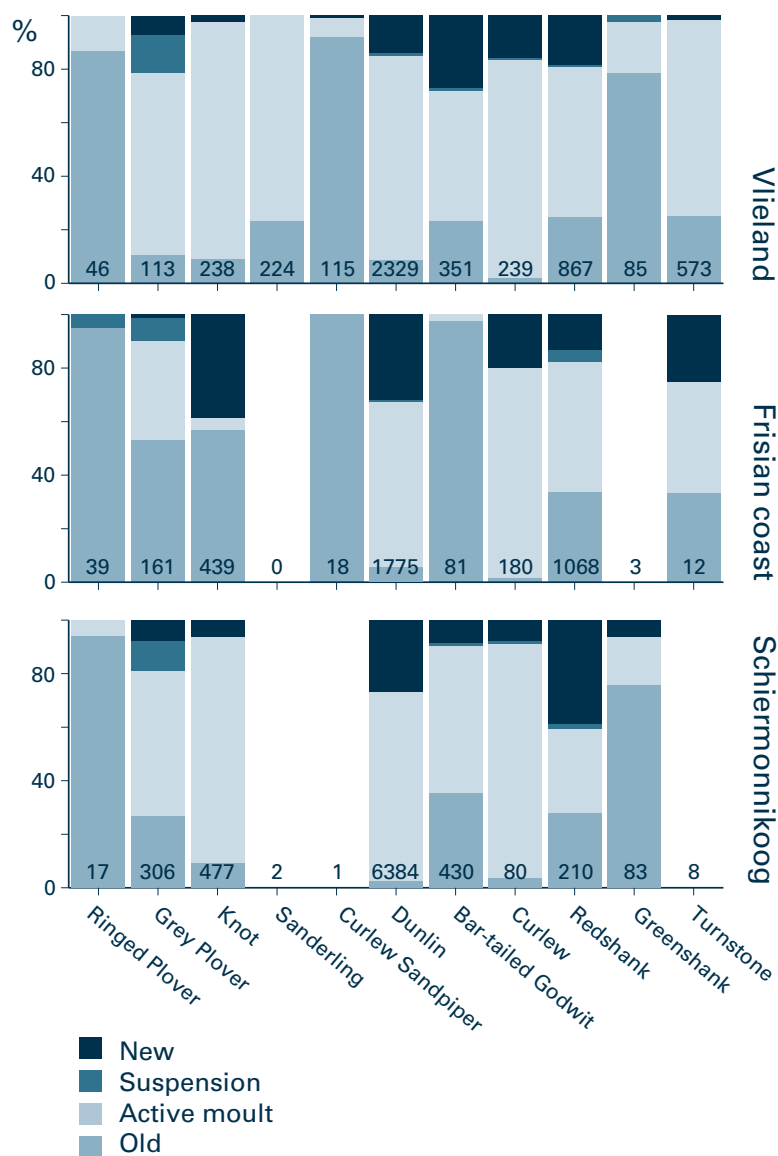7

Figure 20: The distribution in percentages of 4 stages of primary moult for the twelve species and three locations in the Wadden Sea. The data span the period between July and December. For each species and location the number of birds captured is presented just above the X-axis. The four stages of primary moult are from bottom to top: old, actively moulting, suspended moult and completed.

M any of the Ringed Plovers, Curlew Sandpipers, and Greenshanks captured did not moult their primaries in the Wadden Sea (Fig. 20). For all other species moult was observed rather often. Most waders returning from the breeding grounds started their primary moult during August (Fig. 21). Eurasian Curlews were an exception with an estimated mean starting date of 22 July. The estimated mean starting dates of Dunlin and Redshank were respectively 4 and 7 August. Sanderling and Ruddy Turnstone started around 20 August with Red Knot following 8 days later. Bar-tailed Godwit and Grey Plover were the only species, which started as late as early September. Dunlins and Red Knots needed 53-57 days for their primary moult, while Grey Plovers and Eurasian Curlews needed 80-90 days. Occasionally a bird was caught in an advanced stage of primary moult during June, July or August. These birds often had a very worn plumage with remnant characters of first winter or juvenile plumage (Boere 1976) and were considered as summering birds (second summer- & non-breeding birds), which had started their primary moult already in June, a few weeks after the mass departures of the arctic migrants from the Wadden Sea to their breeding grounds. The year-to-year variation in start of primary moult was estimated to range between 20 (Dunlin, Red Knot) and 30 days (Grey Plover, Eurasian Curlew).
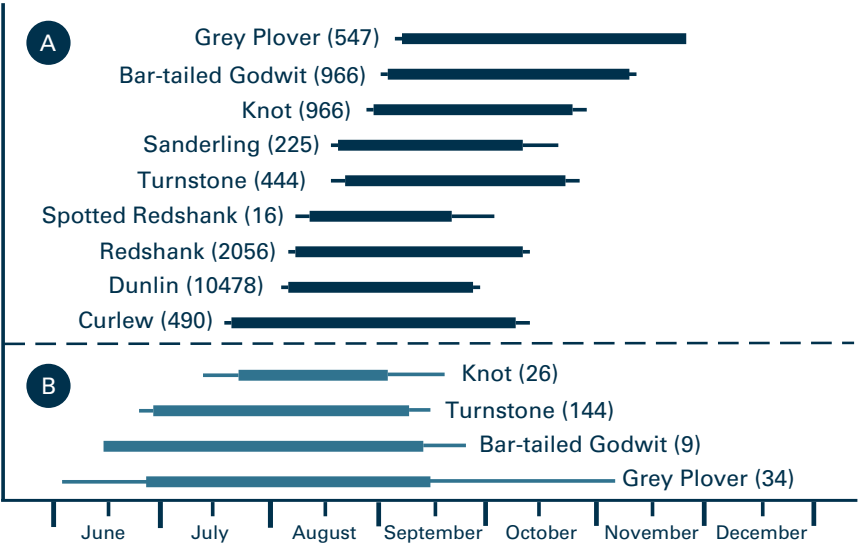

Figure 21: Estimates of the mean start and duration of primary moult in the wader species studied. The thick lines present the mean start and duration. The thin lines present the 95% confidence intervals of the estimates. A. (black lines) birds returning from their breeding grounds, and B. (grey lines) summering birds (non-breeders, immatures) in an advanced stage of primary moult.

There is a large degree of spatial differentiation with respect to occurrence of primary moult (Fig. 20). For instance, the Red Knots and Bar-tailed Godwits on Vlieland and Schiermonnikoog are often moulting, while they nearly never moult along the mainland coast. The moult-data of Grey Plovers, Dunlins, and Ruddy Turnstones show the same pattern but less pronounced.

Redshank seems to be the exception with less moulting individuals on Schiermonnikoog as compared with both other sites. Since temporal variation might cause these differences, the data of July and August were analysed in a bit more detail (Fig. 22). The staging populations of Grey Plover, Red Knot, and Bar-tailed Godwit along the Frisian coast included the highest percentages non-moulters, while they were lowest on Schiermonnikoog. There were also significant differences, once the birds had started primary moult. One bird might start its primary moult intensely with many feathers being shed simultaneously, while another seems to restrict its gap size. Relatively many Redshank and Greenshank tended to have large gaps on Vlieland in comparison to Schiermonnikoog, or additionally relatively many Knot, Dunlin, Bar-tailed Godwit, Eurasian Curlew, and Greenshank tended to have small gaps on Schiermonnikoog. However, this was not tested statistically. Relatively many birds with small gaps were present along the Frisian coast (Dunlin and Redshank) and Schiermonnikoog

Table 17. Results of GLM-analysis relating the number of simultaneously moulted primaries to the number of new primaries already grown and to the catching site. Significance levels: * 0.01 < P < 0.05; ** 0.001 < P < 0.01; *** P < 0.001.

Species	df	F corrected model	R^2	sign. F N new primaries	sign. F catching site	Intercept	N of new primaries	Vlieland	Frisian coast	Schiermonnikoog
Ringed Plover	2/4	6.095	0.629							
Grey Plover	3/317	49.494***	0.313	***	***	3.492	-0.236	-0.051	-0.957	0
Red Knot	3/626	413.728***	0.663	***	**	4.526	-0.377	0.036	-0.578	0
Sanderling	2/170	99.000***	0.533	***		5.000	-0.508			
Curlew Sandpiper	1/6	2.382	0.165							
Dunlin	3/7373	4190.550***	0.630	***	***	4.831	-0.382	0.079	-0.378	0
Bar-tailed Godwit	3/404	129.611***	0.487	***	*	3.766	-0.266	0.200	-0.766	0
Eurasian Curlew	3/401	198.942***	0.595	***	*	4.942	-0.378	0.219	0.076	0
Spotted Redshank	2/5	1.076	0.021							
Redshank	3/1076	176.441***	0.328	***	***	3.830	-0.261	0.225	-0.415	0
Greenshank	2/30	5.033*	0.201	**		3.332	-0.327			
Ruddy Turnstone	3/426	120.066***	0.454	***		5.066	-0.314			

Ringed Plover

%
80
40
0

28 43 14

Grey Plover

$Chi^2 = 17.768; P < 0.000$

106 14 120

Knot

$Chi^2 = 162.40; P < 0.000$

262 20 122

Curlew Sandpiper

80
40
0

18 113 0

Dunlin

$Chi^2 = 146.6; P < 0.000$

1102 623 2429

Bar-tailed Godwit

$Chi^2 = 47.0; P < 0.000$

79 92 242

Curlew

$Chi^2 = 22.42; P < 0.000$

80
40
0

47 16 17

Redshank

$Chi^2 = 134.9; P < 0.000$

758 584 77

Frisian coast   Vlieland   Schiermonnikoog

Greenshank

3 82 66

Frisian coast   Vlieland   Schiermonnikoog

Turnstone

$Chi^2 = 73.706; P < 0.000$

80
40
0

8 541 8

Frisian coast   Vlieland   Schiermonnikoog

■ Large gaps
■ Small gaps
□ No primary moult

Figure 22: The occurrence of primary moult in adult waders captured in the Wadden Sea during July and August. A distinction is made between non-moulters and moulters. In the moulters, a distinction is made between birds with 'small' or 'large' gaps in the wing.
The definition of 'small' gaps is according to Holmgren et al. (1993b): 1 primary shed with raggedness score 3 or lower, 2 primaries shed with score 7 or lower, 3 primaries shed with score 8 or lower, 4 primaries shed with score 7 or lower, 5 primaries shed with score 6 or lower, 6 primaries shed with score 7 or lower, 7 primaries shed with score 6 or lower, 8 or 9 primaries shed with score 4 or lower.

(Eurasian Curlew and Greenshank). In a GLM-analysis the number of simultaneously moulted primaries were analysed in dependence of the number of new primaries already grown and the location (Table 17). Location appeared to be a significantly differentiating factor in 6 of the 12 species. Moulting Dunlin, Bar-tailed Godwits, and Eurasian Curlew have larger gaps on Vlieland than on Schiermonnikoog and moulting Ringed Plovers, Grey Plovers, Red Knots, Dunlin, and Redshank all had significantly smaller gaps along the Frisian coast than on Schiermonnikoog. In most of the species analysed, the Frisian coast populations were extreme because they had the highest proportions non-moulters and/or the smallest gaps in the wings and/or the lowest number of simultaneously growing feathers.

Waders nearly always suspend rather than arrest their moult (Cramp & Simmons 1983). Moult suspenders resume their primary moult: the new feathers continue to grow, but no new feathers are shed. They continue to moult later during that same non-breeding season under warmer circumstances. When they arrest moult, they skip a cycle with a set of new and old feathers and start again next year after the breeding season. Since moult suspension of waders in autumn mostly precedes migration further south, it is of interest to know when and where birds were suspending their moult. The Grey Plover, being the latest species starting
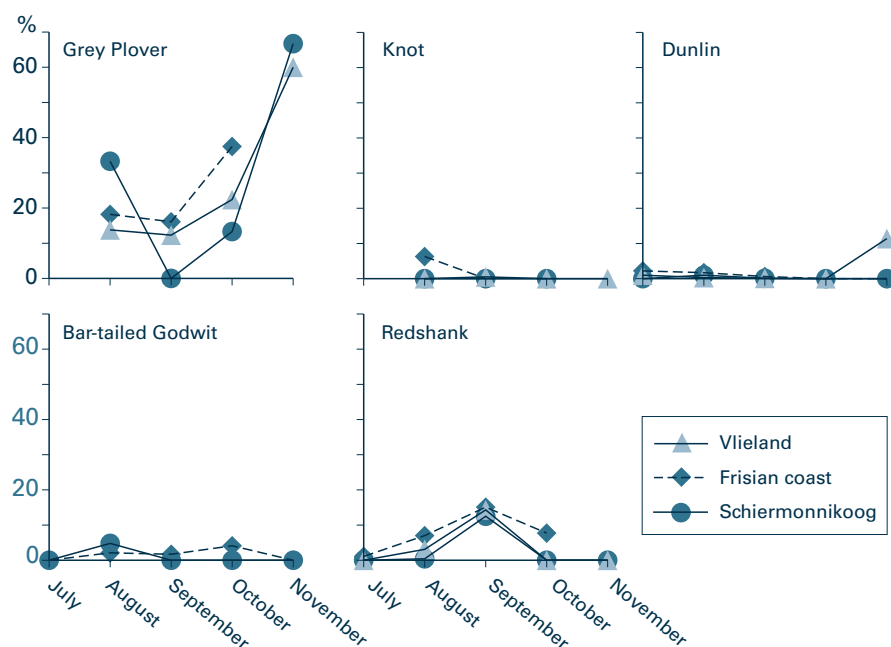

Figure 23: Suspension rates of primary moult in five wader species during post breeding.

its primary moult, is the species with by far the highest percentages moult suspension (Fig. 23). The suspension percentage in this species is increasing to 60% of the adults captured in November. Redshank populations show a peak in suspension percentages during September. The mainland coast populations of Red Knot (Chi^2 = 15.465; df 2; P < 0.000), Dunlin (Chi^2 = 12.594; df 2; P < 0.002), and Redshank (Chi^2 = 22.802; df 2; P < 0.000) have the highest percentages of moult suspension amongst the three locations with resp. 5.3, 1.1, and 8.1%. The duration of primary moult is of influence on the quality of the primaries renewed (Serra 2001): growing more durable primaries -with higher concentrations of melanins- takes more time.

Summarizing, three species hardly ever moult their primaries in the Wadden Sea: Ringed Plovers, Curlew Sandpipers, and Greenshanks. The other species have a large degree of spatial variation with respect to the primary moult pattern. The inhibition of primary moult in the wader populations along the mainland coast is striking with hardly any moulting Red Knots and Bar-tailed Godwits and fewer moulting Grey Plovers, Dunlins, and Ruddy Turnstones. When birds were moulting their primaries, the Ringed Plovers, Grey Plovers, Red Knots, Dunlin, and Redshank along the Frisian coast had smaller gaps, since they shed fewer primaries simultaneously. Incidence of moult suspension was also highest along the mainland coast in Red Knot, Dunlin, and Redshank.

The Vlieland populations of Red Knot, Dunlin, Bar-tailed Godwit, Eurasian Curlew, Redshank, and Greenshank shed more primaries simultaneously or had larger gaps in the wings than their Schiermonnikoog-conspecifics. The Grey Plover had the highest suspension rate amongst the species studied. These differences in primary moult patterns might be caused by differences in migration strategies, time constraints (Serra 2000) or in population composition.

Some of the most pronounced results for species:
1. *Ringed Plover.* Our results agree with Haberer's (1994) results showing low percentages of adult Ringed Plovers with actively moulting primaries in the Wadden Sea. On the other hand, 50-90% of the adult Ringed Plovers caught in the Wash undergo their primary moult in the area (Johnson 1985). Even though the primary moult percentages range between 1 and 86% in other British estuaries (Eades & Okill 1976, Clapham 1978, Insley & Young 1981), they are nearly always higher than the ones in the Wadden Sea.

2. *Grey Plover.* About 10% of the Grey Plovers, captured soon after arrival in August (adults with low energy reserves, n = 231), had suspended primary moult prior to their departure
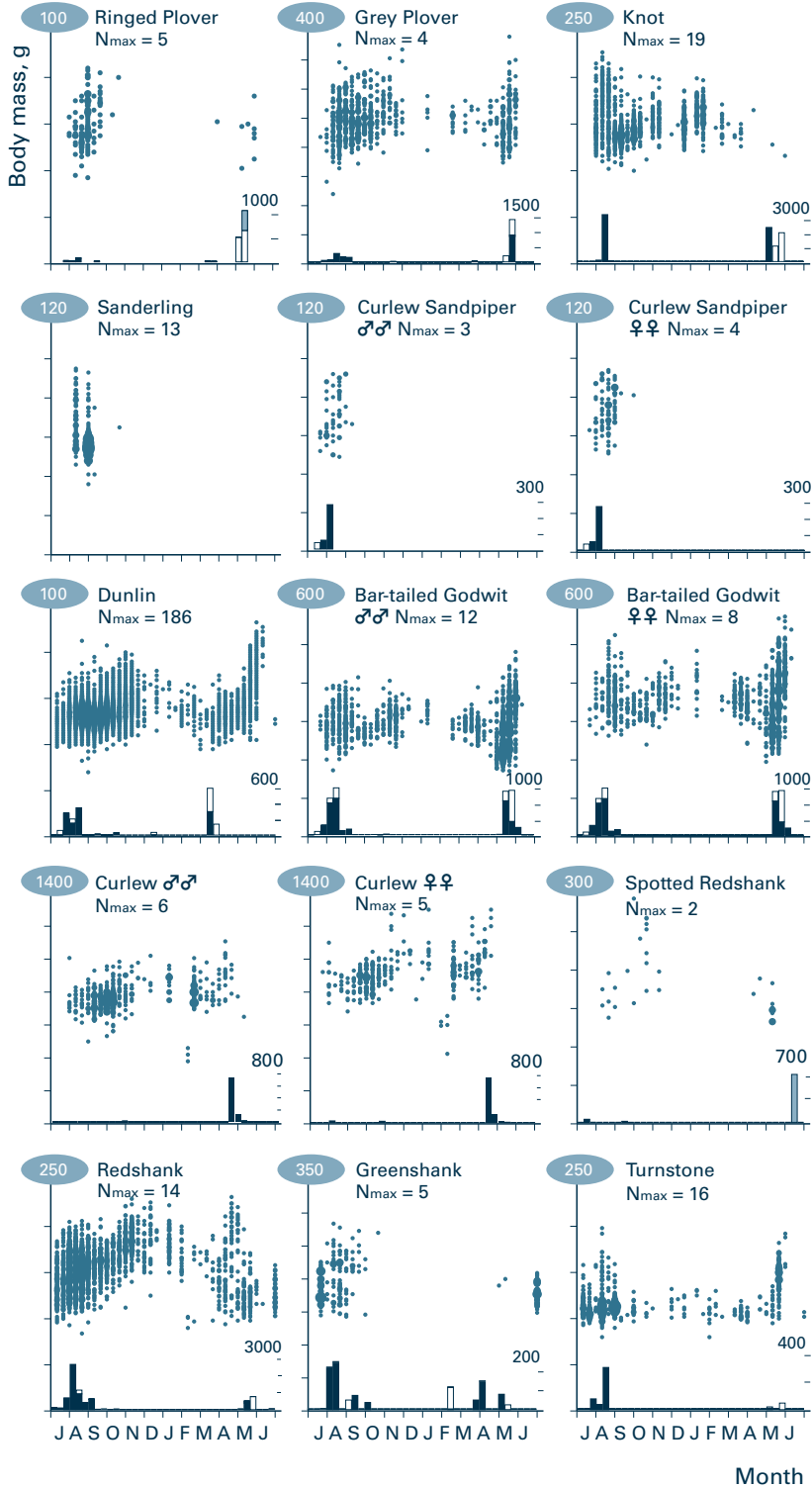
to the Wadden Sea. This percentage is similar to the 11% for the southern Baltic (Gromadzka & Serra 1998), smaller than the 18% in the Polish Puck Bay (Krupa & Krupa 2002) and the 25-40% for the Wash (Branson & Minton 1976) but higher than the 5% presented for the Wash (Serra *et al.* 2006). No moult suspension was detected amongst the recent arrivals at more southerly latitudes like NE-Italy (Serra & Rusticali 1998), SE-India (Balachandran *et al.* 2000), and S-Africa (Serra *et al.* 1999). The Nearctic breeding population starts its primary moult at the breeding grounds, whilst only few birds do so on the Palearctic breeding grounds (Prokosch *et al.* 1993, Engelmoer & Roselaar 1998, Exo & Stepanova 2000).

3. *Dunlin.* Nearly all adults started post-breeding moult immediately after arrival in the area or were moulting when arriving in the area. More than 30% of the Dunlin present on the Baltic staging grounds combine short stays with active primary moult (Gromadzka 1989, Holmgren *et al.* 1993a). These birds thus enter the Wadden Sea with growing primaries. The proportion of birds not in primary moult in the Wadden Sea immediately after the breeding season is accordingly small compared with other species in the area. Dunlins on the island sites also started their primary moult 2-3 weeks earlier than the ones captured along the Frisian coast.

BODY MASS AND FLIGHT RANGE ESTIMATES

8

Body mass, g

Ringed Plover
Nmax = 5

Grey Plover
Nmax = 4

Knot
Nmax = 19

Sanderling
Nmax = 13

Curlew Sandpiper
♂♂ Nmax = 3

Curlew Sandpiper
♀♀ Nmax = 4

Dunlin
Nmax = 186

Bar-tailed Godwit
♂♂ Nmax = 12

Bar-tailed Godwit
♀♀ Nmax = 8

Curlew ♂♂
Nmax = 6

Curlew ♀♀
Nmax = 5

Spotted Redshank
Nmax = 2

Redshank
Nmax = 14

Greenshank
Nmax = 5

Turnstone
Nmax = 16

J A S O N D J F M A M J   J A S O N D J F M A M J   J A S O N D J F M A M J

Month

N early all involved wader species are long-distance migrants. Their migrations require the capacity to build up large energy reserves prior to migration. These birds have the ability to double their body mass 4-6 times a year. This results in large fluctuations of body masses measured in the Wadden Sea during the non-breeding season (figs. 24 & 25). The average body masses of adults and first winter birds are presented in Table 18.

In this section, body mass fluctuations were analysed with three goals in mind: (1) to visualize the periods of low and high energy reserves in the wader populations of the Wadden Sea, (2) to present some indication of the potential flight ranges with the body masses measured in the Wadden Sea, and (3) to establish the occurrence of spatial variation in body masses during the period of primary moult. The first two goals can only be reached, if we decide upon some estimate for 'energy reserve'. Therefore, attention is firstly given to the question on how to estimate energy reserves with our data.

8.1 ESTIMATING ENERGY RESERVES

S everal authors (Lindström & Piersma (1993), Piersma (1994), Battley *et al.* 2000, and Lindström *et al.* 2000) already showed the complexity of the processes underlying the deposition and depletion of energy reserves. This complexity includes differences in fat or protein storage, different types of fat, varying levels of water content, seasonal variations in lean mass, non-linear relationships between fat reserves and lean mass, and the burning

Figure 24: Body masses (in grams) of adult waders captured in the Wadden Sea. The data are presented per species in bubble graphs with the size of each bubble depending on the frequency of occurrence. This frequency ranges between 1 and Nmax. The value of Nmax differs per species and is presented within each graph. In Curlew Sandpiper, Bar-tailed Godwit and Eurasian Curlew, the data were split per sex following the results obtained with POSCON-analysis in Curlew Sandpiper and Eurasian Curlew. The bar graphs along the bottom of each graph represent the accumulated observations on visible migration in the Wadden Sea: black bars - departure, grey - passage and striped - arrival . About 80% of the observations were done by Leo Zwarts and colleagues (Ens et al. 1990a), the remaining 20% concerns own observations.

Figure 25 (over leaf): Body masses (in grams) of juvenile waders captured in the Wadden Sea. The data are presented per species in bubble graphs with the size of each bubble depending on the frequency of occurrence. This frequency ranges between 1 and Nmax. The value of Nmax differs per species and is presented within each graph. In Curlew Sandpiper, Bar-tailed Godwit and Eurasian Curlew, the data were split per sex following the results obtained with POS-CON-analysis in Curlew Sandpiper and Eurasian Curlew.

Body mass, g

100	Ringed Plover	400	Grey Plover	250	Knot
	$N_{max} = 5$		$N_{max} = 5$		$N_{max} = 7$

120	Sanderling	120	Curlew Sandpiper	120	Curlew Sandpiper
	$N_{max} = 2$		♂♂ $N_{max} = 3$		♀♀ $N_{max} = 5$

100	Dunlin	600	Bar-tailed Godwit	600	Bar-tailed Godwit
	$N_{max} = 58$		♂♂ $N_{max} = 2$		♀♀ $N_{max} = 2$

1400	Curlew ♂♂	1400	Curlew ♀♀	300	Spotted Redshank
	$N_{max} = 2$		$N_{max} = 2$		$N_{max} = 1$

250	Redshank	350	Greenshank	250	Turnstone
	$N_{max} = 8$		$N_{max} = 2$		$N_{max} = 5$

J A S O N D J F M A M J   J A S O N D J F M A M J   J A S O N D J F M A M J
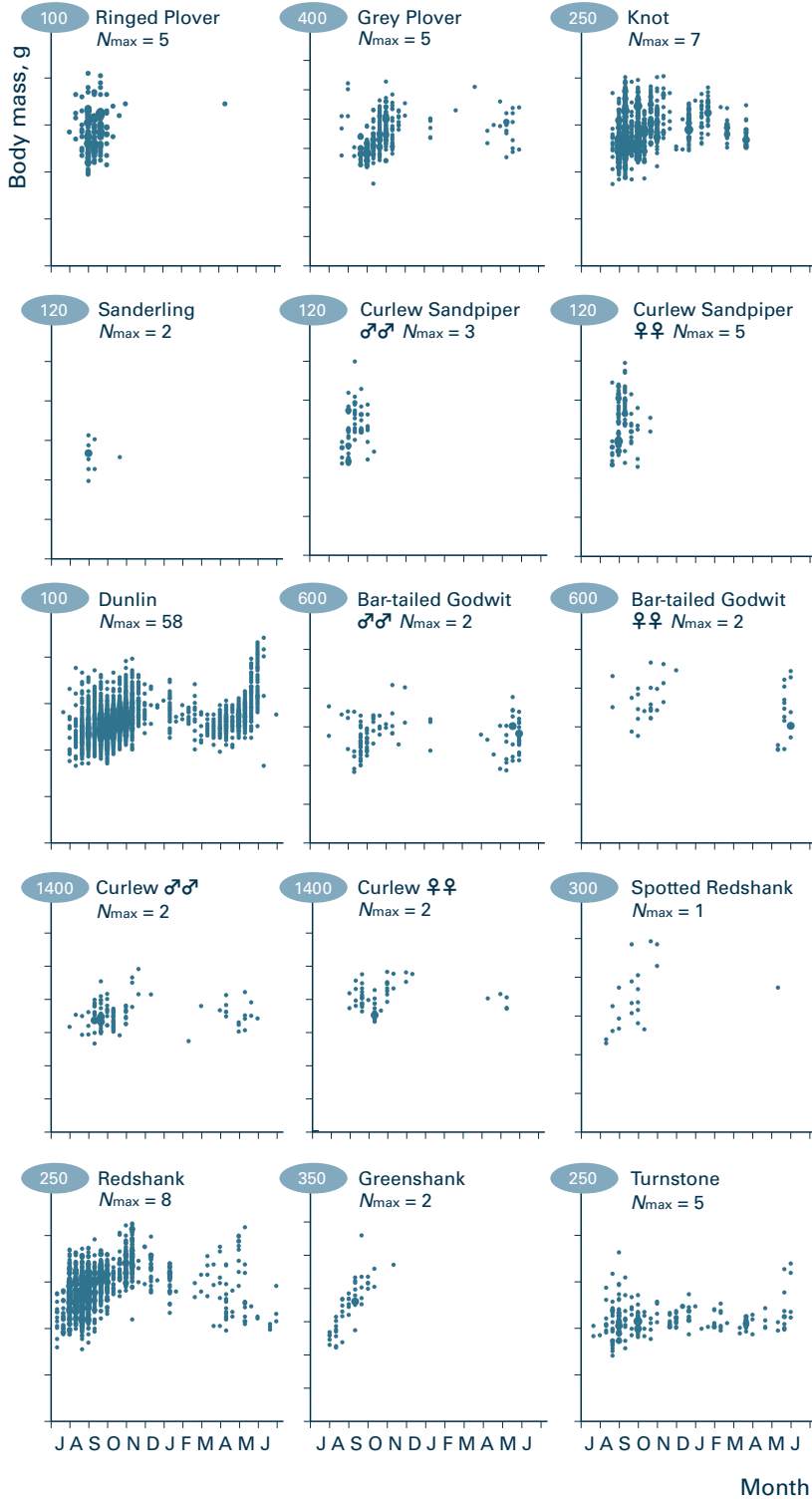
Month

Table 18. Body masses of waders in the Wadden Sea. Presented are the mean body masses in grams after correction for the period of captivity with standard deviation, sample size and range (second and third column). Estimated 'minimal moulting masses' (explained in text) with standard deviation and sample size are also given and finally the estimated body masses assuming these species were W-African wintering birds with standard deviation and sample size. The before last and last column are added, since these masses are used to estimate energy reserves and potential flight ranges of waders in the Wadden Sea.

| Species | Corrected body mass | | Minimal moulting mass | winter mass W-Africa |
	Mean ± SD (n)	range	Mean ± SD (n)	Mean ± SD (n)
First winter birds				
Ringed Plover	57.5 ± 8.8 (157)	39.4 - 82.1	50.1 ± 3.3 (160)	42.1 ± 5.3 (160)
Grey Plover	221.1 ± 30.7 (285)	140.0 - 314.5	218.6 ± 8.7 (278)	177.8 ± 6.1 (278)
Red Knot	144.1 ± 21.5 (791)	87.0 - 202.1	128.2 ± 4.3 (788)	112.8 ± 4.9 (788)
Sanderling	51.5 ± 7.1 (10)	39.4 - 61.8	54.7 ± 1.5 (10)	46.0 ± 1.3 (10)
Curlew Sandpiper ♂	64.1 ± 11.3 (62)	47.0 - 99.0	57.4 ± 1.5 (64)	51.1 ± 1.3 (64)
Curlew Sandpiper ♀	67.8 ± 12.5 (94)	44.5 - 98.0	57.7 ± 1.4 (95)	51.4 ± 1.2 (95)
Dunlin	52.2 ± 6.8 (4564)	33.0 - 88.3	46.2 ± 1.6 (4583)	44.5 ± 1.9 (4583)
Bar-tailed Godwit ♂	273.6 ± 45.1 (110)	182.0 - 406.0	244.0 ± 27.2 (117)	230.3 ± 23.6 (117)
Bar-tailed Godwit ♀	350.7 ± 60.5 (41)	239.0 - 464.1	286.0 ± 32.8 (44)	266.6 ± 28.4 (44)
Eurasian Curlew ♂	702.8 ± 79.3 (107)	530.0 - 980.0	676.0 ± 63.3 (110)	606.3 ± 56.1 (110)
Eurasian Curlew ♀	803.6 ± 81.6 (54)	662.4 - 963.2	796.9 ± 62.6 (56)	713.4 ± 55.4 (56)
Spotted Redshank	172.2 ± 40.3 (21)	114.1 - 246.3	138.4 ± 14.8 (21)	
Redshank	146.9 ± 23.4 (1276)	80.0 - 214.8	134.8 ± 11.9 (1339)	110.4 ± 8.1 (1339)
Greenshank	179.8 ± 37.7 (45)	116.6 - 285.0	192.4 ± 16.4 (47)	
Ruddy Turnstone	112.0 ± 15.6 (225)	73.7 - 185.4	105.4 ± 4.0 (226)	97.4 ± 1.6 (226)
Adults				
Ringed Plover	60.7 ± 10.0 (127)	37.3 - 84.2	53.6 ± 2.9 (129)	47.6 ± 4.6 (129)
Grey Plover	247.9 ± 34.5 (780)	119.6 - 390.0	231.8 ± 8.9 (720)	187.2 ± 6.3 (720)
Red Knot	151.1 ± 19.0 (1411)	100.0 - 227.4	138.1 ± 5.0 (1278)	124.3 ± 5.8 (1278)
Sanderling	60.5 ± 10.8 (225)	36.3 - 95.4	56.0 ± 1.8 (298)	47.1 ± 1.6 (298)
Curlew Sandpiper ♂	70.8 ± 12.4 (54)	49.0 - 92.5	59.0 ± 1.0 (54)	52.4 ± 0.8 (54)
Curlew Sandpiper ♀	73.9 ± 11.1 (84)	51.0 - 94.3	59.9 ± 1.2 (84)	53.2 ± 1.0 (84)
Dunlin	54.2 ± 5.9 (12587)	27.6 - 92.8	46.5 ± 1.6 (9317)	44.8 ± 1.9 (9317)
Bar-tailed Godwit ♂	291.5 ± 52.0 (1429)	170.8 - 481.4	262.8 ± 19.0 (1340)	246.5 ± 16.5 (1340)
Bar-tailed Godwit ♀	359.5 ± 63.3 (956)	194.9 - 573.1	308.5 ± 21.4 (894)	286.1 ± 18.5 (894)
Eurasian Curlew ♂	777.0 ± 92.3 (397)	380.0 - 1107.9	734.5 ± 74.6 (277)	658.2 ± 66.1 (277)
Eurasian Curlew ♀	917.7 ± 112.2 (323)	425.0 - 1300.0	867.2 ± 72.3 (213)	775.7 ± 64.0 (213)
Spotted Redshank	187.3 ± 45.2 (30)	133.4 - 293.0	146.6 ± 14.1 (28)	
Redshank	155.5 ± 24.6 (2513)	84.0 - 231.8	140.4 ± 11.6 (2970)	114.2 ± 7.9 (2970)
Greenshank	194.8 ± 28.8 (220)	142.6 - 283.7	209.8 ± 18.2 (221)	
Ruddy Turnstone	118.9 ± 18.7 (763)	80.0 - 198.0	110.3 ± 4.8 (723)	99.4 ± 1.9 (723)

Table 19. The results of regression analysis with the body masses of adults in primary moult in the Wadden Sea depending on wing length and/or gap size in the wing. Only the significant results with the derived equations are presented. The analyses of the Eurasian Curlew and Ruddy Turnstone data showed no significant improvement with the inclusion of gap size and in Greenshank the influence of wing length was insignificant.

Species	N	Variable(s)	Variation explained (R^2)	F-value	s	Equation derived Constant	Wing	Gap size
Grey Plover	253	wing	0.066	17.912	0.000			
		wing & gap	0.264	45.026	0.000	-27.318	1.453	-1.318
Red Knot	468	wing	0.099	51.282	0.000			
		wing & gap	0.134	35.943	0.000	33.751	0.654	-0.339
Sanderling	163	wing	0.274	61.137	0.000			
		wing & gap	0.344	42.240	0.000	-47.540	0.865	-0.261
Dunlin	4071	wing	0.163	790.932	0.000			
		wing & gap	0.167	407.370	0.000	-5.553	0.492	-0.033
Bar-tailed Godwit	195	wing	0.256	66.872	0.000			
		wing & gap	0.338	49.167	0.000	-175.577	2.335	-1.759
Eurasian Curlew	104	wing	0.221	29.150	0.000	-253.716	3.467	
Redshank	880	wing	0.134	136.594	0.000			
		wing & gap	0.289	178.589	0.000	-71.339	1.417	-0.753
Greenshank	28	gap	0.320	12.700	0.001	210.755		-1.316
Ruddy Turnstone	334	wing	0.141	54.559	0.000	36.340	0.472	

of tissue like muscles and organs during migration flights. This means that lean masses are not stable during the year. As our data were not detailed enough, I did not even try to estimate these varying levels of lean masses from our data-sets.

A rough approach was chosen to quantify the energy reserves. The approach starts with correcting the measured body masses for the period of captivity as described in Chapter 3. Then a predictor of the lowest masses from which recovery is possible in the Wadden Sea was sought. The solution was found in analysing body masses of adults, which were intensely moulting their primaries. It was already known, that fat percentages of moulting waders in the Wadden Sea are low, ranging between 1 and 10 % (Pons unpubl., Cronau in De Goede *et al.* 1985). The body masses of moulting birds of Grey Plover, Knot, Sanderling, Dunlin, Bar-tailed Godwit, and Redshank in the Wadden Sea appear to increase with increasing wing length and to decrease with increasing gap size in the wing (Table 19). Since the

body masses of these waders in primary moult with low fat percentages show a negative relationship with gap size, the birds with the largest gaps in the wing might well have body masses close to the lean masses. Therefore, I determined the upper quartile of gap sizes in every species being followed by a selection on birds with gap sizes larger than this quartile, i.e. 22.9 in Ringed Plover, 22.0 in Grey Plover, 24.0 in Red Knot, 26.4 in Sanderling, 18.9 in Curlew Sandpiper, 27.2 in Dunlin, 24.1 in Bar-tailed Godwit, 28.2 in Eurasian Curlew, 31.5 in Spotted Redshank, 26.1 in Redshank, 20.4 in Greenshank, and 25.6 in Ruddy Turnstone. The masses of these moulting birds with large gaps in the wings were then taken as representative for birds with minimal energy reserves. In order to avoid confusion with the term 'lean mass', the masses of these moulting birds with large gaps in the wing are called 'minimal moulting masses'.

The body masses of moulting adults with large gaps in the wing are positively related to wing lengths (Table 20). The resulting regression equations can be used to establish minimal moulting masses of all individual waders with known wing length in the area. No species-specific equations could be derived for Spotted Redshank and Greenshank. For both an all-species equation was derived:

$$\ln(\text{minimal moulting mass}) = -9.976 + 2.908 * \ln(\text{wing length})$$
$$R^2 = 0.973; \; df = 3361; \; F = 61384.278; \; P = 0.000)$$

Table 20. Regression analysis relating body mass and wing length in moulting adults with large gaps in the wing. The regression statistics are presented together with the resulting formulae needed to predict the minimal moulting masses (see text for definition) of waders in the Wadden Sea.

Species	R^2	df	F-value	s	Regression	
					Intercept	Slope
Ringed Plover	0.546	48	56.566	0.000	-62.388	0.880
Grey Plover	0.608	267	205.889	0.000	-88.537	1.589
Red Knot	0.406	594	202.459	0.000	-39.704	1.031
Sanderling	0.786	57	101.175	0.000	-8.987	0.512
Curlew Sandpiper	0.199	280	34.502	0.000	-2.463	0.461
Dunlin	0.644	1205	1085.943	0.000	-8.433	0.461
Bar-tailed Godwit	0.639	262	461.058	0.000	-478.667	3.452
Eurasian Curlew	0.553	42	50.639	0.000	-1737.885	8.309
Redshank	0.784	309	558.667	0.000	-136.447	1.681
Greenshank	0.032	7	0.201	0.670	-	-
Ruddy Turnstone	0.426	279	102.796	0.000	-43.035	0.975

Energy reserves built up for the non-stop flight to W-Africa were estimated using the formulae, presented by Zwarts *et al.* 1990, for the W-African wintering situation. Waders wintering in W-Africa have nearly no fat reserves (Piersma & Van Brederode 1990). When waders leave the Wadden Sea on their way to W-Africa, they will arrive with body masses close to the W-African wintering levels. Therefore, two separate estimates of body masses with nearly no energy reserves are presented per species in Table 18. In order to present figures as trust-worthy as possible, the sexes of Curlew Sandpiper, Bar-tailed Godwit, and Eurasian Curlew are treated separately, since the sexes of these species can be distinguished either in the field (Bar-tailed Godwit) or by using the outcome of the POSCON-analyses (Curlew Sandpiper, Eurasian Curlew). By doing so, we run ahead of the findings to be presented in Chapter 9.

Are the estimated minimal moulting masses reliable? Red Knots in the Wadden Sea have lean masses of 120-130 g (Piersma & Poot 1993). Our results are within that range with a mean 128 g minimal moulting mass. Using minimal moulting masses in order to approach the lean masses of the various wader species in the Wadden Sea, thus seems to work at least for the Red Knot. However, the systematically heavier masses of moulting birds in the Wadden Sea as compared with the W-African wintering masses are intriguing, and needs more attention. Here, I can merely speculate about the backgrounds. It was decided to use the minimal moulting mass as the best possible measure to approach Lean Body Masses (LBM) in the Wadden Sea. The difference between a bird's factual mass on the one side and the minimal moulting mass or the W-African wintering mass on the other side is considered to approach the energy reserves.
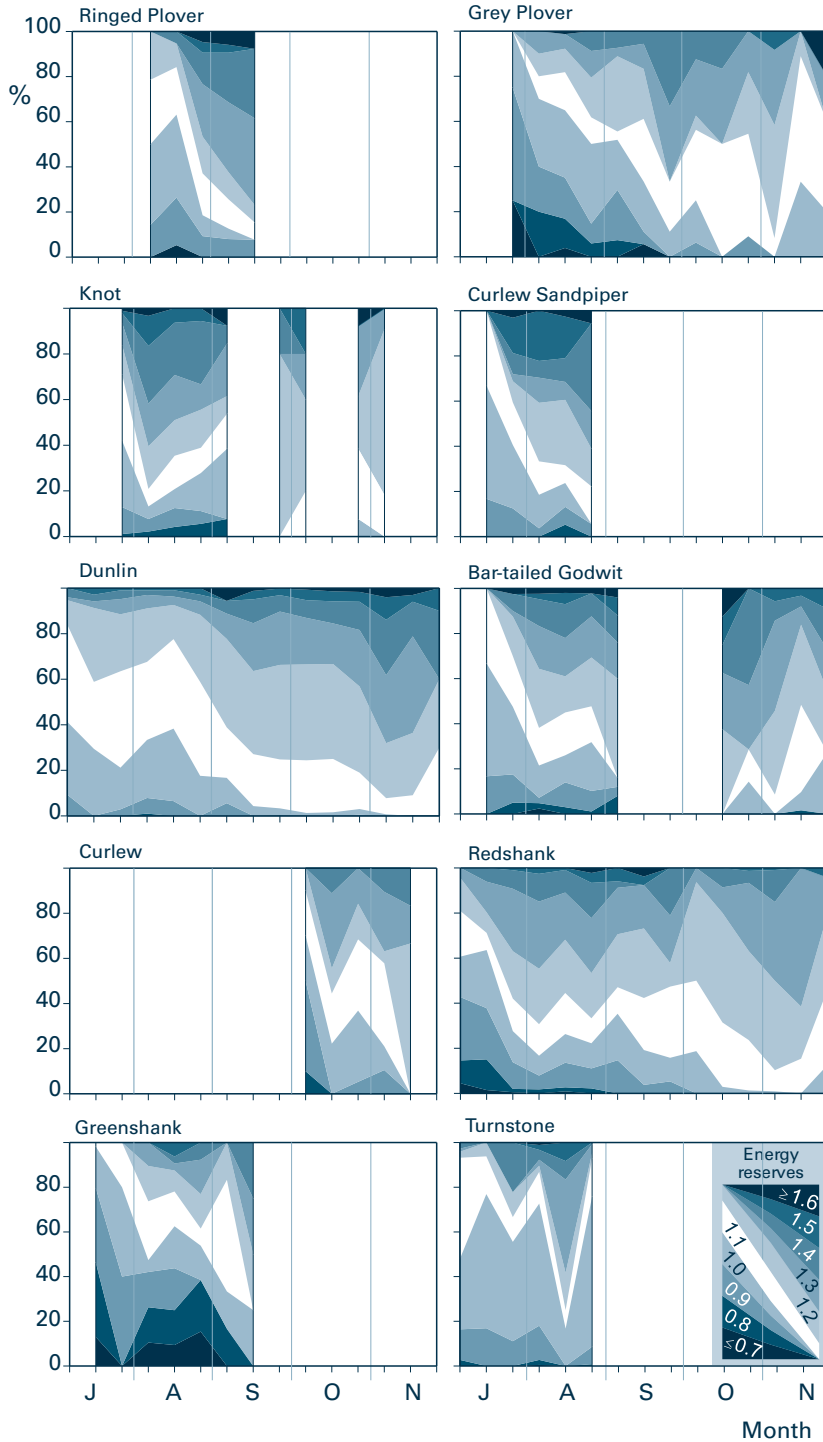
8.2 VARIABILITY OF ENERGY RESERVES

The masses of the Wadden Sea waders were related to their minimal moulting masses. We thus obtained estimates of energy reserves: masses relative to minimal moulting masses. These estimates were clustered in groups mostly ranging between 0.7 and 1.6.

Figure 26: Energy reserves in non-moulting adults captured in the Wadden Sea during late summer and autumn. The energy reserves are expressed relative to the minimal moulting masses. The minimal moulting mass is defined as 1.0 and all estimates are given as proportions. The energy reserves are categorized in groups of 0.1 each and cover the range in classes between ≤0.7 to ≥1.6. Only samples with 5 birds or more are presented.

Figure 27 (over leaf): Energy reserves in juveniles captured in the Wadden Sea during late summer and autumn. The energy reserves are expressed relative to the minimal moulting mas-ses, are categorized in groups of 0.1 each and cover the range in classes between ≤0.7 to ≥1.6. Only samples with 5 birds or more are presented.

Non-moulting adults

Ringed Plover, Grey Plover, Knot, Curlew Sandpiper, Dunlin, Bar-tailed Godwit, Curlew, Redshank, Greenshank, Turnstone

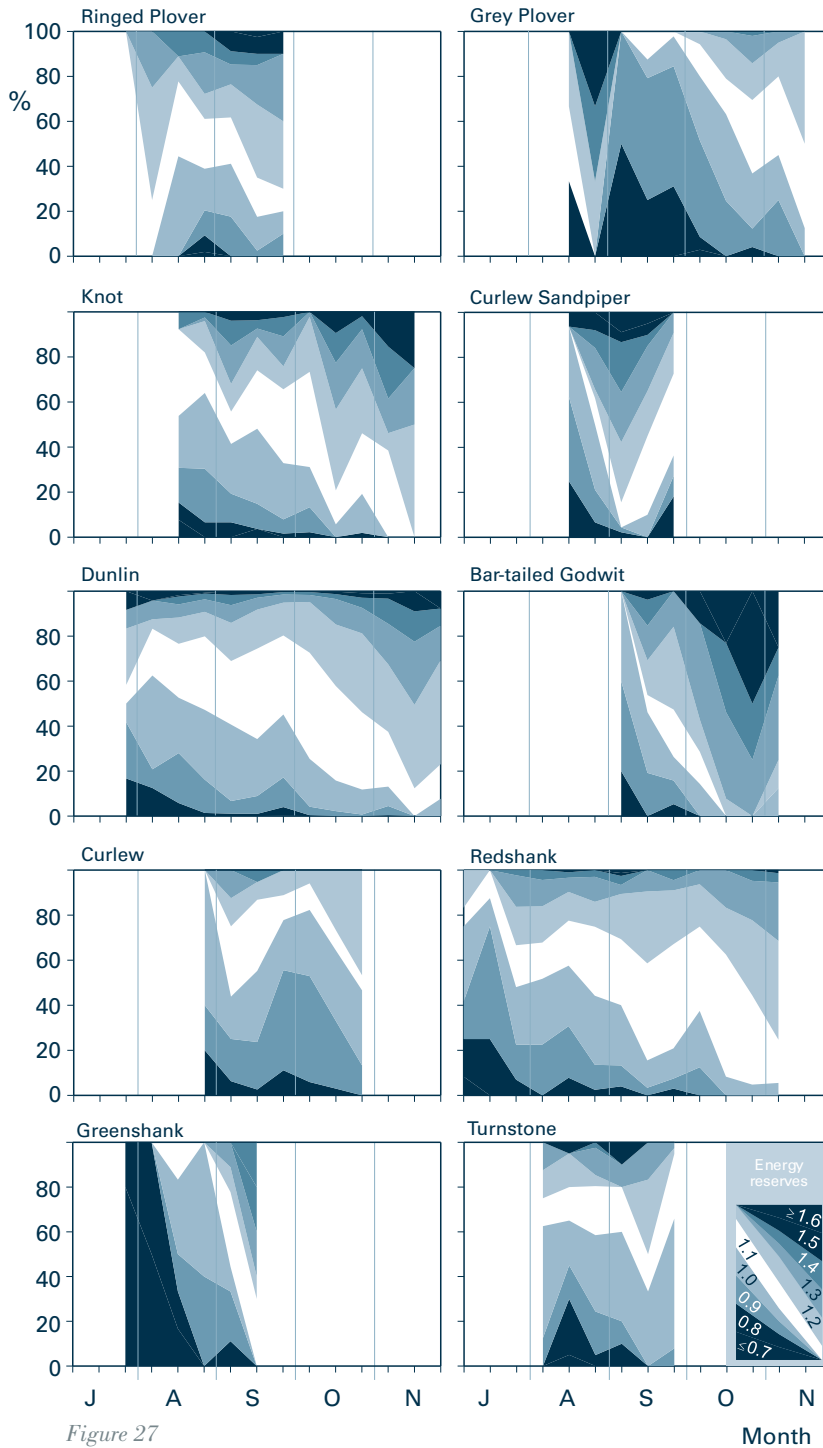Energy reserves: ≥1.6, 1.5, 1.4, 1.3, 1.2, 1.1, 1.0, 0.9, 0.8, ≤0.7

Month

Juveniles

Figure 27

Birds with values smaller than 1 had masses lower than the minimal moulting masses (negative energy reserves) and birds with values larger than 1 weighed more than the minimal moulting masses (positive energy reserves). The outcome was plotted per 10-day period resp. for non-moulting adults during post-breeding in Fig. 26, for juveniles during post-breeding in Fig. 27, and for adults and first winter birds during spring in Fig. 28. Only periods with sample size of 5 birds or more are shown. The sample sizes are given in Table 21.

Table 21. Sizes of the samples used in the figures 26, 27 and 28. Adults in a stage of active primary moult were excluded from the samples.

| | Post-breeding period | | | | | | | | | | | | | | | Spring | | | | | | | | |
	July			August			September			October			November			March			April			May		
Species	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
Non-moulting adults (figs. 26 & 28)																								
Ringed Plover	-	-	2	14	19	43	2	13	-	-	1	-	-	-	-	-	-	1	-	-	-	2	1	5
Grey Plover	-	-	4	30	77	34	27	18	9	16	6	11	12	9	5	2	1	-	1	7	7	51	74	24
Red Knot	-	-	93	91	96	18	13	1	5	5	1	13	11	-	1	2	8	-	1	-	-	1	-	1
Sanderling	-	-	-	31	-	21	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Curlew Sandpiper	-	6	32	27	38	18	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dunlin	75	34	104	102	107	34	18	162	419	437	432	564	423	33	10	6	48	97	243	119	160	232	273	148
Bar-tailed Godwit	-	6	40	42	100	88	25	3	1	-	8	7	35	62	11	45	56	107	12	20	83	510	483	223
Eurasian Curlew	-	-	3	1	-	3	3	3	3	10	9	19	19	6	3	13	19	25	29	8	1	1	-	-
Spotted Redshank	-	-	-	-	-	1	-	1	-	1	7	-	2	-	-	-	-	-	1	1	-	8	-	-
Redshank	89	66	195	114	110	45	34	26	19	16	35	76	106	13	24	6	9	27	45	35	35	49	50	7
Greenshank	-	54	5	19	32	13	6	4	2	-	1	-	-	-	-	-	-	-	-	-	1	1	-	-
Ruddy Turnstone	44	16	8	64	6	11	-	-	2	-	-	1	-	-	3	4	18	13	-	4	3	14	116	4
Juveniles & first winter birds (figs. 27 & 28)																								
Ringed Plover	-	-	1	4	9	54	34	40	10	2	1	1	-	-	-	-	-	-	1	-	-	-	-	-
Grey Plover	-	-	-	-	3	3	2	24	45	35	57	49	20	8	2	-	-	-	2	1	2	8	6	2
Red Knot	-	-	-	-	13	122	181	27	128	45	53	52	13	4	2	-	23	-	-	-	-	-	-	-
Sanderling	-	-	-	-	-	7	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Curlew Sandpiper	-	-	-	-	16	76	45	20	13	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Dunlin	-	1	12	24	171	284	177	584	565	554	450	604	268	89	13	13	20	44	105	30	152	114	90	74
Bar-tailed Godwit	-	-	2	-	4	3	5	26	19	7	13	4	8	1	2	-	-	1	1	1	2	9	19	23
Eurasian Curlew	-	-	1	1	2	5	16	38	9	34	2	17	5	2	2	-	-	1	6	-	4	7	2	1
Spotted Redshank	-	-	-	2	2	3	-	4	5	1	1	2	-	-	-	-	-	-	-	-	-	1	-	-
Redshank	12	24	129	137	205	199	75	116	67	16	24	63	73	3	3	4	3	6	14	3	9	12	1	2
Greenshank	-	-	5	8	6	5	9	5	4	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Ruddy Turnstone	-	2	1	8	20	42	10	6	38	4	4	4	-	8	10	2	17	3	-	2	-	2	6	4
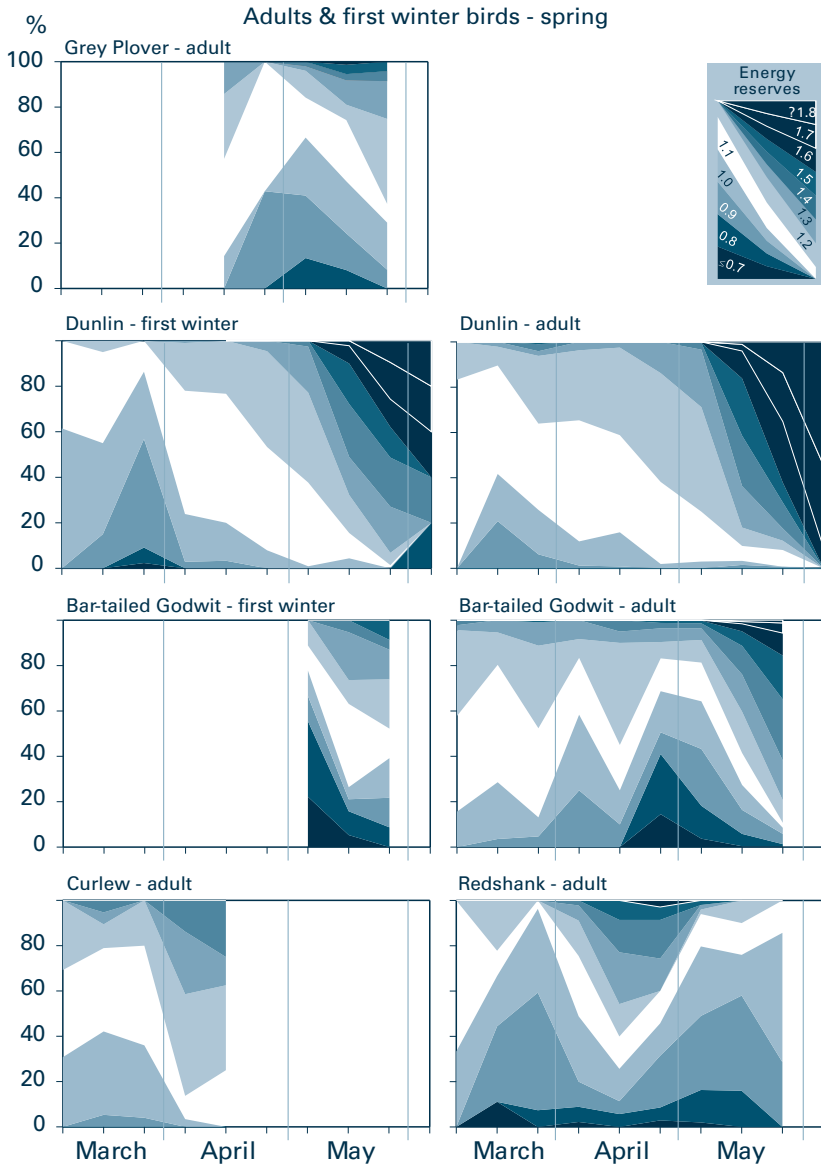
Figure 28: Energy reserves in adults and first winter birds captured in the Wadden Sea during March, April and May. The energy reserves are expressed relative to the minimal moulting masses They are categorized in groups of 0.1 each and cover the range in classes between ≤0.7 to ≥1.8. Only samples with 5 birds or more are presented.

The increase in numbers during the post-breeding period of Fig. 17 already showed the steady arrival of most species towards September except for Spotted Redshank, Redshank, and Ruddy Turnstone. This pattern returns in Fig. 26, where birds with negative estimated energy reserves are mostly found during these months. In some species relatively more birds with negative energy reserves appear again in the catches during November, for instance Grey Plover, Dunlin, Bar-tailed Godwit, and Redshank. Peak occurrence of birds carrying large energy reserves (40% or higher) did not correspond with the periods of increase or decline of population numbers in the area. This is logical, if attention is paid to the major periods of departure or passage (bars in Fig. 24). Most observations of departures occur in July and August. Peak occurrence of birds carrying large energy reserves can also be recognized after August: Dunlin and Greenshank by mid September, Grey Plover and Redshank by end September, Eurasian Curlew by mid October, and Dunlin by early November. These peak occurrences invariably occur simultaneously with declining population numbers in the area (Fig. 26 compared with Fig. 17).

Peak occurrence of juveniles with large energy reserves (40% or higher) is in some species evident: Grey Plovers by end August, Red Knot by early September, mid October, and early November, Curlew Sandpiper by early September, Dunlin by mid November, Bar-tailed Godwit in the second half of October and Greenshank by mid September. These peak occurrences are more evident than in the adults. Juveniles appear to have a more synchronized migration pattern, which is less complicated then for the adults where males and females have different migration schedules being interrupted by different moult schedules.

The emerging patterns during spring migration are mostly in agreement with existing knowledge. Birds leaving earlier, do not weigh as much as the ones departing by end May - early June. The first group concerns more southerly breeders than the last group of high-arctic breeders. The first group is able to start breeding earlier and head for their breeding areas during March and April (Ringed Plover, Dunlin, Eurasian Curlew, and Redshank). Their energy reserves are generally not estimated to be higher than 30% of the minimal moulting mass. The energy reserves of the late departing groups are regularly higher than 60% of the minimal moulting masses in Dunlin (both first winter birds and adults), Bar-tailed Godwit, and Ruddy Turnstone. They sometimes even reach levels of up to 90% of the minimal moulting masses. The Grey Plover is the exception to this rule with maximum levels up to 50% of the minimal moulting mass. Grey Plover, Dunlin, Bar-tailed Godwit, and Ruddy Turnstone reach higher body mass levels during May - early June than during post-breeding. It supports the findings of Soloviev & Tomkovich (1997). Morrison *et al.* (2007) and Tulp (2007), that waders try to arrive in relatively good condition on the breeding grounds, since these areas might still be snow-covered. They also have to cope with unpredictable weather conditions during migration, and thus higher departure masses might be profitable.

8.3 FLIGHT RANGE ESTIMATES

Long-distance migrants store energy reserves prior to migration, using these reserves as fuel during flight and often arrive in a completely depleted state (e.g. Piersma & Jukema 1990, Lindström & Piersma 1993, Piersma 1994). These species developed the ability to double and deplete their body mass several times a year. During flight, they spend it as fuel during a few days non-stop flight. These patterns of preparation for non-stop long-distance migration during post-breeding are visible amongst juveniles and adults in at least eleven of the twelve species (Fig. 29 - adults; Fig. 30 - juveniles). These figures were produced by using the Castro & Myers' (1989) formula, which produces estimates of the potential maximum flight ranges. We assumed, that the arrival masses in W-Africa equal the W-African wintering masses. An average air speed of 75 km/h was taken following the measured air speeds by Green (2004). Adults trapped during August and September had sometimes potential flight ranges as large as 4000 km: 25% of the Curlew Sandpipers, 13% of the Grey Plovers, 13% of the Ringed Plovers, 12% of the Sanderlings, 10% of the Red-shank, 6% of the Bar-tailed Godwits (more females than males), 6% of the Red Knots and Eurasian Curlews (more males than females in the latter), 3% of the Ruddy Turnstones and <1% of the Dunlin. Juveniles pass through the Wadden Sea somewhat later. The percentages of juveniles trapped during August, September or October with estimated potential flight ranges of 3000 km or longer are as follows: 27% Ringed Plover, 13% Curlew Sandpiper, 10% Bar-tailed Godwit, 5% Red Knot, 4% Redshank, 3% Grey Plover, 2% Eurasian Curlew, 2% Ruddy Turnstone, and <1% Dunlin.

With a flight of 4,000 km the Mauritanian Banc d'Arguin can be reached. Piersma & Jukema (1990), Alerstam (1990), Zwarts *et al.* (1990), Gudmundsson *et al.* (1991), Butler *et al.* (1997), and Weber & Houston (1997) were in agreement that flight range calculations, including the Castro & Myers (1989) formula used here, often produce too conservative estimates. They generally used flight speeds between 57 and 65 km/h. Alerstam *et al.* (2007) related the flight speeds to the average body mass of a series of bird species and show heavier species to fly faster. Their range of flight speeds of the relevant wader species range between 35 and 75 km/h. Airspeeds of 75 km/h were measured from radar tracks over S Sweden by Green (2004) and co-workers. Waders on migration fly as cheap and fast as possible by flying in group formations and by adjusting their flight altitude to the most advantageous winds en route (e.g. Piersma & Van de Sant 1992). Therefore air speeds of up to 75 km/h were used here. When an air speed of 55 km/h was used, the reductions in calculated flight ranges fluctuated between 20 and 40%, depending on the species. When the Davidson (1984) formula was used flight ranges of the smaller-sized species were estimated to be 10-20% smaller, while the ones of Bar-tailed Godwit and Curlew were resp. 30 and 60% larger.
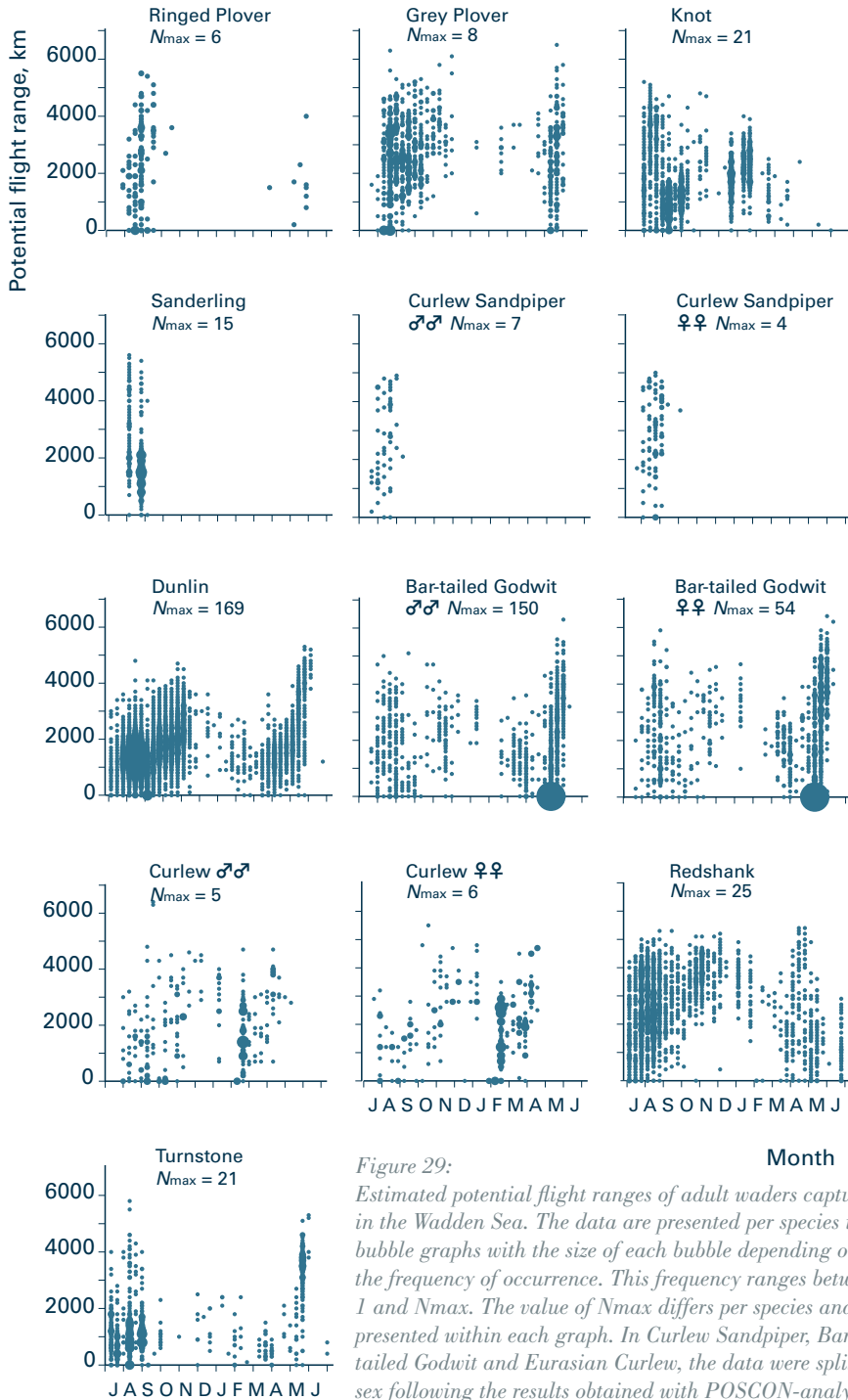
Figure 29:
Estimated potential flight ranges of adult waders captured in the Wadden Sea. The data are presented per species in bubble graphs with the size of each bubble depending on the frequency of occurrence. This frequency ranges between 1 and Nmax. The value of Nmax differs per species and is presented within each graph. In Curlew Sandpiper, Bar-tailed Godwit and Eurasian Curlew, the data were split per sex following the results obtained with POSCON-analysis in Curlew Sandpiper and Eurasian Curlew.
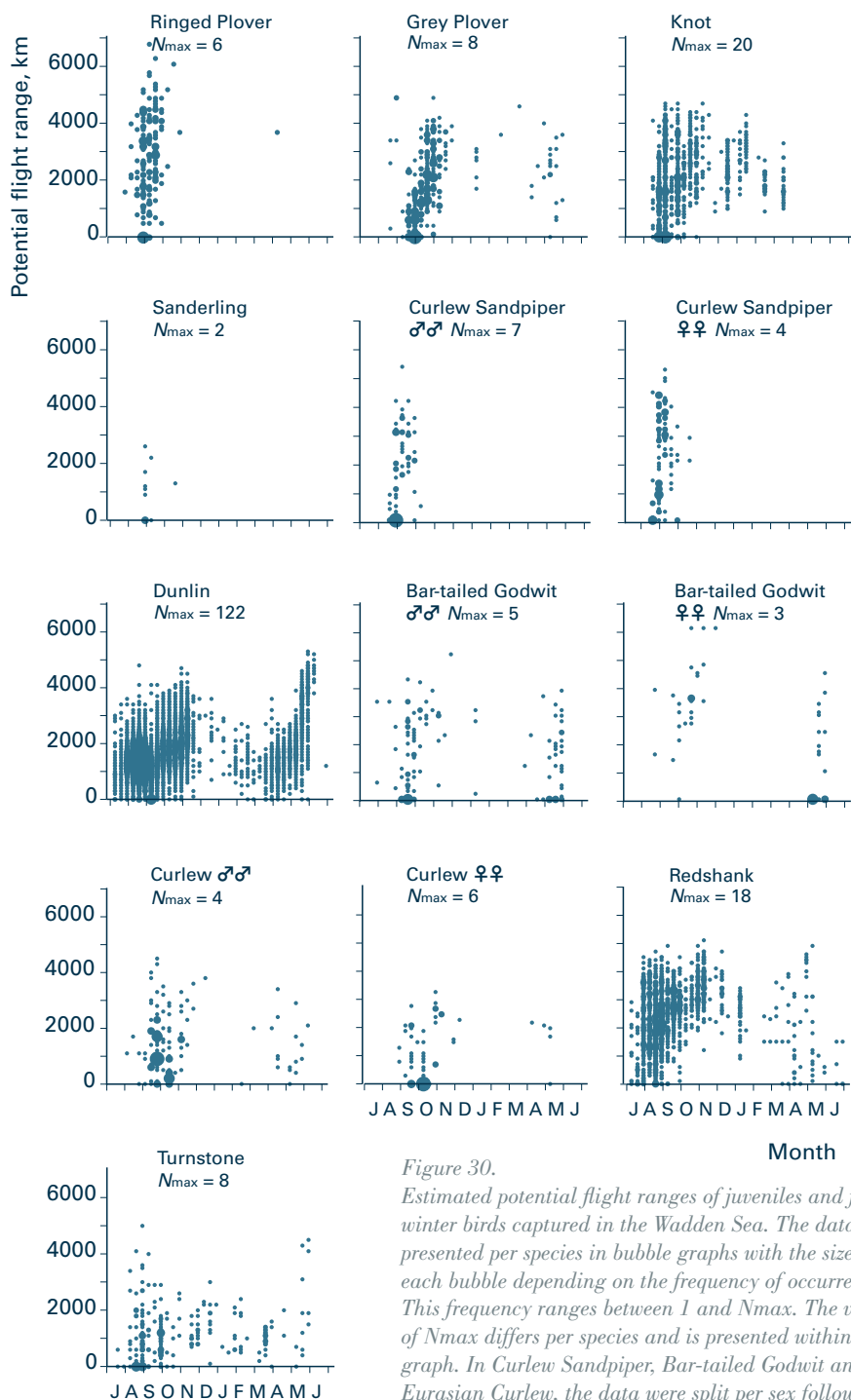
Figure 30.
Estimated potential flight ranges of juveniles and first winter birds captured in the Wadden Sea. The data are presented per species in bubble graphs with the size of each bubble depending on the frequency of occurrence. This frequency ranges between 1 and Nmax. The value of Nmax differs per species and is presented within each graph. In Curlew Sandpiper, Bar-tailed Godwit and Eurasian Curlew, the data were split per sex following the results obtained with POSCON-analysis in Curlew Sandpiper and Eurasian Curlew.

8.4 SPATIAL VARIATION IN THE BODY MASS OF WADERS IN PRIMARY MOULT

Waders appeared not to deplete their energy reserves to the same level on the various catching sites in the Wadden Sea, when they were moulting their primaries (Table 22). The moulting birds on Vlieland always had the smallest reserves in the nine possible comparisons. Moulting Grey Plovers, Red Knots, and Redshank on the Frisian coast were heavier than their conspecifics on Schiermonnikoog, while moulting Eurasian Curlews were heavier on Schiermonnikoog. There was no difference between both sites with respect to the moulting populations of Dunlin. The sample sizes of Bar-tailed Godwit and Ruddy Turnstone were too small to allow comparison between both sites. These differences are in line with the finding that most species along the coast had smaller gaps in the wing during primary moult (Chapter 7).

Table 22. Mean energy reserves, expressed relative to the minimal moulting mass, of adults moulting their primaries on the different catching sites in the Wadden Sea. Minimal moulting mass is defined as 1.0, all estimates given as proportions. The means, standard deviations and sample size are presented per species and catching site. Whether the mean energy reserves differed significantly between the three catching sites, was tested with ANOVA.

Species	Vlieland			Frisian coast			Schiermonnikoog			ANOVA		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	df	F	s
Ringed Plover	1.19	0.18	6	-	-	-	1.06	-	1	1	0.470	0.523
Grey Plover	1.00	0.10	60	1.12	0.12	58	1.06	0.11	136	2	16.408	0.000
Red Knot	0.99	0.05	184	1.16	0.18	16	1.02	0.06	269	2	58.527	0.000
Sanderling	1.01	0.09	163	-	-	-	0.65	-	1	-	-	-
Curlew Sandpiper	1.19	0.19	8	-	-	-	-	-	-	-	-	-
Dunlin	1.12	0.08	949	1.13	0.07	670	1.13	0.09	2457	2	9.676	0.000
Bar-tailed Godwit	1.03	0.11	60	1.24	0.03	2	1.09	0.15	134	2	6.496	0.002
Eurasian Curlew	0.95	0.11	22	1.03	0.10	58	1.13	0.26	23	2	8.628	0.000
Spotted Redshank	-	-	-	1.18	0.20	4	-	-	-	-	-	-
Redshank	0.99	0.09	408	1.11	0.14	440	1.07	0.12	37	2	103.085	0.000
Greenshank	0.88	0.09	16	-	-	-	1.03	0.22	13	1	6.000	0.021
Ruddy Turnstone	1.01	0.06	327	1.10	0.12	5	1.11	0.17	3	2	10.229	0.000

BREEDING ORIGINS PER SPECIES

9

This chapter aims to establish breeding origins of waders present in the Wadden Sea by comparing wing- and culmen length of Wadden Sea birds with the measurements of breeding populations. Only species showing morphometric differences between breeding grounds and/or sexes and captured in reasonable numbers in the Wadden Sea, are included. The eight species selected are Ringed Plover, Grey Plover, Red Knot, Curlew Sandpiper, Dunlin, Bar-tailed Godwit, Eurasian Curlew, and Redshank. Their wing- and culmen lengths are presented in Table 10.

Every species' section starts with an introduction, describing the present-day knowledge concerning their breeding distribution, morphometric variation, and the migratory patterns of the species in the East Atlantic Flyway. No attention is given to the empirical basis of the statements given: they are taken to be solid. The statements only try to summarize the available knowledge, as short as possible. If necessary, the reader has to return to the original references.

The following part of every species' section starts with estimating the population composition. These estimates were produced sometimes using POSCON, sometimes with NAG-optimization, and sometimes with both. Standard errors are not presented because of reasons formulated in Remark 1, section 4.3. However, they are expected to be considerable, say in the order of 5-10%.

A serious drawback is, that only wing- and culmen lengths were measured in the past Wadden Sea studies. Engelmoer & Roselaar (1998) already showed, that the simultaneous inclusion of more dimensions might produce better results, though measurement errors and biological variations expressed as coefficients of variation were smallest for wing- and culmen length. It is thus uncertain whether additional inclusion of measurements other than wing- and culmen lengths, and with larger breeding samples, the composition estimates should be less unreliable. In this paper, I have done the utmost with the old material. It is obvious that high degrees of overlap cause a lot of trouble (Fig. 14). If anyone wants to continue on this path, better data have to be collected, possibly using other sources of information in addition to plumage and morphology, but then it must seriously be doubted that it can still be done in our present-day society by organizing large-scale catching activities by unpaid volunteers.

All interpretation in the population composition sections should be considered with scepticism. In many cases the estimation of population composition is a rather uncertain affair. Estimates, however, may be useful in an exploratory analysis leading to the formulation of new hypotheses. When the results are discussed, the statistical uncertainties are more or less ignored.

I will concentrate on general trends, e.g. from a series of months, which makes the findings hopefully somewhat less unreliable.

9.1 RINGED PLOVER

Introduction

The Ringed Plover has a primarily Palearctic breeding distribution under temperate, boreal, and arctic conditions (Map 1). It closely resembles the Nearctic Semipalmated Plover Charadrius semipalmatus, which also breeds in more or less the same breeding habitats. Some overlap in breeding range occurs (Wynne-Edwards 1952, Bock 1959, Smith 1969, Sutton & Parmelee 1955, Godfrey 1986, Stishov *et al.* 1991, Engelmoer & Roselaar 1998).

Several subspecies have been recognized in the past. Here the subspecies' distinction follows Hale (1980) and Engelmoer & Roselaar (1998): (1) nominate *hiaticula* breeding in W-Europe, (2) *psammodroma* breeding in NE-Canada, on Greenland, Jan Mayen, and Iceland, and (3) *tundrae* breeding in N-Europe and Siberia. Nominate *hiaticula* and *tundrae* show some degree of variability in body dimensions. Since the features of *psammodroma* are intermediate, this subspecies has not always been recognized. *C.h. tundrae* is gradually replaced by nominate *hiaticula* in Fennoscandia during the 20th century (Väisänen 1969, Engelmoer & Roselaar 1998). Smit & Wolff (1981) and Meltofte *et al.* (1994) considered *psammodroma* as nominate *hiaticula*.

The migratory patterns of the Ringed Plover populations in various parts of the East Atlantic flyway are described by Boere (1976), Clapham (1978), Ferns (1980a), Taylor (1980), Insley & Young (1981), Moser & Carrier (1983), Pienkowski (1984), Siefke & Kastepold (1985), Smit & Piersma (1989), Smit & Wymenga (1989), Wymenga *et al.* (1990), Meltofte (1993), Haberer (1994), Meltofte *et al.* (1994), Wernham *et al.* (2002), Bakken *et al.* (2003), Stroud *et al.* (2004) and Meissner (2007b). Here a short summary is given. W-European breeding

Table 23. The predicted breeding origin of adult Ringed Plovers during August and September as derived from the POSCON predictions. The predictions for both sexes within a subspecies were combined. Presented are the estimated proportions and the sample sizes. The seasonal changes in proportions are not significant (Chi²= 9.176; df= 8; s= 0.328).

Period	psammodroma	hiaticula	tundrae	N
1/8-10/8	0.30	0.20	0.50	10
11/8-20/8	0.14	0.14	0.73	22
21/8 - 31/8	0.36	0.06	0.59	53
1/9 - 10/9	0.43	0.29	0.29	7
11/9 - 20/9	0.31	0.15	0.54	13
Average/ total	0.31	0.11	0.58	105

hiaticula winter on the British isles, in SW-Europe and NW-Africa. They depart from the W-European breeding grounds during August and return by March (also Annex 1 - Table 1). Siberian and N-European *tundrae* winter in W-Africa and stage frequently in the Wadden Sea after the breeding season during the first half of August and the first half of September. During spring, *tundrae* is mainly present in the Wadden Sea during May, but the first *tundrae* may be present amidst nominate *hiaticula* in W-Europe already by March. Nearctic *psammodroma* regularly stage in the Wadden Sea during the second half of August. They generally winter in NW-Africa N of *tundrae*. During spring migration probably all *psammodroma* migrate from W-France to the British isles without entering the Wadden Sea.

Population composition

The composition estimates of the Ringed Plover population in the Wadden Sea are based on the subspecies *psammodroma*, *hiaticula*, and *tundrae*. W-European *hiaticula* have the largest and N-European/Siberian *tundrae* the smallest dimensions (Table 10). Six sample groups need to be distinguished due to sexual dimorphism. Morphometric analysis with the NAG-optimization technique is preferable, but did not produce clear results. Therefore, POSCON-analysis was used in addition. The results obtained with this technique indicate the presence of all three subspecies, but do not reveal clear temporal changes (Table 23). On average, 56% of the captured birds resembled the N-European/ Siberian subspecies *tundrae* most (the P-value of Hotelling's sample test was largest), 33% the Iceland/ Green-land subspecies *psammodroma*, and 11% the W-European subspecies *hiaticula*. Too few adults were captured to reveal temporal changes from early August to end September. Only two adults were trapped in February and March. These were evidently W-European breeding birds because of their large measurements.

9.2 GREY PLOVER

Introduction

The breeding range of the Grey Plover extends from the Kanin Peninsula in N-Europe throughout arctic Siberia and Alaska to Baffin Island in N-Canada (Map 2). The species breeds on Wrangel Island, but not on most other high arctic islands. The breeding season starts from the second half of May depending on the climatic conditions at the breeding grounds. The Grey Plover is mostly considered to be a monotypic species with some clinal variation (Peters 1934, Low 1938, Dement'ev 1939, AOU 1957, Vaurie 1964, Glutz *et al.* 1975, Cramp & Simmons 1983, Hayman *et al.* 1986, Stepanyan 1990,

Byrkjedal & Thompson 1998). Siberian breeding birds have been described as *hypomelaena* by Pallas in 1827, those of N-Canada as *cynosurae* by Thayer & Bangs (1914). Hartert (1912-21) also recognized *hypomelaena*, but had no material to check the validity of *cynosurae*. Roselaar in Cramp & Simmons (1983) showed that the variation in bill dimension in Siberia was discontinuous, Alaskan and E-Siberian samples were morphometrically similar but N-Canadian breeders had distinctly smaller measurements. Engelmoer & Roselaar (1998) recognized three subspecies: *Pluvialis s. squatarola* breeding in the Palearctic (excluding Wrangel Island), and in Alaska, *cynosurae* breeding in N-Canada, and *tomkovichi* breeding on Wrangel Island. The distinction between the subspecies was based upon measurements (in order of importance: lengths of wing, first secondary, tarsus, tail, culmen, and middle toe), and plumage characters (degree of contrast in breeding plumage). Both *squatarola* and *cynosurae* are polymorphic. Morphometric differences between the sexes are regularly lacking or not systematic amongst all populations. When sexes had to be distinguished only tail length had good discriminatory power (Engelmoer & Roselaar 1998).

The migratory patterns of the Grey Plover populations in various parts of the East Atlantic flyway are described by Boere (1976), Branson & Minton (1976), Smit & Wolff (1981), Townshend (1982), Speek & Speek (1984), Prokosch (1988), Nottrot (1981), Smit & Piersma (1989), Wymenga *et al.* (1990), Meltofte (1993), Meltofte *et al.* (1994), Exo & Wahls (1996), Krupa (1997), Byrkjedal & Thompson (1998), Serra *et al.* (1999), Tomkovich *et al.* (2000), Wernham *et al.* (2002), Stroud *et al.* (2004), Nieboer (2005), and Serra *et al.* (2006). A brief summary is as follows. Grey Plovers breeding as far east as the Russian Taimyr Peninsula (83ºE) arrive in the Wadden Sea from mid July onwards with the adult females arriving prior to the adult males, which arrive on their turn prior to the juveniles. Juveniles arrive mostly in the Wadden Sea in the first half of September when peak numbers of about 60,000 birds are reached in the international Wadden Sea.

The arriving adults include both the European and African wintering populations. Three categories of adult Grey Plovers are identified in E. England on the basis of primary moult and body mass (Branson & Minton 1976): (1) non-moulting birds, which increase body mass, and migrate further south, (2) birds moulting 1-3 inner primaries, and suspend then followed by body mass increase and departure, and (3) birds, which complete or suspend primary moult, and winter locally.

The European wintering birds go through (part of) their post-breeding moult in the Wadden Sea. African wintering birds only stage for a few weeks in the Wadden Sea in order to replenish their energy reserves, and start their post-breeding moult on the wintering grounds. Many Grey Plovers staging in the Wadden Sea winter in Africa as far south as the Gulf of Guinea (also Annex 1 - Table 3) but some winter in N-Africa and along the coast of

the Mediterranean as far east as Turkey. Many of the moulting Grey Plovers leave the Wadden Sea after having completed their post-breeding moult. On average, about 10,000 birds stay to winter in the Wadden Sea. The Grey Plover is one of the most vulnerable wader species with respect to extreme winter weather (Clark *et al.* 1993), and relatively many leave the Wadden Sea under severe weather circumstances in order to winter along the British E- and SE-coasts or along the French Atlantic coastline. The number of Grey Plovers in the Wadden Sea starts to increase from February onwards indicating the start of spring passage. Peak spring numbers of about 100,000 birds are reached in the first half of May when the African wintering birds also have returned to the Wadden Sea. Many Grey Plovers leave the area by late May, and important passage is observed to occur over S-Sweden between end May - early June in easterly directions (Green 2004). Second year birds stay to summer in the Wadden Sea. The population of Grey Plovers in the East Atlantic Flyway strongly increased over the past decades (Prater 1981, Townshend 1986, Moser 1988, Tubbs 1991, Meltofte *et al.* 1994, Byrkjedal & Thompson 1998, Pollitt *et al.* 2003, Stroud *et al.* 2004). The population increase is attributed to a western expansion of the breeding range from Siberian origin (Hagemeijer & Blair 1997).

Population composition

The composition estimates of the Grey Plover population in the Wadden Sea are restricted to the subspecies *squatarola*. The breeding samples were not split according to sex following

Table 24. Estimates of the population composition of Grey Plovers according to their breeding origin in the Wadden Sea during migration and wintering. Data from all catching sites were combined. Presented are the estimated proportions.

Period	N	Arkhangelsk region	Yamal & Taymyr	E-Siberia & Alaska
21/7 - 10/8	28	0.69	0.27	0.04
11/8 - 20/8	49	0.68	0.28	0.04
21/8 - 31/8	48	0.63	0.37	0.00
1/9 - 10/9	58	0.70	0.30	0.00
11/9 - 21/9	44	1.00	0.00	0.00
21/9 - 30/9	36	0.72	0.28	0.00
1/10 - 10/10	46	0.97	0.00	0.03
11/10 - 31/10	29	0.67	0.19	0.14
1/11 - 31/12	31	0.69	0.06	0.25
1/1 - 31/3	13	1.00	0.00	0.00
1/4 - 30/4	8	1.00	0.00	0.00
1/5 - 10/5	24	0.92	0.08	0.00
11/5 - 31/5	22	0.27	0.34	0.39

Engelmoer & Roselaar (1998), and contra the results of Exo & Stepanova (2001) for the Lena Delta population. The breeding samples of low arctic Canadian *cynosurae* and Wrangel Island *tomkovichi* were not included in the optimization processes, since their occurrence in the Wadden Sea is rather unlikely (Smit & Wymenga 1989 and Wymenga *et al.* 1990). Moreover, the size of the Arkhangelsk region sample is as yet rather small, whilst the wing- and culmen lengths are rather similar to the ones of the N-Canada population. Since the presence in the Wadden Sea of breeding birds from the Arkhangelsk region is much more likely than the occurrence of low arctic Canadian cynosurae, the latter were not included in the analyses in order to avoid exploding standard errors.

The optimizations showed the Arkhangelsk region population to be most numerous in the Wadden Sea with an average of 76% occurrence (Table 24). The Arkhangelsk region population dominated the Wadden Sea populations between mid September and early May with percentages ranging between 69 and 100%. The Yamal & Taimyr populations occurred more frequently with 27-37% prior to 10 September and between 10 and 31 May (34%). The Yamal & Taimyr birds showed their highest occurrence in the last ten days of August and stay in lower proportions in the area until end December. Grey Plovers from E-Siberia or Alaska were infrequently predicted to occur and if so in particular between mid October and end December (14-25%) or in the second half of May (37-39%). There was a rapid change in population composition around 10 May with increasing proportions of both easterly breeding populations (Yamal & Taimyr and E-Siberia & Alaska) and a decrease of the Arkhangelsk region population.

The Grey Plover populations, present on Vlieland during post-breeding, might all originate from the N-Europe breeding population, whilst the occurrence of Arkhangelsk region breeding

Table 25. The estimated composition of the Grey Plover populations on Vlieland and Schiermonnikoog during post-breeding. Presented are the estimated proportions.

Period	N	Arkhangelsk region	Yamal & Taymyr	E-Siberia & Alaska
Vlieland				
11/8 - 10/9	20	1.00	0.00	0.00
11/9 - 30/9	32	1.00	0.00	0.00
October	28	0.93	0.02	0.04
November	13	1.00	0.00	0.00
Schiermonnikoog				
11/8 - 10/9	132	0.64	0.35	0.00
11/9 - 30/9	48	0.77	0.23	0.00
October	45	0.74	0.22	0.05
November	17	0.45	0.16	0.39

birds ranged between 45 and 77% on Schiermonnikoog during the same time of year (Table 25). The occurrence of the Yamal & Taimyr population on Schiermonnikoog seems to decrease from about 35 to 16%. These results might suggest a homogeneous post-breeding population on Vlieland and a more mixed population on Schiermonnikoog.

9.3 RED KNOT

Introduction

The Red Knot breeds scattered throughout the high arctic regions of the Nearctic and the Pale-arctic (Map 3). The species mostly breeds on peninsulas and islands north of the continental mainland, near but not on the coast (Cramp & Simmons 1983). Our knowledge of the variability in body dimensions in the Red Knot has advanced by leaps and bounds in the past decades. The close similarity in the mitochondrial DNA of the different breeding populations as studied by Baker *et al.* (1994), did not allow intraspecific taxonomical conclusions. Much of the species' morphometrical variation was unknown or not well understood until the early 1980s, since migrant birds with unknown breeding origins were regularly used to describe subspecific variation. The species shows sexual and spatial variability in body dimensions in measurements and plumage characters (Dick *et al.* 1976, Roselaar 1983, Tomkovich 1990 & 1992, Godfrey 1992, Piersma 1994, Tomkovich & Solo-viev 1996, Engelmoer & Roselaar 1998, Tomkovich 2001). The differences between both sexes are larger than those between subspecies. Males are smaller than females. Sexual dimorphism is smallest in the breeding population of low arctic Canada and largest in the one of the New Siberian Islands. Also, females show less variation in body dimensions than males. Engelmoer & Roselaar (1998) proposed to distinguish five sub-species: nominate *canutus* breeding on N-Taimyr, *islandica* breeding in high arctic Canada, NE-Greenland and on Svalbard, *rogersi* breeding on the New Siberian Islands, *roselaari* breeding on Wrangel Island and *rufa* breeding in low arctic Canada. The differences between the various sub-species included both measurements (in order of importance: culmen-, secondary-, tarsus- and wing lengths) and colouration patterns. Tomkovich & Serra (1999) did not agree with assigning *rogersi* to the breeding population of the New Siberian Islands. They agreed on the morphometrical differences between the New Siberian Islands population and the Taimyr one. And they were in favour to split both populations contra Tomkovich (1992). Tomkovich (2001) then proposed to distinguish the breeding population of the New Siberian Islands as *piersmai* and to assign the Chukotsk population as *rogersi*. This proposal is followed in the current paper.

The migratory patterns of the Red Knot populations in various parts of the East Atlantic flyway are described by Prater (1974), Morrison (1975), Boere (1976), Dick *et al.* (1976), Gromadzka (1985c), Davidson *et al.* (1986a), Dick *et al.* (1987), Uttley *et al.* (1987), Prokosch (1988), Smit & Piersma (1989), Underhill *et al.* (1989), Davidson & Wilson (1992), Piersma & Davidson (1992), Piersma *et al.* (1992), Gudmundsson (1994), Meltofte *et al.* (1994), Piersma (1994), Tomkovich & Soloviev 1996, Nebel *et al.* (2000), Tomkovich *et al.* (2000), Boyd & Piersma (2001a & b), Koopman (2002), Wernham *et al.* (2002), Bakken *et al.* (2003), Stroud *et al.* (2004), Nieboer (2005), Helseth *et al.* (2005), Meisner & Kamont (2005) and Meissner (2005, 2007a). Two subspecies of Red Knot stage in W-Europe during migration and winter. Nominate *canutus* is passing through the area between end July and end September and during May and early June to and from the W-African wintering grounds. *C.c. islandica* arrives during August and stays until the end of April. This sub-species goes through the post-breeding moult in W-Europe. C.c. *canutus* does not perform the post-breeding moult in W-Europe but instead on the W-African wintering grounds. Females *canutus* are considered to skip the western Wadden Sea after the breeding season in some years and males *canutus* in most years.

The W-European wintering birds depart from the Wadden Sea before early May, heading for staging grounds on Iceland and in N-Norway and continue their migrations to E-Greenland

Table 26. Estimated population composition of Red Knots staging in the Wadden Sea. Presented are the estimated proportions.

Period	N	piersmai ♂	islandica ♂	islandica ♀	canutus ♂	canutus ♀	roselaari ♀
21/7 - 31/7	29	0.02	0.09	0.00	0.18	0.72	0.00
1/8 - 20/8	20	0.00	0.17	0.00	0.52	0.31	0.00
21/8 - 31/8	92	0.00	0.40	0.03	0.37	0.17	0.03
1/9 - 10/9	204	0.01	0.17	0.60	0.20	0.01	0.01
11/9 - 20/9	19	0.05	0.17	0.11	0.67	0.00	0.00
21/9 - 31/9	151	0.00	0.22	0.52	0.21	0.00	0.04
1/10 - 10/10	26	0.00	0.19	0.53	0.28	0.00	0.00
11/10 - 30/11	29	0.00	0.59	0.30	0.00	0.11	0.00
1/12 - 31/12	168	0.00	0.23	0.73	0.03	0.00	0.01
1/1 - 10/1	90	0.00	0.10	0.86	0.00	0.00	0.04
11/1 - 20/1	134	0.00	0.18	0.82	0.00	0.00	0.00
21/1 - 20/2	27	0.00	0.21	0.77	0.00	0.00	0.02
20/2 - 10/4	14	0.00	0.43	0.44	0.00	0.13	0.00

and NE-Canada. The W-African wintering population arrives in the Wadden Sea mainly between 5 and 10 May, they leave the area by the end of May and pass S-Sweden between end May - early June in easterly directions (Green 2004). These Red Knots are recovered as far east as N-Taimyr and the Lena River.

Population composition

The estimates of the population composition are based upon the inclusion of six breeding samples: *piersmai* males, *islandica* males, *islandica* females, *canutus* males, *canutus* females and *roselaari* females (Table 10). Both breeding samples *piersmai* males and *roselaari* females were only included to investigate the probable occurrence of these extreme-sized populations. If both groups were recognized in significant proportions, *piersmai* females and *roselaari* males might also be amongst the captured birds in the Wadden Sea. In that case the selection of breeding samples ought to include these samples as well, resulting in a large degree of overlap between the breeding samples and thus in difficulties with interpreting the results. Thus, the presented results are based upon two assumptions. The first concerns N-Canadian rufa being assumed not to migrate to the Wadden Sea. Secondly, no sexual differentiation is assumed in the migratory patterns of *piersmai* and *roselaari*.
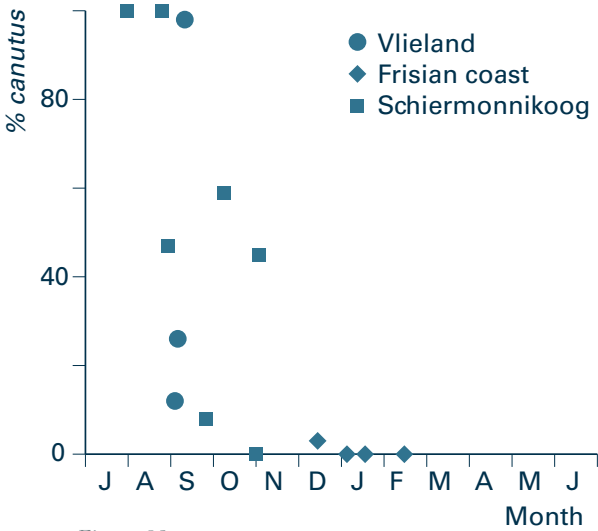

The NAG-optimizations show a scarce occurrence (< 5%) of *piersmai* males or *roselaari* females (Table 26). They were often predicted to be absent: *piersmai* males in ten out 13 estimates and *roselaari* females in seven out of 13 estimates. Therefore, a probable occurrence of both these subspecies in the Wadden Sea will be ignored here, even though individuals might well have a large enough probability to belong to these subspecies.

Both other populations islandica and *canutus* showed a pattern of temporal segregation with *canutus* dominating immediately after the breeding season until the end of August or mid September.

Figure 31:
The estimated proportional occurrence (%) of the nominate subspecies of the Red Knot in the Wadden Sea during post-breeding and winter, as based upon the site-specific population composition estimates with the NAG-optimisations (males and females canutus *combined).*

C.c. *canutus* gradually disappeared from August onwards, which modifies the general idea of an abrupt departure of *canutus* to W-Africa in the second half of August without even starting its post-breeding moult (e.g. Dick *et al.* 1987, Piersma *et al.* 1992, Piersma 1994). Our results indicate the presence of significant numbers of moulting *canutus* in the Wadden Sea, since *canutus* was predicted to occur regularly until mid October, whilst practically all adults captured in the Wadden Sea after end August were moulting their primaries. Analysis of only the large catches showed the same pattern (Fig. 31), but there was a large variation in estimates of the population composition during the moulting period. It did not seem to be caused by spatial differences between the three catching sites.

C.c. *islandica* dominated from September throughout winter and spring until at least 10 April. Males *islandica* arrived earlier than females in the Wadden Sea after breeding. Among females *islandica* dominated during December - February and constituted about half in the samples from September and October. This predominance of females was less evident after February due to a lack of data.

C.c. *canutus* dominated in the Wadden Sea during July and August (also Koopman 2002). Females were the first to arrive in the Wadden Sea causing a predominance of females during July. This predomination decreased during August. Males *canutus* stayed longer in the Wadden Sea than females, since they occurred until mid October. Females had left by early September. Measurements of Red Knots captured in the Wadden Sea from the second half of April and during May were lacking.

9.4 CURLEW SANDPIPER

Introduction

The Curlew Sandpiper is a regular breeding species of high arctic Siberia between the Gydansk tundra and the Chukotsk peninsula (Map 4, also Lappo & Tomkovich 2006). The species is considered monotypic (Glutz *et al.* 1975, Prater *et al.* 1977, Cramp & Simmons 1983, Engelmoer & Roselaar 1998). Both sexes differ importantly with respect to measurements and plumage characters. Females are larger than males. They are best distinguished with culmen- and tarsus lengths.

The migratory patterns of the Curlew Sandpiper populations in various parts of the East Atlantic flyway are described by Boere (1976), Elliott *et al.* (1976), Smit & Wolff (1981), O.A.G. Münster (1983), Wilson *et al.* (1980), Gromadzka (1985a), Smit & Piersma (1989),

Wymenga *et al.* (1990), Zeiske (1992), Underhill *et al.* (1993), Meltofte *et al.* (1994), Dodman *et al.* 1997, Figuerola & Bertolero (1998), Tomkovich *et al.* (2000), Koopman (2001), Wernham *et al.* (2002), Bakken *et al.* (2003), Stroud *et al.* (2004) and a series of authors in Underhill *et al.* (2006). The presence of Curlew Sandpipers in W-Europe is restricted to the post-breeding season. Staging numbers in the Wadden Sea are low as related to the total population size. The few staging birds in the area are present for a few weeks while refuelling for their migration to the NW-and W-African wintering grounds (also Annex 1 - Table 3). The W-European migrants originate from the Siberian breeding grounds east to N-Taimyr at 98oE. Curlew Sandpipers breeding on N-Taimyr appear to migrate just as well in a SE direction to the Indian sub-continent, the E coast of Africa and Australia.

The population substantially increased during the past decades. This resulted in increasing post-breeding numbers in the Wadden Sea with important concentrations near the estuaries of the Elbe and the Eider. Curlew Sandpipers regularly complete part of their post-breeding moult on these staging sites. In general, males depart a month earlier than females from the breeding grounds. Males stayed longer on a stopover site in NE-Spain than females. In good breeding seasons males arrive ten days ahead of the females in NE-Spain against four days in a bad breeding season. Spring migration from W-Africa follows a more easterly route than during autumn and is mainly passing through the Mediterranean and the Black Sea region.

Population composition

No geographical races are distinguished in this species. Since both sexes differ clearly, the samples collected in Engelmoer & Roselaar (1998) could be used to estimate the population composition with respect to both sexes of the Curlew Sandpipers in the Wadden Sea. Males arrived ahead of the females: 85% of the adults present by end July were males. During the following weeks the male percentages decreased to maximally 27% during August (Table 27).

Table 27. Estimated sex ratios in the Curlew Sandpiper populations present in the Wadden Sea. Presented are the estimated proportions. 'V&F&S' stands for Vlieland, Frisian coast and Schiermonnikoog.

Period	Catching site	N	♂♂	♀♀
11/7 - 20/7	V&F&S	6	no optimal solution	
21/7 - 31/7	V&F&S	29	0.85	0.15
1/8 - 10/8	V&F&S	29	0.00	1.00
11/8 - 20/8	V&F&S	48	0.26	0.73
21/8 - 20/9	V&F&S	29	no optimal solution	
11/8 - 20/8	Vlieland	32	0.27	0.73
11/8 - 20/8	Frisian coast	16	no optimal solution	

9.5 DUNLIN

Introduction

The breeding areas of the Dunlin cover coastal grasslands, salt marshes, and upland moors of the temperate zone, mires in forests of the boreal zone and tundras of the subarctic and arctic (Map 5 and Lappo & Tomkovich 1998).The variability in body dimensions in the Dunlin has received much attention during the past 30 years (Glutz *et al.* 1975, Browning 1977 & 1991, Ferns & Green 1979, Hale 1980, Ferns 1981a, Cramp & Simmons 1983, Greenwood 1986, Tomkovich 1986, Nechaev & Tomkovich 1987 & 1988, Wenink *et al.* 1993, Wenink *et al.* 1996, Engelmoer & Roselaar 1998, Wennerberg *et al.* 1999 and Stroud *et al.* 2004). Cramp & Simmons, Browning, Nechaev & Tomkovich studied both plumage characters and morphometrics, Greenwood and Engelmoer & Roselaar pre-dominantly morphometrics, and both Wenink *et al.* as well as Wennerberg *et al.* differences in mtDNA. These studies resulted in the recognition of ten sub-species, which however are not all recognized by all authors. Four of them are of potential interest for this study, since they use the East Atlantic Flyway in various intensities. These four sub-species are from west to east: (1) *arctica* - breeding in arctic NE-Greenland, (2) *schinzii* - mainly breeding in the temperate and boreal zones of the NE-Atlantic region and W-and NW-Europe, (3) nominate *alpina* - breeding in subarctic and arctic N-Europe breed as far east as 85°E, where it intermixes with *centralis* and (4) *centralis* breeding from Taimyr eastwards. The other subspecies breed in E-Siberia, the N-Pacific, Alaska and low arctic N-Canada and are reviewed in detail by Engelmoer & Roselaar (1998). The separating characters included both measurements and plumage characters. The Atlantic populations are small-sized, have less black bellies in breeding plumage and their mantle feathers include yellowish-red colours. The N-Pacific populations are large-sized, have relatively whitish head-feathers, more extensively black bellies and more chestnut-red mantle feathers. The small-sized actites on the E-Palearctic Sakhalin Island is an exception on this rule. Nearctic *hudsonia* has intermediate characters between the Atlantic and N-Pacific populations. MtDNA studies showed the existence of five major phylogeographic groups: three in the Palearctic and two in the Nearctic. The three subspecies *arctica*, *schinzii*, and nominate *alpina* (east to Yamal) are grouped in the European (phylogeographic) group, *centralis* (from Yamal east to the Lena River) in the Central Siberian group and sakhalina and kistchinski in the E-Siberian group. Within *arctica*, *schinzii*, *alpina* and *centralis* six breeding populations are generally distinguished due to the distinction of three separate *schinzii* populations: Iceland (& SE-Greenland), the British isles (incl. continental W-Europe) and the S-Baltic. Worldwide most Dunlin-populations moult primaries on the breeding grounds, though with differences in speed and timing. The Atlantic populations of the Dunlin are an exception on this rule: they do not start primary moult on the breeding grounds.

The migratory patterns of the Dunlin populations in various parts of the East Atlantic flyway are described by Ogilvie (1963), Mascher (1971), Boere *et al.* (1973), Pienkowski & Dick (1975), Boere (1976), O.A.G. Münster (1976), Leslie & Lessells (1989), Pienkowski *et al.* (1979), Hardy & Minton (1980), Ferns (1981b), Smit & Wolff (1981), Gromadzka (1981, 1983, 1985b & 1989), Pienkowski & Prokosch (1982), Clark (1983), Greenwood (1984), Speek & Speek (1984), Van der Have *et al.* (1984), Jönsson (1986), Brenning (1989), Gromadzka (1989), Smit & Piersma (1989), Stiefel & Scheufler (1989), Rösner (1990), Goede *et al.* (1990), Fokker (1991), Meltofte (1991), Holmgren *et al.* (1993b), Meltofte *et al.* (1994), Rösner (1997), Lappo & Tomkovich (1998), Thorup (1998), Serra *et al.* (1998), Gromadzka & Ryabitsev (1998), Wernham *et al.* (2002), Bakken *et al.* (2003), Stroud *et al.* (2004) and Nieboer (2005), Tjørve & Tjørve (2007). The 20-45,000 Greenlandic *arctica* winter in W-Africa. Part of this population is present in the Wadden Sea during autumn but virtually none during spring. The 950,000 Icelandic *schinzii* (including SE-Greenland) winter in NW-and W-Africa. Icelandic *schinzii* migrate through the Wadden Sea (also Speek & Speek 1984). The 30,000 British *schinzii* mainly winter in NW-Africa and SW-Europe. Some may occur in the Wadden Sea region. The Baltic *schinzii* population is the smallest and most threatened one. It involves 6,000 birds. Some of them breed as far west as the German and Danish part of the Wadden Sea. They pass through the Wadden Sea (Annex 1 - Table 1) and mainly winter along the Atlantic coast of S-Britain, W-France and the Iberian Peninsula. The N-European *alpina* population is the largest one with 1.3 million birds estimated. The great majority of Dunlins visiting the Wadden Sea belongs to this subspecies. *C.a. alpina* mainly winters in W-and SW-Europe with about 130 - 260,000 wintering in the Wadden Sea.

By end February westerly wintering Dunlin start to return to the Wadden Sea. By end April - early May 90% of the whole *alpina* population is present in the Wadden Sea. Finally, W-Siberian *centralis* mainly winter around the Caspian Sea and in the Mediterranean, NE-Africa and in the Middle East. The population is estimated at nearly 300,000 birds. Subarctic breeding *alpina* depart from the Wadden Sea by early May, while the Siberian breeders stage throughout May and depart by end May/ early June. Important passage is observed to occur over S-Sweden between end May - early June in easterly directions (Green 2004). These Siberian Dunlin are either *alpina* or *centralis*. Dunlins breeding as far east as Yamal and Gydan are known to pass through the Baltic region (Koopman 1993, Gromadzka & Ryabitsev 1998, Tomkovich *et al.* 2000).

Population composition
Morphometric analysis based on the wing- and culmen lengths of Dunlin is complicated. If more than only wing- and culmen lengths were measured in the Wadden Sea, and both sexes would have been distinguished, analysis would have been less complicated. There is a large

degree of polymorphism within the ten distinguished subspecies: *arctica*, *schinzii*, *alpina*, *centralis*, *actites*, *kistchinski*, *sakhalina*, *arcticola*, *pacifica* and *hudsonia* (Hale 1980, Greenwood 1986, Tomkovich 1986, Nechaev & Tomkovich 1987 & 1988, Browning 1991 Wenink *et al.* 1996, Engelmoer & Roselaar 1998). Morphometric differences between the sexes increase the complexity, since females are generally larger than males. These potential 20 breeding samples have partly overlapping measurements. The predictive analyses in this study were therefore limited to *arctica*, *schinzii*, *alpina* and *centralis*. These subspecies have the smallest measurements of the various Dunlin subspecies.

Table 28. Estimated population composition of Dunlin staging in the Wadden Sea. Both subspecies arctica and schinzii are included. Presented are the estimated proportions.

Period	N	arctica ♂	schinzii ♂	arctica ♀/ schinzii ♀/ Fenno-scandia alpina ♂	Fennoscandia alpina ♀/ N-Europe alpina ♂/ Siberia centralis ♂	N-Europe ♂/ Siberia centralis ♀
Vlieland						
1/7 - 10/7	85	0.00	0.00	0.15	0.50	0.35
11/7 - 17/7	64	0.00	0.00	0.38	0.00	0.62
18/7 - 24/7	75	0.00	0.00	0.28	0.21	0.51
25/7 - 31/7	150	0.00	0.00	0.21	0.30	0.49
1/8 - 7/8	50	0.00	0.00	0.00	0.00	1.00
8/8 - 14/8	279	0.00	0.11	0.00	0.54	0.35
15/8 - 21/8	113	0.00	0.14	0.00	0.53	0.33
22/8 - 28/8	102	0.00	0.00	0.59	0.07	0.34
29/8 - 4/9	48	0.00	0.03	0.40	0.08	0.49
Schiermonnikoog - until season 1980/81						
18/7 - 31/7	153	0.00	0.00	0.57	0.04	0.39
1/8 - 7/8	124	0.00	0.00	0.00	0.50	0.50
8/8 - 14/8	436	0.00	0.00	0.60	0.07	0.33
15/8 - 21/8	606	0.06	0.00	0.37	0.18	0.39
22/8 - 28/8	368	0.00	0.05	0.14	0.19	0.62
29/8 - 4/9	166	0.00	0.07	0.00	0.59	0.34
Schiermonnikoog - seasons 1981/82 until 1990/91						
18/7 - 31/7	32	0.00	0.04	0.00	0.39	0.57
1/8 - 7/8	116	0.25	0.00	0.00	0.00	0.75
8/8 - 14/8	81	0.14	0.06	0.14	0.00	0.66
15/8 - 21/8	134	0.00	0.00	0.42	0.00	0.58
22/8 - 28/8	342	0.08	0.00	0.12	0.40	0.39
29/8 - 4/9	48	0.00	0.00	0.54	0.00	0.46

Another complication is the variability in body dimensions within nominate *alpina*. The 'Fennoscandian' population (breeding from the east coast of the White Sea westwards) has smaller culmen lengths than the 'N-European' one (breeding east of the White Sea), while the latter have more or less the same culmen lengths as *centralis* (also Wennerberg *et al.* 1999), and differ from *centralis* by not starting their primary moult on the breeding grounds (also Kania 1990). Therefore, two separate sample groups were created, one including the small-sized Fennoscandian *alpina* (White Sea to the west) and the other including larger-sized N-European *alpina* and *centralis* (east of the White Sea to the Anabar River). And there is also considerable overlap in measurements between the various populations and sexes (Table 10). Nevertheless, a first set of samples was created with the primary aim to estimate the occurrence of *arctica* males and *schinzii* males. This set was composed as follows: (1) *arctica* males, (2) *schinzii* males, (3) Fennoscandian *alpina* males with *arctica* females and *schinzii* females, (4) Fennoscandian *alpina* females, N-European *alpina* males & *centralis* males and (5) N-European *alpina* females & *centralis* females. The results are
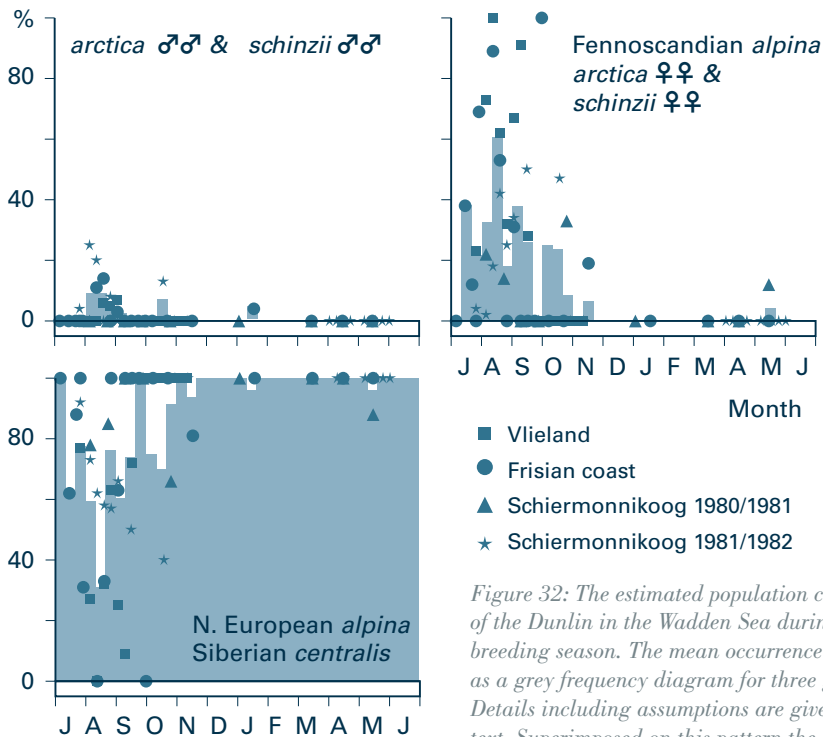

Figure 32: The estimated population composition of the Dunlin in the Wadden Sea during the non-breeding season. The mean occurrence is shown as a grey frequency diagram for three groups. Details including assumptions are given in the text. Superimposed on this pattern the site-specific values are given (see key).

Table 29. Estimated population composition of Dunlin staging in the Wadden Sea. Since arctica and schinzii were not predicted to occur along the Frisian mainland coast and observed to be absent after 4 September on Vlieland and Schiermonnikoog (Table 28), both subspecies were excluded from this series of optimisations. Presented are the estimated proportions.

Period	N	Fennoscandian alpina ♂	Fennoscandian alpina ♀	N-European alpina ♂ Siberian centralis ♂	N-European alpina ♀ Siberian centralis ♀
Vlieland					
5/9 - 11/9	82	0.00	0.00	0.63	0.37
12/9 - 18/9	76	0.00	0.00	1.00	0.00
19/9 - 25/9	50	0.00	0.00	0.38	0.62
26/9 - 2/10	49	0.00	1.00	0.00	0.00
3/10 - 9/10	51	0.00	0.00	0.76	0.24
10/10 - 31/10	90	0.00	0.00	1.00	0.00
1/11 - 30/11	35	0.00	0.19	0.00	0.81
1/12 - 28/2	38	0.00	0.00	0.81	0.19
March	41	0.00	0.00	0.57	0.43
April	21	0.00	0.00	0.47	0.53
May	75	0.00	0.00	0.55	0.45
Frisian coast					
18/7 - 14/8	101	0.22	0.00	0.00	0.78
15/8 - 28/8	87	0.00	0.14	0.35	0.50
29/8 - 18/9	54	0.00	0.00	0.00	1.00
19/9 - 2/10	24	0.00	0.00	0.71	0.29
10/10 - 7/11	99	0.00	0.33	0.06	0.60
1/11 - 28/2	107	0.00	0.00	0.54	0.46
March	102	0.00	0.00	0.41	0.59
April	34	0.00	0.00	0.87	0.13
May	39	0.00	0.12	0.00	0.88
Schiermonnikoog - until season 1980/81					
5/9 - 11/9	59	0.00	0.91	0.09	0.00
12/9 - 18/9	207	0.00	0.28	0.36	0.36
19/9 - 25/9	159	0.00	0.00	0.52	0.48
26/9 - 2/10	159	0.00	0.00	0.61	0.39
3/10 - 9/10	241	0.00	0.00	0.16	0.84
10/10 - 16/10	349	0.00	0.00	0.92	0.09
17/10 - 30/10	185	0.00	0.00	0.51	0.49
31/10 - 6/11	52	0.00	0.00	0.00	1.00
7/11 - 13/11	325	0.00	0.00	0.44	0.56

Schiermonnikoog - seasons 1981/82 until 1990/91				
5/9 - 2/10	121	0.19	0.31	0.00	0.50
3/10 - 23/10	48	0.60	0.00	0.00	0.40
24/10 - 30/10	38	0.00	0.00	0.31	0.69
31/10 - 20/11	65	0.00	0.00	1.00	0.00
27/3 - 9/4	88	no optimal solution			
10/4 - 16/4	57	0.00	0.00	0.73	0.27
17/4 - 23/4	41	0.00	0.00	0.58	0.42
24/4 - 30/4	21	no optimal solution			
1/5 - 14/5	119	0.00	0.00	0.81	0.19
15/5 - 21/5	137	0.00	0.00	0.42	0.59
22/5 - 28/5	44	0.00	0.00	0.48	0.52
29/5 - 4/6	47	0.00	0.00	0.17	0.83

presented in Table 28. Since *arctica* males and *schinzii* males occurred rarely, a second set of samples was constructed with four sample groups: (1) Fennoscandian *alpina* males, (2) Fennoscandian *alpina* females, (3) N-European *alpina* males & *centralis* males and (4) N-European *alpina* females & *centralis* females. These results can be found in Table 29. Since the occurrence of *arctica* and *schinzii* was rejected, the results of these second series of analyses had to be corrected for their probable occurrence. These corrections were based upon the estimates resulting from the first series of analyses. Since Dunlin resembling *arctica* or *schinzii* in the first series of analyses were usually recognized as small-sized Fennoscandian *alpina* males in this second series, only the estimated proportions of Fenno-scandian *alpina* males were corrected by subtracting the estimated proportions of *arctica* and *schinzii* under the assumption of equal sex-ratios in *arctica* and *schinzii*.

Geographical breeding origins - temporal variation *arctica* and *schinzii*

The males of both subspecies were nearly exclusively present during August as deduced from the NAG-optimizations (Fig. 32). The data from the 1970s on Vlieland showed a regular occurrence of *schinzii* males between 8 August and 4 September. Their occurrence peaked between 15 and 21 August when up to 14% of the captured birds was recognized as *schinzii* males. When equal sex-ratios are assumed, the relative occurrence of both subspecies can be estimated. Declining proportions are recognizable since the 1970s (Fig. 33). C.a. *arctica* was regularly estimated to occur with 5% or more until the early 1990s, but no *arctica* were estimated to occur in the second half of the 1990s. The proportional occurrence of *schinzii* decreased as well since the 1970s. It seems as if these changes have taken place throughout the Wadden Sea, since the pattern was recognized on all three catching sites.

Fennoscandian *alpina*

The post-breeding period appeared the major period of passage for the sample group of Fenno-scandian *alpina*, *arctica* females and *schinzii* females. Nearly 40% of the numbers present by mid July resembled this sample group. Their occurrence even peaked at 60% by mid August. They had left the Wadden Sea by mid November and were virtually absent during winter and spring. The percentages Fennoscandian *alpina* could be estimated by assuming equal sex-ratios for *schinzii* and *arctica*. The relative occurrence of Fennoscandian *alpina* declined since the 1970s as was the case with *arctica* and *schinzii*. In 6 out of 9 estimates Fennoscandian *alpina* were more common than N-European *alpina* or Siberian *centralis* on both barrier islands Vlieland and Schiermonnikoog during August in the 1970s (Table 29). But in 4 samples collected during the 1980s on Schiermonnikoog Fennoscandian *alpina* were less common. When the wing- and culmen lengths of adult Dunlin captured during August and September in the Wadden Sea were analysed with POSCON and grouped per trapping effort, the same pattern emerged (Fig. 33).
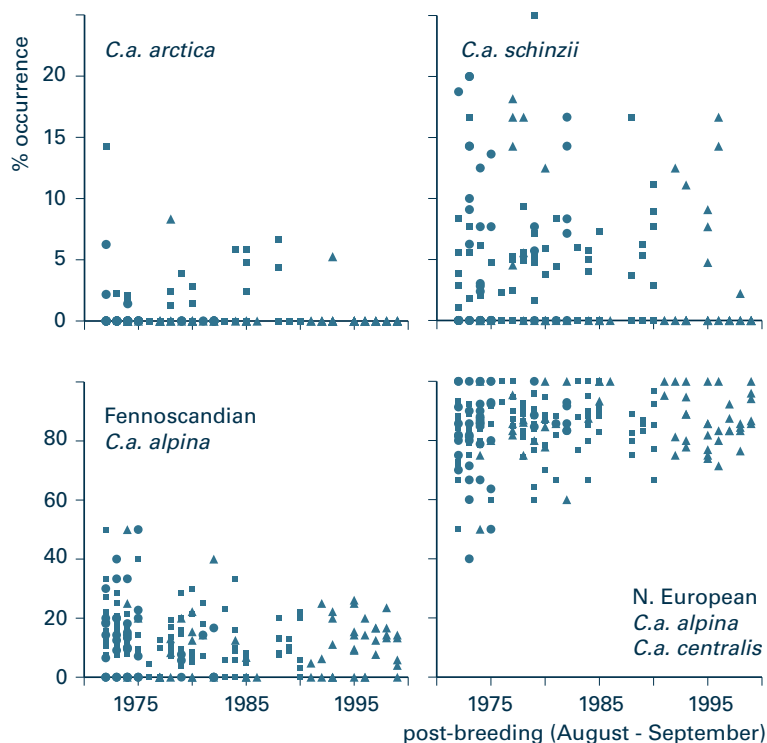

Figure 33: Estimates of the occurrence of the four subspecies of Dunlin in the Wadden Sea since the early 1970s during the months August and September. POSCON-analysis was used with the following a-priori probabilities: arctica ♂♂ *0.01,* arctica ♀♀ *0.01,* schinzii ♂♂ *0.05,* schinzii ♀♀ *0.05, Fennoscandian* alpina ♂♂ *0.15, Fennoscandian* alpina ♀♀ *0.15, Siberian ♂♂ 0.29, Siberian ♀♀ 0.29. These a-priori probabilities were estimated according to (1) the results of the NAG-optimizations, and (2) the sizes of the various breeding populations (Rose & Scott 1997, Hagemeijer & Blair 1997). Explanation of the symbols: '●' Vlieland, '▲' Frisian coast, '■' Schiermonnikoog.*

The proportional presence of Fennoscandian *alpina* gradually declined during the past 30 years. These differences in occurrence between the 1970s and 1980s might reflect reality, but they might also have been caused by the assumption of equal sex-ratios in *arctica* and *schinzii*. When, in reality, more females than males of both these subspecies were captured during the 1970s, a declining occurrence of *arctica* and *schinzii* (as estimated by the male samples) will then correspondingly have a profound effect on the occurrence of the sample group with *arctica* females and *schinzii* females. A sex-ratio in favour of females *arctica* and *schinzii* will affect the August-estimates in particular.

N-European *alpina* and/or Siberian *centralis*

Their proportional occurrence during post-breeding counterbalanced the Fennoscandian *alpina*: relatively low proportions during August in the 1970s and during September - October during the 1980s. Generally, this group of Dunlins dominated the flocks after mid August and nearly all wintering Dunlin and spring migrants in the Wadden Sea resembled this sample group. In general, the estimated proportions of N-European *alpina* and/or Siberian *centralis* in the Wadden Sea increased during the last 30 years. This increase was linked to a reduced occurrence of the other populations (Fig. 33).
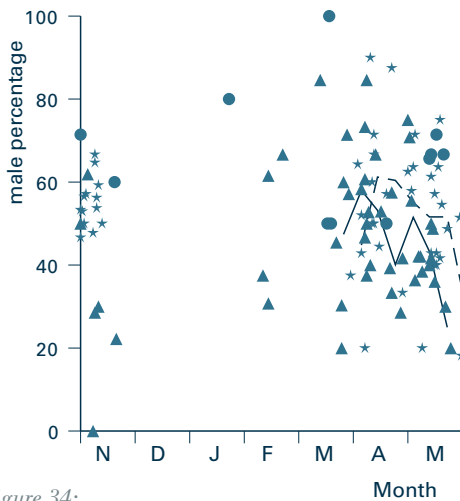

Figure 34:
Estimated male percentages in the Dunlin populations of the Wadden Sea between November and June. The NAG-optimizations, presented in Fig. 35, showed the near exclusive occurrence of centralis *during these months. Explanation of the symbols: '●' Vlieland, '▲' Frisian coast (also drawn line), '★' Schiermon-nikoog (also dotted line).*

Regular occurrence of Siberian *centralis* in the Wadden Sea might be deduced from the moulting data, since *centralis* is moulting (nearly all) primaries on the breeding grounds. If *centralis* is a regular migrant, adults with 8-10 new primaries must be captured regularly in the Wadden Sea during July or August. Such is not the case. No adults were captured during July in an advanced stage of primary moult, which had started moulting after suspension earlier (*N*= 593). Birds with suspended moult were found during August with the following percentages: Vlieland 1.6% (*N*= 716), Frisian coast 0.4% (*N*= 554) and Schiermonnikoog 2.7% (*N*= 2287). Furthermore, our ringed birds were not recovered from the breeding grounds of *centralis* (own data). Wernham *et al.* (2002) report the easternmost recovery along the east coast of Yamal, which is still part of the *alpina* breeding range. Tomkovich *et al.* (2000) report a total of two recoveries of birds breeding

on the Gydan Peninsula. One of them was a breeding 2 c.y. bird, which was controlled during September along the Polish coast. The catching details of the other bird are unknown. The conclusion is that the large majority of wintering Dunlin in the Wadden Sea are N-European *alpina* with some *centralis* amongst them. As long as no further information is available on the degree of occurrence of birds with 'adult buff' coverts (Gromadzka 1989), no estimates can be made of the proportional occurrence of *centralis* in the Wadden Sea.

Sex-ratio

Since N-European *alpina* and/or Siberian *centralis* were the only ones present from mid November onwards, measurement data were used to estimate the male percentages for the various catching sites in the Wadden Sea (Fig. 34). A mean male percentage of 28.5% (SD= 22.2, *N*= 5) is estimated along the mainland coast during November, against 65.7% on Vlieland (SD= 8.1, *N*= 2) and 55.9% on Schiermonnikoog (SD= 6.0, *N*= 11). Thus, females predominate with these predictions along the mainland coast and males on the island sites. The conclusion of higher male percentages on the island sites seems to hold for winter and spring as well. The male percentages on Schiermonnikoog decreased from about 60% males by early April to 35% by the end of May and along the Frisian coast from 55% to 25%. In total, 37% of the variation in estimated male percentages sampled throughout the Wadden Sea during May could be explained from either the day of catching or the catching site (*F*day= 7.681, *df* = 1, s.= 0.009; *F*site= 7.675, *df*= 2, *s.*= 0.002).

Geographical breeding origins - spatial variation

The NAG-optimization results do not indicate the occurrence of *arctica* males on Vlieland during post-breeding. In the 1970s, *schinzii* males appear to occur less regularly on Schier-monnikoog than on Vlieland (Schiermonnikoog 0-7% against 3-14% on Vlieland). Males *arctica* are predicted to occur on Schiermonnikoog during August in the 1970s and 1980s, but not on Vlieland. Neither *schinzii* males nor *arctica* males are predicted to occur along the Frisian coast. This point will be further discussed in Chapter 10.

9.6 BAR-TAILED GODWIT

Introduction

The Bar-tailed Godwit breeds in the subarctic regions of the Palearctic and Alaska both on coastal and inland sites. The species has some degree of variability in body dimensions (Vaurie 1965, Prater *et al.* 1977, Glutz *et al.* 1977, Hale 1980, Cramp & Simmons 1983, Hayman *et al.* 1986, Stepanyan 1990, Paulson 1993, Del Hoyo *et al.* 1996,

Engelmoer & Roselaar 1998). Five disjunct breeding ranges are currently known (Map 6) These separate breeding populations are distinguished at the subspecies level: (1) nominate *lapponica* - breeding in N-Fennoscandia, the north part of the White Sea and on the Kanin Peninsula; (2) *taymyrensis* - breeding from Yamal east to the delta of the Anabar River; (3) *menzbieri* - breeding from the Lena Delta east to the Chaunsk Bay; (4) *anadyrensis*, breeding at Anadyr and along the south part of the Chukotsk Peninsula; and (5) *baueri* - breeding in Alaska. Tomkovich & Serra (1999) originally did not agree with the distinction of *anadyrensis* as a separate subspecies. However, recent work of Tomkovich (in prep.) showed the distinction between *anadyrensis* and *baueri* to be a correct one. *L.l. lapponica* and *taymyrensis*, the two westerly subspecies, are generally considered to use the East Atlantic Flyway.
The species shows marked sexual and spatial variability in body dimensions. Sexual differences are larger than geographical differences and males are smaller-sized than females. Measurements as well as plumage characters contribute to the distinction between subspecies (also Nieboer *et al.* 1985). Primary moult is not started during breeding.

The migratory patterns of the Bar-tailed Godwit populations in various parts of the East Atlantic flyway are described by Boere (1976), Benthem (1981), Smit & Wolff (1981), Speek & Speek (1984), De Goede *et al.* (1985), Prokosch (1988), Smit & Piersma (1989), Piersma & Jukema (1990), Drent & Piersma (1990), Wymenga *et al.* (1990), Meltofte *et al.* (1994), Atkinson (1996), Tomkovich *et al.* (2000), Scheiffarth *et al.* (2002), Wernham *et al.* (2002), Bakken *et al.* 2003, Scheiffarth (2003), Stroud *et al.* (2004) and Nieboer (2005). W-European migrants are recovered east to SE-Taimyr at 102oE (Nieboer 2005). Large numbers of adults enter the Wadden Sea between mid July and mid August, followed by the juveniles a month later. These birds winter both in W-Europe and along the Atlantic coast of Africa (Annex 1 - Table 3). The European wintering birds undergo their post-breeding moult in the Wadden Sea, but the African wintering birds only stage for a few weeks to replenish their energy reserves. They undergo their post-breeding moult on the African wintering grounds. The European wintering birds are considered to be nominate *lapponica* and the W-African wintering birds as *taymyrensis*. Part of the moulting population at completion moves away from the Wadden Sea to estuaries elsewhere in W-and SW-Europe. For instance, Bar-tailed Godwits from the German part of the Wadden Sea were mostly recovered from wintering sites along the E-coast of Britain (Prokosch 1988). From the end of February the numbers in the Wadden Sea increase from about 35,000 to more than 90,000 by mid March due to the arrival of other European wintering birds. The W-African wintering Bar-tailed Godwits arrive by early May (Annex 1 - Table 3). *L.l. lapponica* leaves the Wadden Sea in the first half of May and *taymyrensis* by late May. *L.l.taymyrensis* passes S-Sweden between 25 May and 10 June with median date June 2nd (De Goeij *et al.* 2000, Green *et al.* 2002). There was no difference in timing of migration between both sexes when passing S-Sweden.

Table 30. Population composition of Bar-tailed Godwits. Sexes were analysed separately. Data from all catching sites were combined. Presented are the estimated proportions.

Period	N	lapponica	taymyrensis	menzbieri	anadyrensis	baueri
♂♂						
21/7 - 31/7	22	0.00	1.00	0.00	0.00	0.00
1/8 - 10/8	24	0.00	1.00	0.00	0.00	0.00
11/8 - 20/8	37	0.00	0.96	0.03	0.00	0.00
21/8 - 31/8	39	0.13	0.84	0.00	0.00	0.03
1/9 - 10/9	20	0.18	0.82	0.00	0.00	0.00
11/9 - 20/9	13	0.82	0.16	0.00	0.02	0.00
21/9 - 31/9	13	0.46	0.54	0.00	0.00	0.00
1/10 - 31/10	11	0.13	0.87	0.00	0.00	0.00
1/11 - 30/11	74	1.00	0.00	0.00	0.00	0.00
1/12 - 28/2	30	0.58	0.42	0.00	0.00	0.00
1/3 - 10/3	24	0.38	0.57	0.00	0.00	0.05
11/3 - 20/3	25	0.94	0.00	0.00	0.00	0.06
21/3 - 31/3	67	0.89	0.09	0.00	0.02	0.00
1/4 - 30/4	63	0.00	0.83	0.17	0.00	0.00
1/5 - 10/5	256	0.00	0.96	0.04	0.00	0.00
11/5 - 20/5	241	0.00	0.98	0.02	0.00	0.00
21/5 - 10/6	126	0.00	1.00	0.00	0.00	0.00
♀♀						
21/7 - 10/8	11	1.00	0.00	0.00	0.00	0.00
11/8 - 20/8	26	0.00	0.92	0.08	0.00	0.00
21/8 - 31/8	29	0.10	0.69	0.12	0.09	0.00
1/9 - 20/9	40	0.17	0.70	0.09	0.04	0.00
21/9 - 10/10	22	0.49	0.51	0.00	0.00	0.00
11/10 - 20/11	35	0.76	0.23	0.00	0.00	0.00
21/11 - 20/2	26	0.72	0.16	0.12	0.00	0.00
21/2 - 10/3	22	1.00	0.00	0.00	0.00	0.00
11/3 - 20/3	31	0.74	0.00	0.00	0.24	0.02
21/3 - 31/3	40	1.00	0.00	0.00	0.00	0.00
1/4 - 20/4	17	1.00	0.00	0.00	0.00	0.00
21/4 - 30/4	27	0.48	0.52	0.00	0.00	0.00
1/5 - 10/5	162	0.30	0.69	0.00	0.00	0.00
11/5 - 20/5	179	0.00	0.95	0.04	0.02	0.00
21/5 - 10/6	98	0.00	1.00	0.00	0.00	0.00

Population composition

Since Bar-tailed Godwits were sexed during catching, it was possible to estimate the population composition separately for both sexes. According to Engelmoer & Roselaar (1998), five breeding samples were distinguished per sex: (1) nominate *lapponica* - N-Fennoscandia, (2) *taymyrensis* - Yamal & Taimyr, (3) *menzbieri* - Central Siberia, (4) *anadyrensis* - E-Siberia and (5) *baueri* - Alaska. The results from the NAG-optimizations showed the regular occurrence of nominate *lapponica* and *taymyrensis* and the virtual absence of *menzbieri*, *anadyrensis* and *baueri* (Table 30).

The first *lapponica* males arrived by end August and stayed throughout winter until the end of March. Female *lapponica* were also present throughout winter. However, they arrived earlier (July - August) and stayed longer (until early May). *L.l. taymyrensis* dominated the staging populations in the Wadden Sea immediately after the breeding season until mid September (both males and females) and during April (males) and May (both males and females). Thus, *taymyrensis* females arrived somewhat later than the males in the Wadden Sea. Females from this population were not predicted to occur between 21 February and 20 April. males *taymyrensis* occasionally occurred between late autumn and April.

Significant proportions of the easterly populations were estimated to occur amongst the males during March, April and May (2-17%) and in the females from mid August to end September (8-21%), between end November and end March (12-26%) and around mid May (6%). Our easternmost recovery concerns an adult Bar-tailed Godwit shot in July 1997 in the delta of the Anabar River (73.050N 113.500E), which is the easternmost part of the breeding range of *taymyrensis*.

Spatial variation in the occurrence of different breeding populations

Males *lapponica* were proportionally more abundant on Vlieland than on Schiermonnikoog during post-breeding (Table 31). It is even more extreme in the females with no *lapponica* females estimated on Schiermonnikoog in contrast to the most important fraction of the Vlieland females. As a consequence, *taymyrensis* females were relatively scarce on Vlieland during post-breeding as compared to Schiermonnikoog. Whenever any of the three easterly subspecies was predicted to occur, this concerned mostly Schiermonnikoog (5-18% of the birds present) and less Vlieland (5% of the birds present - tables 31 & 32). Thus, easterly subspecies seem to occur more often in the eastern Wadden Sea than in the western part.

During spring, males *lapponica* were relatively abundant on Vlieland and Schiermonnikoog until 11 May, but virtually absent on Texel in May and along the Frisian coast during April and May (Table 31). Female *lapponica* were captured more frequently than male *lapponica* on Vlieland, Schiermonnikoog and along the Frisian mainland coast. Consequently, *taymyrensis*

Table 31. Population composition of Bar-tailed Godwits on Vlieland and Schiermonnikoog between July and November (sexes differntiated): Presented are the estimated proportions.

Period	N	lapponica	taymyrensis	menzbieri	anadyrensis	baueri
Vlieland ♂♂						
before 21/8	39	0.03	0.97	0.00	0.00	0.00
21/8 - 11/9	23	0.27	0.68	0.00	0.00	0.05
11/9 - 31/10	13	1.00	0.00	0.00	0.00	0.00
Schiermonnikoog ♂♂						
before 21/8	35	0.00	1.00	0.00	0.00	0.00
21/8 - 11/9	36	0.10	0.90	0.00	0.00	0.00
11/9 - 31/10	15	0.25	0.62	0.11	0.02	0.00
Vlieland ♀♀						
1/7 - 31/8	35	0.68	0.32	0.00	0.00	0.00
1/9 - 31/10	31	1.00	0.00	0.00	0.00	0.00
Schiermonnikoog ♀♀						
1/7 - 31/8	31	0.00	0.83	0.11	0.07	0.00
1/9 - 31/10	23	0.00	0.95	0.05	0.00	0.00

predominated on Schiermonnikoog, Texel, and the Frisian coast during May. Males from the eastern subspecies occurred with percentages higher than 10% on Vlieland during April and May and along the Frisian coast during April. This occurred in the female groups only once on Schiermonnikoog in the period 11-21 May.

9.7 EURASIAN CURLEW

Introduction

The Eurasian Curlew breeds in temperate, boreal and subarctic habitats scattered over the Palearctic (Map 7). The variability in body dimensions in the species was analysed by Sushkin (1925), Johansen (1960 & 1961), Vaurie (1965), Glutz *et al.* (1977), Cramp & Simmons (1983), Stepanyan (1990) and Engelmoer & Roselaar (1998). There is marked sexual and spatial variability in body dimensions. Sexual differences are larger than geographical differences and males are smaller than females. The species is polytypic and three subspecies are distinguished nowadays:

(1) nominate *arquata*, breeding in Europe, (2) *orientalis*, breeding in Central Siberia, and (3) *suschkini*, breeding in the S-Ural & Kazakhstan. Nominate *arquata* and *orientalis* intergrade

Table 32. Population composition of Bar-tailed Godwits during April and May: Vlieland, Schiermonnikoog, Texel and the Frisian coast compared. Catching sites are specified along the Frisian coast (P = Paesens, H = Holwerd). Presented are the estimated proportions.

Period	N	lapponica	taymyrensis	menzbieri	anadyrensis	baueri
Vlieland ♂♂						
1/4 - 31/5	24	0.36	0.51	0.13	0.00	0.00
Schiermonnikoog ♂♂						
1/4 - 30/4	22	0.33	0.67	0.00	0.00	0.00
1/5 - 11/5	55	0.23	0.77	0.00	0.00	0.00
11/5 - 21/5	52	0.00	1.00	0.00	0.00	0.00
21/5 - 31/5	18	0.00	0.99	0.01	0.00	0.00
Texel ♂♂						
11/5 - 21/5	27	0.00	0.91	0.09	0.00	0.00
21/5 - 31/5	59	0.00	1.00	0.00	0.00	0.00
Frisian coast ♂♂						
21/4 - 30/4 (H&P)	29	0.00	0.85	0.15	0.00	0.00
1/5 - 11/5 (P)	91	0.02	0.96	0.00	0.02	0.00
1/5 - 11/5 (H)	96	0.00	0.97	0.03	0.00	0.00
11/5 - 21/5 (P)	79	0.00	0.99	0.00	0.01	0.00
11/5 - 21/5 (H)	78	0.00	0.99	0.01	0.00	0.00
21/5 - 31/5 (P)	43	0.00	1.00	0.00	0.00	0.00
Vlieland ♀♀						
1/4 - 30/4	8	1.00	0.00	0.00	0.00	0.00
Schiermonnikoog ♀♀						
1/4 - 30/4	28	1.00	0.00	0.00	0.00	0.00
1/5 - 11/5	45	0.28	0.70	0.00	0.00	0.02
11/5 - 21/5	74	0.08	0.80	0.08	0.04	0.00
21/5 - 11/6	22	0.00	0.96	0.00	0.04	0.00
Texel ♀♀						
11/5 - 21/5	25	0.00	1.00	0.00	0.00	0.00
21/5 - 31/5	48	0.00	1.00	0.00	0.00	0.00
Frisian coast ♀♀						
1/5 - 11/5 (P)	57	0.20	0.80	0.00	0.00	0.00
1/5 - 11/5 (H)	51	0.00	0.92	0.08	0.00	0.00
11/5 - 21/5 (P)	40	0.00	1.00	0.00	0.00	0.00
11/5 - 21/5 (H)	36	0.00	0.98	0.02	0.00	0.00
21/5 - 31/5 (P)	19	0.19	0.81	0.00	0.00	0.00

in SE-Europe and W-Siberia. These three subspecies are characterized by a combination of measurements and plumage characters. Eurasian Curlews do not moult their primaries at the breeding grounds.

The migratory patterns of the Eurasian Curlew populations in various parts of the East Atlantic flyway are described by Boere (1976), Bainbridge & Minton (1978), Smit & Wolff (1981), Speek & Speek (1984), Kastepold (1985), Smit & Piersma (1989), Berg (1992), Meltofte *et al.* (1994), Butiev & Lebedeva (1998), Currie & Valkama (2000), Currie *et al.* (2001), Wernham *et al.* (2002), Bakken *et al.* (2003) and Stroud *et al.* (2004). Staging Eurasian Curlews in the Wadden Sea breed mostly in eastern Fennoscandia and NW-Russia east to about 50oE (also Annex 1 - tables 1 & 2). Norwegian breeding Eurasian Curlews winter on the British isles and are absent from the international Wadden Sea. Also British breeding Eurasian Curlews hardly ever reach the Wadden Sea.

The W-European breeding population is not as numerous as the Fennoscandian one. Dutch breeding birds stage outside the breeding season close near the Atlantic coastline of W-and SW-Europe. Fennoscandian breeding birds arrive in mid- to late April and usually lay their first eggs in the first half of May. At the end of the breeding season, females leave the breeding grounds 14 d ahead of the males from the first half of July onwards. Numbers in the Wadden Sea start to increase from the second half of July. During summer, a resident population of about 6,000 birds stays in the Wadden Sea being mostly immature non-breeders. These non-breeders start their primary moult already by June. With the arrival of the breeders the total in the international Wadden Sea adds up to about 180,000 birds by mid August. Post-breeding moult in the adults starts immediately after arrival. Departure from the Wadden Sea takes place by the end of the moulting period and during winter numbers remain on a lower level, but relatively stable.

Under severe weather conditions the totals often increase in the area. Pre-breeding movements start already by February when Eurasian Curlews enter the Wadden Sea and departure to the breeding grounds takes place during April. Most Fennoscandian and NW-Russian Eurasian Curlews tend to arrive at the breeding grounds by mid April.

Population composition
In the Eurasian Curlew four breeding samples were used according to Engelmoer & Roselaar (1998). These samples were: *arquata* ♂, *arquata* ♀, *orientalis* ♂ and *orientalis* ♀. Wing- and culmen lengths from the W-European and Fennoscandian population were combined in the *arquata*-samples used here. The NAG-optimizations clearly showed the exclusive presence of *arquata* and the absence of *orientalis* in the Wadden Sea (Table 33).

Table 33. Population composition in the Eurasian Curlew populations of the Wadden Sea. Presented are the estimated proportions.

Site	Period	N	arquata ♂	arquata ♀	orientalis ♂	orientalis ♀
Vlieland	July & August	17	no optimal solution			
Vlieland	September	30	no optimal solution			
Vlieland	October	39	1.00	0.00	0.00	0.00
Vlieland	November	21	0.08	0.92	0.00	0.00
Vlieland	December	14	0.00	1.00	0.00	0.00
Vlieland	January	23	0.33	0.67	0.00	0.00
Vlieland	1/2 - 10/3	17	0.40	0.60	0.00	0.00
Vlieland	11/3 - 20/3	19	0.33	0.67	0.00	0.00
Vlieland	21/3 - 31/3	7	no optimal solution			
Vlieland	April & May	12	0.00	1.00	0.00	0.00
Frisian coast	July - September	48	no optimal solution			
Frisian coast	October	69	1.00	0.00	0.00	0.00
Frisian coast	November	10	no optimal solution			
Frisian coast	December - February	13	no optimal solution			
Frisian coast	March - May	18	1.00	0.00	0.00	0.00
Schiermonnikoog	July & August	25	no optimal solution			
Schiermonnikoog	September	64	1.00	0.00	0.00	0.00
Schiermonnikoog	October - November	27	no optimal solution			

Table 34. Male percentages in Eurasian Curlew populations of the Wadden Sea as estimated with POSCON-analysis.

	Vlieland		Frisian coast		Schiermonnikoog	
Month	% ♂♂	N	% ♂♂	N	% ♂♂	N
July/ August	78	9	75	24	56	18
September	72	36	62	21	60	20
October	70	20	33	9		
November	29	21	50	10		
December	43	14			-	-
January	59	22	33	12	-	-
February	49	73			-	-
March	34	53	70	10	-	-
April/ May	42	12			-	-

Spatial variation in the occurrence of different breeding populations. The optimizations show the exclusive presence of males on Vlieland during October, along the Frisian coast during October and March - May and on Schiermonnikoog during September and the exclusive presence of females on Vlieland during December and April - May. Since the outcome of the NAG optimizations was not in line with the visual observations in the area, in a second run POSCON-analysis was performed (Table 34). These results showed a predominance of males on Vlieland and along the Frisian coast immediately after the breeding season. On both sites the male percentages decreased towards November/ December. The male percentages stabilized around 50% on Vlieland during winter and decreased again after February. The male percentages on Schiermonnikoog tended to fluctuate around 50%, but the sample size is small.

9.8 REDSHANK

Introduction

Redshank breed in moist and wet grasslands in different climate zones of the Palearctic ranging from Mediterranean to subalpine and subarctic zones (Map 8). The variability in body dimensions in the species was analysed by Hale (1971 & 1980), Glutz *et al.* (1977), Cramp & Simmons (1983), Summers *et al.* 1988, Stepanyan (1990), Engelmoer & Roselaar (1998) and Ottvall & Gunnarsson (2007). The species shows a fair degree of sexual and spatial variability in body dimensions. In general, males are smaller than females. The species is polytypic and three subspecies are identified in the W-Palearctic: (1) nominate *totanus*, breeding in Fennoscandia, (2) *robusta*, breeding on Iceland, the Faeroes and the Orkneys and (3) *britannica*, breeding at least in the North Sea countries but probably as far east as the Black Sea. Broad intergradation zones occur in between the various subspecies. Sexual dimorphism is smaller in the smaller-sized subspecies. The migratory patterns of the Redshank populations in various parts of the East Atlantic flyway are described by Ogilvie (1963), Hale (1973), Dick (1975), Boere (1976), Tamis (1980), Smit & Wolff (1981), Speek & Speek (1984), Gromadzki (1985), Summers *et al.* (1988b), Wymenga *et al.* (1990), Meltofte (1993), Meltofte *et al.* (1994), Meissner (2000), Wernham *et al.* (2002), Bakken *et al.* (2003), Stroud *et al.* (2004) and Nieboer (2005). The migrations of Redshank in the Wadden Sea concern the movements of three subspecies having different migration schedules:

1. *Local breeding birds* belong to the subspecies *britannica*. They gather in the area from mid June onwards and most adults depart during July to the W-African wintering grounds, followed by the juveniles between mid July and early August. This local population returns in the Wadden Sea during March and April.

2. *Fennoscandian totanus* arrive in large numbers in the Wadden Sea during July - early
   August. Most adults continue their migrations to the W-African wintering grounds by
   early September and juveniles follow during that month. SE-and E-Baltic breeding adults
   winter near the Atlantic Channel and in the Mediterranean, from where they return to the
   Wadden Sea during April. N-Fennoscandian *totanus* leave the wintering grounds from
   March to late May.
3. *Icelandic robusta* arrive by mid July - early August and moult in the Wadden Sea. Almost
   all Redshanks wintering in the Wadden Sea are robusta (also Annex 1 - Table 1). Most
   Redshank leave the Wadden Sea under severe weather circumstances, since it is the most
   vulnerable wader species with respect to extreme winter weather (Clark *et al.* 1993) The
   Icelandic population departs by end April to the breeding grounds. Long-winged Icelan-
   dic *robusta* start to breed earlier than short-winged ones (Summers & Underhill 1991).
   A small part of the N-British breeding population, possibly *robusta*, is staging in the
   Wadden Sea as well.

Population composition

The measurements of Redshanks captured in the Wadden Sea were compared with six
different breeding samples of breeding populations: britannica males, britannica females,
robusta males, *robusta* females, *totanus* males and *totanus* females (Table 10). Spatial and
temporal variation were analysed simultaneously, since the three catching sites showed large
differences in population composition, especially during post-breeding and spring (Table 35
and Fig. 35).

All three subspecies were regularly captured in the Wadden Sea during post-breeding. *T.t.
britannica* and nominate *totanus* occurred most frequently immediately after the breeding
season. These subspecies were gradually replaced by *robusta* towards the end of the post-
breeding period. *Robusta* appeared to be the only subspecies wintering in the Wadden Sea.
Both *britannica* and *totanus* were lacking until March when the return migration started.
Females were evidently more abundant than males on all three locations. The proportional
occurrence of *robusta* decreased from February/ March onwards in favour of both *britannica*
and *totanus*. *T.t. robusta* was completely lacking by May.

T.t. britannica was virtually absent during post-breeding on Schiermonnikoog, while it was
quite abundant on Vlieland and along the Frisian coast. *T.t. robusta* was already present on
both island sites during June and July, opposite to the situation along the Frisian coast.
Nominate *totanus* was captured more often on Vlieland than on both other sites during
August and September. Within this subspecies females occurred more regularly than males
on Vlieland, whilst males *totanus* were more often captured than females along the Frisian

coast during post-breeding. Females *robusta* were more numerous than males *robusta* on all three sites during post-breeding.

The spring population on Vlieland mainly consisted of *britannica*, whilst *totanus* was not present. Both subspecies occurred along the Frisian coast during spring with *totanus* being more numerous than *britannica*. Thus, *totanus* exclusively occurred along the coast and within this subspecies the occurrence of females decreased towards the end of the spring migration period. The *britannica* on Vlieland during spring migration were nearly all males.
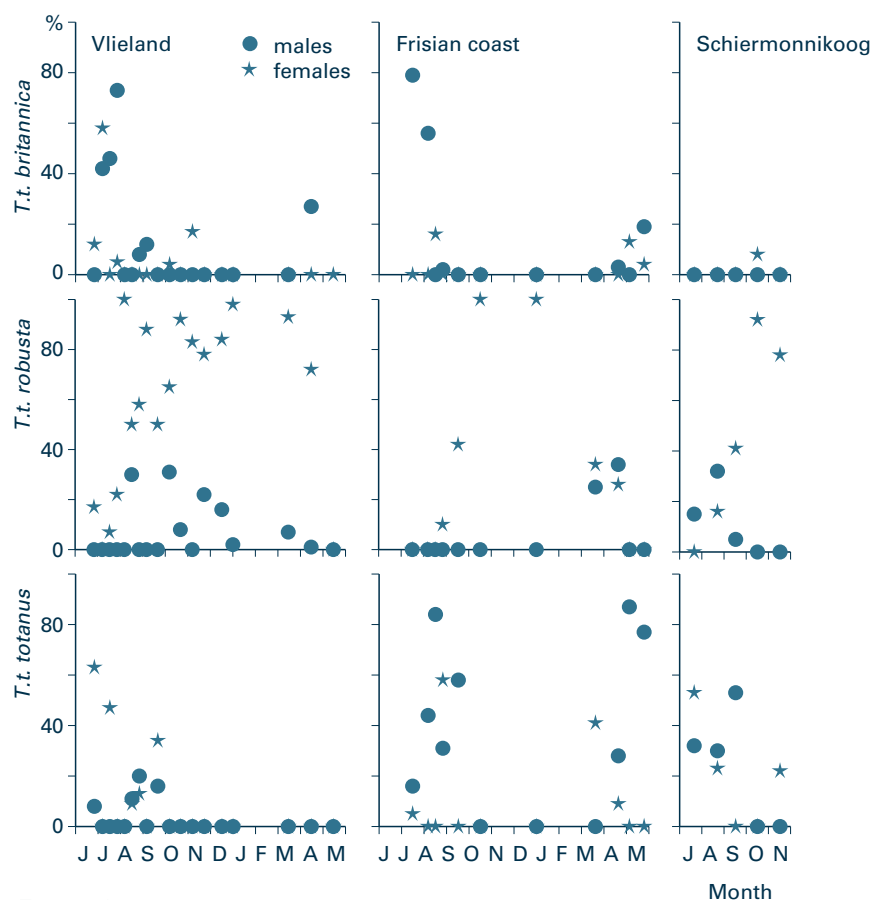
Figure 35:
Population composition of Redshanks on the 3 trapping sites in the Wadden Sea. The estimated occurrence per period of the 6 sample groups (both sexes of britannica, robusta *and* totanus*) results in 100%. The graphs are based upon the estimates presented in Table 36.*

Table 35. Population composition in the Redshank (adults). Presented are the estimated proportions.

Period	N	britannica ♂	britannica ♀	robusta ♂	robusta ♀	totanus ♂	totanus ♀
Vlieland							
21/6 - 30/6	50	0.00	0.12	0.00	0.17	0.08	0.63
1/7 - 10/7	109	0.42	0.58	0.00	0.00	0.00	0.00
11/7 - 20/7	99	0.46	0.00	0.00	0.07	0.00	0.47
21/7 - 31/7	106	0.73	0.05	0.00	0.22	0.00	0.00
1/8 - 10/8	47	0.00	0.00	0.00	1.00	0.00	0.00
11/8 - 20/8	163	0.00	0.00	0.30	0.50	0.11	0.09
21/8 - 31/8	42	0.08	0.00	0.00	0.58	0.20	0.13
1/9 - 10/9	14	0.12	0.00	0.00	0.88	0.00	0.00
10/9 - 30/9	21	0.00	0.00	0.00	0.50	0.16	0.34
1/10 - 10/10	12	0.00	0.04	0.31	0.65	0.00	0.00
11/10 - 31/10	40	0.00	0.00	0.08	0.92	0.00	0.00
1/11 - 10/11	52	0.00	0.17	0.00	0.83	0.00	0.00
11/11 - 30/11	32	0.00	0.00	0.22	0.78	0.00	0.00
1/12 - 31/12	30	0.00	0.00	0.16	0.84	0.00	0.00
1/1 - 28/2	62	0.00	0.00	0.02	0.98	0.00	0.00
1/3 - 31/3	29	0.00	0.00	0.07	0.93	0.00	0.00
1/4 - 30/4	34	0.27	0.00	0.01	0.72	0.00	0.00
1/5 - 31/5	21	1.00	0.00	0.00	0.00	0.00	0.00
Schiermonnikoog							
1/7 - 10/8	27	0.00	0.00	0.15	0.00	0.32	0.53
11/8 - 31/8	50	0.00	0.00	0.32	0.16	0.30	0.23
1/9 - 30/9	28	0.00	0.00	0.05	0.41	0.53	0.00
1/10 - 31/10	29	0.00	0.08	0.00	0.92	0.00	0.00
1/11 - 30/11	90	0.00	0.00	0.00	0.78	0.00	0.22
Frisian coast							
1/7 - 31/7	49	0.79	0.00	0.00	0.00	0.16	0.05
1/8 - 10/8	46	0.56	0.00	0.00	0.00	0.44	0.00
11/8 - 20/8	23	0.00	0.16	0.00	0.00	0.84	0.00
21/8 - 31/8	22	0.02	0.00	0.00	0.10	0.31	0.58
1/9 - 30/9	50	0.00	0.00	0.00	0.42	0.58	0.00
1/10 - 31/10	17	0.00	0.00	0.00	1.00	0.00	0.00
1/11 - 28/2	24	0.00	0.00	0.00	1.00	0.00	0.00
1/3 - 10/4	21	0.00	0.00	0.25	0.34	0.00	0.41
11/4 - 30/4	22	0.03	0.00	0.34	0.26	0.28	0.09
1/5 - 10/5	13	0.00	0.13	0.00	0.00	0.87	0.00
11/5 - 10/6	11	0.19	0.04	0.00	0.00	0.77	0.00

DISCUSSION

10

In the 1960s and 1970s ornithologists were confronted with difficulties associated with the analysis of spatial distribution of wader populations on the basis of ring recoveries. One of these difficulties is that rings are recovered in areas with people but not in the ones without people. Also, most recoveries are in countries with a heavy hunting pressure, giving the wrong impression that countries like France and Spain are more important for waders than the British isles or the Wadden Sea countries. Moreover, recoveries are strongly biassed towards juveniles and first winter birds, since these are easiest to be shot because of their inexperience. To overcome these difficulties ornithologists started to promote the taking of measurements like wing- and culmen lengths during ringing studies, since breeding populations were known to differ from each other with respect to their body dimensions. Many studies followed, in which sample statistics of measurements collected in different areas were compared on a one-dimensional basis. For instance, sample statistics of wing length at site A were compared with those at site B by using Percentage Cumulative Frequency-paper. Later, methods from multivariate linear discriminant analysis were used and the computer was introduced. But the results from these methods had their drawbacks as well, as for instance only a-typical birds were selected. Regularly results were meagre and methods inadequate. The aim was clear but far beyond the reach of what was possible at that time. It was aimed to produce quantitative estimates of the population composition of the migrant wader populations in the Wadden Sea during the non-breeding season. By that time, the work for this thesis was started. We started out to measure as many variables as possible, from as many as possible skins of breeding waders in museum collections, from as many as possible breeding populations around the world, and to analyse the resulting data-set with methods from multivariate statistics. This resulted in the compendium of Engelmoer & Roselaar (1998). After completing this task, the Wadden Sea database with 32,446 captured waders had to be analysed using an update of the breeding wader database.
The main results can be found in the preceding chapters, especially Chapter 9.
The reliability of the population composition is critically examined in the sections 10.1 and 10.2. Interpretations are made in the later sections. The aim formulated has been reached in the sense that estimates have been produced. It has not been reached and, possibly, will never be reached in the sense that the statistical uncertainties in these estimates are not expressed, but assessed to be large.

10.1 THE APPROPRIATENESS OF THE METHODOLOGY USED

Restricting ourselves to the methodological basis of Chapter 9, we note that the first method used to estimate breeding-origin proportions (POSCON, based on p-values and successive manipulations) is too indirect to be satisfactory. The second method -NAG-optimization- is more satisfactory since it concentrates the attention on estimating population composition. Nevertheless, there are still some drawbacks:

1. The attention is focussed on the estimation of proportions in a hypothetical population: the birds actually captured and measured can be regarded as a sample from this population. The estimated relative frequencies $\alpha_1,...,\alpha_k$ refer to this hypothetical population and are not equivalent to the relative frequencies in the group captured, measured, and used as the basis of the analysis.

2. The statistical uncertainties in the estimates $\alpha_1,...,\alpha_k$ of $\alpha_1,...,\alpha_k$, obtainable from the inverse of the Hessian, are not trustworthy because (1) the statistical uncertainties in Table 10 would be ignored, (2) they are based on simplifying assumptions (e.g. equality of covariance matrices), and (3) there is a personal component involved: measurements of wing- and culmen length depend upon the person taking the measurements (errors being in the order of 1 resp 2% - section 3.2).

3. The uncertainty about these uncertainties had the effect that the attention in Chapter 9 had to be restricted to qualitative interpretations of the estimates of the proportions. With the NAG-optimisations, actually used, estimates of the proportions could be produced with which drawback (1) is partly avoided, but not the others.

10.2 RELIABILITY OF THE POPULATION COMPOSITION ESTIMATES

In Chapter 9, quantitative estimates of the population composition of migrant wader populations in the Wadden Sea were presented. Little attention was given to the reliability of these estimates. The reason for this lack of attention was argued in Section 4.3 under step 4 - remark 2. The individual estimates of the proportions are considerably unreliable, but when they are considered as a whole, a 'concerted' is obtained, which we consider to be fairly reliable. An analogy with the large-scale counting activities of birds is instructive. A single flock of birds is regularly estimated 50% off the real number. Nevertheless, Rappoldt *et al.* (1985) showed, that -apart of a systematic underestimation- the estimated total number of Oystercatchers in the Wadden Sea was within limits of 5% due to the large number of

groups counted. They argued that many other biological estimates like prey density, food intake, or available foraging area are generally not more accurate. The population composition estimates presented in this thesis have a similar epistemological status.

We partly caused the trouble ourselves, because we wanted to distinguish at the subspecies' level using the 75 % rule in taxonomy, stating that 75% of the individuals in a population should be distinguishable from any individual from other geographical areas (Amadon 1949). This results in about 10 % overlap of the distinguishing characteristics between the subspecies recognized in the best situation: when birds are sexed and in summer plumage. But it is a totally different situation when the breeding origins of non-breeding birds in winter plumage, which are not sexed, have to be predicted. Especially when only wing- and culmen lengths are available while the distinction between the subspecies is only partly based upon these characters and often includes other characters. If there is no overlap in measurements between two groups, both can easily be distinguished at the species-level and we would not need statistics to recognize both species. This displays a discrepancy between the need for statistics and taxonomical distinction and between distinction and prediction. On the other hand, when differences are small and overlap is large, then statistics cannot provide us with certainties. This shows that much depends on the separatory quality of the characteristics used. Ornithologists working on the breeding grounds and taxonomists have the possibility to distinguish subspecies on the basis of breeding plumage characteristics, which is not possible during winter. Taxidermists have the comforting knowledge of a bird's sex, according to the pre- or absence of gonads. But a ringer in the Wadden Sea is nearly never sure about the sex of a captured bird. This person has to cope with the presence of several subspecies, many having overlap in measurements, providing population composition estimates with low reliabilities. In physical anthropology experiences with skull measurements are similar: the sexual dimorphism is of the same order of magnitude as the difference between sub-populations of the same sex, resulting in overlap in the order of 75% (Van Vark & Howells 1984, Saunders & Katzenberg 1992).

Even though from a mathematical statistical point of view the statistical uncertainties of the point estimates were considered to be considerable (possibly standard errors in order of 10%), most of these estimates were fortunately in line with ornithological opinions at large. This was the case in most estimates of Grey Plover, Red Knot, Dunlin, Bar-tailed Godwit, and Redshank, but not with the ones of Ringed Plover, Curlew Sandpiper, and Eurasian Curlew. Hence the estimates gave us some improved understanding but they also gave us some 'strange' outcomes. The two major surprises were the possibility of moulting Taymyr Red Knot *canutus* in the Wadden Sea and the long staging period of Taymyr Bar-tailed Godwit *taymyrensis*.

Table 36. Testing the results of POSCON predictions on Redshanks and Knots originating from known subspecies, since they were captured or controlled on their breeding grounds.

Subspecies	Predicted as		
Ringed Plover	*psammodromma*	*hiaticula*	*tundrae*
psammodroma	-	-	-
hiaticula	-	-	-
tundrae	1	-	-
Red Knot	*canutus*	*islandica*	
canutus	-	-	
islandica	1	5	
Dunlin	*schinzii/arctica*	*alpina*	*centralis*
schinzii/arctica	1	-	-
alpina	-	2	-
centralis	-	1	-
Bar-tailed Godwit	*lapponica*	*taymyrensis*	*menzbieri*
lapponica	-	-	-
taymyrensis	-	3	-
menzbieri	-	-	-
Redshank	*britannica*	*robusta*	*totanus*
britannica	8	-	4
robusta	-	5	1
totanus	1	-	1

A positive experience was that when we used POSCON analysis most of the waders with known breeding origins were assigned to the right breeding sample (Table 36). In total 25 out of 34 birds (73.5%) were assigned to the right subspecies. The distinction between *britannica* and nominate *totanus* in the Redshank appears to be more difficult than that between both these and *robusta* (95% correct), which is logical since robusta is the most distinctive of the three subspecies. In the Red Knot, five out of six (83%) Icelandic migrants were allocated as *islandica*. Some additional support is provided by the fact that 21 out of 26 migrant and wintering Red Knots (81%) visiting both Great Britain and the Wadden Sea were assigned to *islandica*.

To conclude, it will not be possible to assign a single individual caught in the Wadden Sea with complete certainty to a breeding population, if only wing- and culmen lengths available. It is also difficult if a group of individuals in the Wadden Sea has to be compared with breeding populations having considerable overlap in characteristics and thus cannot be distinguished at the subspecies level. The results improve when breeding populations can be distinguished as subspecies on the basis of wing- and culmen lengths. Difficult statistical

procedures can be avoided if almost no overlap exists, i.e. if differences are large enough for distinction at the species level. To improve the situation, the degree of overlap should be reduced. Some ideas are as follows:

When birds can systematically be sexed the amount of overlap can strongly be reduced in the majority of the species studied. Reduction in overlap can, in principle, also be reached by taking better diagnostic measurements. Engelmoer & Roselaar (1998) presented for 14 wader species a priority list of measurements to be collected. The measuring of wing- and culmen lengths might only be an option for Eurasian Curlew, since in all other distinctions additional measurements are needed for the reduction of overlap (Table 126 in Engelmoer & Roselaar 1998).

Several plumage characters are available for birds in breeding plumage, but also the adult-buff coverts in the winter plumage of Siberian Dunlin provide an indication of their breeding origin. When plumage characters are collected, close attention should be given to the type of data: categorical or at the interval level. It makes a large difference in the sample sizes needed. In the search for variables, there is a preference for the latter type of measurements, especially when they have a normal distribution and under circumstances that statistical analyses have to produce sophisticated inferences.

Finally, population composition estimates, such as the ones presented here, are point estimates based on all birds caught at a given catching site and during a given time-period, even though such a sample itself is a composition of sub-samples. It might be better to consider the composition estimates of these latter samples as separate point estimates before grouping them in one overall sample with only one composition estimate and little information on the variability. Analysis of sets of samples (per trapping night/day or a short series of nights/days and/or catching site) might be better. The statistical uncertainties can be reduced if one assumes that for these sub-samples all birds have the same breeding origin.

10.3 AREAS OF ORIGIN: AN OVERVIEW

The composition estimates of the Wadden Sea populations help us in increasing our understanding of the function of the Wadden Sea in international perspective. Here, this function is discussed with the following questions in mind: (1) what breeding populations were found to occur?, (2) when are these breeding populations present?, and (3) what proportion of a breeding population frequents the Wadden Sea? These findings will form the basis for a judgement of the functional role of the Wadden Sea for the populations we have been able to trace.

Table 37. Population composition estimates in six wader species present in the Wadden Sea during resp.
July/ August, September/ October, November - February, March/ April and May. These six species have in
common, that more than one subspecies or breeding population per species occur in the area. The per-
centages are mean values derived from the tables of composition estimates in the species chapters. The
estimated population composition estimates in the Bar-tailed Godwit are split per sex and the estimates
for each sex total 100 percent. The male percentages in this species are presented as well. The estimated
juvenile percentages are derived from the trapping results. The mean staging numbers are derived from
the results of the large-scale counting activities until November 1998 (Zegers 1985, Zegers & Kwint 1992,
Meltofte et al. 1994, Koffijberg et al. 1999, De Boer et al. 2001). A figure between brackets indicates the
uncertain character of the estimate. A '?' is placed when no estimate was available.

Species	July/ August	September/ October	November - February	March/ April	May
Ringed Plover					
psammodroma	(45.0)	-	?	-	-
hiaticula	(10.0)	(5.0)	?	(100.0)	(10.0)
tundrae	(45.0)	(95.0)	?	-	(90.0)
N Wadden Sea	1862	1812	48	544	1208
% juveniles/ first winter	41.8	80.4	-	?	0.0
Grey Plover - nominate subspecies					
West of Yamal	67.0	81.0	84.0	100.0	59.0
Yamal & Taymyr	31.0	15.5	3.0	0.0	21.0
East of Taymyr	2.0	3.5	12.5	0.0	19.5
N Wadden Sea	11215	21618	7898	7136	28109
% juveniles/ first winter	2.3	41.5	39.6	17.1	9.4
Red Knot					
islandica	24.0	69.0	97.0	87.0	20.0?
canutus	76.0	31.0	3.0	13.0	80.0?
N Wadden Sea	33084	67895	54501	38547	9881
% juveniles/ first winter	25.3	48.1	22.5	64.9	?
Dunlin					
arctica	5.0	1.4	0.0	0.0	0.0
schinzii	4.0	1.0	0.0	0.0	0.0
alpina	91.0	97.6	100.0	100.0	100.0
N Wadden Sea	117941	241779	88331	171614	178132
% juveniles/ first winter	9.7	32.6	41.3	34.5	29.8
Bar-tailed Godwit					
♂♂ - lapponica	3.0	39.8	79.0	55.3	0.0
♂♂ - taymyrensis	95.0	59.7	21.0	37.2	98.0
♂♂ - East of Taymyr	2.0	0.5	0.0	7.5	2.0
♀♀ - lapponica	36.7	47.3	82.7	80.5	10.0

♀♀ - *taymyrensis*	53.6	48.4	13.0	13.0	88.0
♀♀ - East of Taymyr	9.7	4.3	4.3	6.5	2.0
N Wadden Sea	38975	34810	18823	32550	93379
% juveniles/ first winter	2.0	26.6	5.5	1.5	3.9
% males	61.2	59.0	64.3	54.0	62.1
Redshank					
totanus	42.0	20.1	3.7	19.5	54.7
britannica	30.3	3.0	2.8	7.5	45.3
robusta	27.7	76.9	93.5	73.0	0.0
N Wadden Sea	22494	16335	7462	11046	7376
% juveniles/ first winter	30.4	39.6	26.0	13.5	11.3

The non-breeding season was subdivided in late summer (July/ August), autumn (September/ October), winter (November - February), early spring (March/ April), and late spring (May). All estimates of population composition were averaged per species over these five periods under the assumption that the whole set of samples from various catching sites represent the Wadden Sea population as a whole. The resulting estimates of the six species, present with more than one breeding population, are presented in Table 37. Curlew Sandpiper, Spotted Redshank and Greenshank were not included, since they are regarded as monomorphic (Table 10). Too few Sanderling-data were collected to allow an all-season analysis. All Eurasian Curlew samples showed the exclusive occurrence of nominate *arquata* and likewise all Ruddy Turnstone samples concerned the subspecies *interpres*.

Most Grey Plovers in the Wadden Sea apparently belong to the westernmost N-European breeding population. This breeding population increased in numbers over the last thirty years (Hagemeijer & Blair 1997). The wintering numbers in W-Europe increased as well (e.g. Meltofte *et al.* 1994, Pollitt *et al.* 2003, Van Roomen *et al.* 2004, this study), but then also other than N-European breeding birds might be involved. Grey Plovers from Yamal and Taimyr particularly seem to occur during July/August and May in the Wadden Sea. The estimates from the Wadden Sea persistently show the occurrence of a small proportion of Grey Plovers originating from the east of Taimyr.

The majority of Red Knots in the Wadden Sea concerns the Nearctic subspecies *islandica*, particularly during winter. Siberian *canutus* is most numerous during July/ August and May, but this subspecies is present as well during September/ October. Also, a S-African wintering bird was controlled with moulting primaries in the Wadden Sea during October (Annex 1 - Table 3). This finding deviates from the general picture, in which nominate *canutus* is not expected to be present in the Wadden Sea during the period of primary moult (e.g. Davidson

Table 38. Comparing the population composition of Red Knots wintering in the Wadden Sea, on the Banc d'Arguin, and in the Arquipelago dos Bijagos. Presented are the estimated proportions.

Period	N	piersmai ♂	islandica ♂	islandica ♀	canutus ♂	canutus ♀	roselaari ♀
Wadden Sea - Netherlands							
11/10 - 30/11	29	0.00	0.59	0.30	0.00	0.11	0.00
1/12 - 31/12	168	0.00	0.23	0.73	0.03	0.00	0.01
1/1 - 10/1	90	0.00	0.10	0.86	0.00	0.00	0.04
11/1 - 20/1	134	0.00	0.18	0.82	0.00	0.00	0.00
21/1 - 20/2	27	0.00	0.21	0.77	0.00	0.00	0.02
20/2 - 10/4	14	0.00	0.43	0.44	0.00	0.13	0.00
Banc d'Arguin - Mauritania							
1/1 - 31/3	37	0.00	0.07	0.00	0.93	0.00	0.00
1/4 - 10/4	81	0.00	0.00	0.00	0.91	0.00	0.09
11/4 - 20/4	122	0.00	0.00	0.00	0.42	0.58	0.00
21/4 - 30/4	44	0.00	0.00	0.00	0.31	0.69	0.00
all	284	0.00	0.00	0.00	0.41	0.56	0.02
Arquipelago dos Bijagos - Guinea Bissau							
11/12 - 20/12	95	0.00	0.03	0.00	0.91	0.00	0.04
21/12 - 10/1	105	0.01	0.00	0.00	0.96	0.00	0.03
1/2 - 10/2	67	0.00	0.03	0.00	0.93	0.00	0.04
all	267	0.02	0.02	0.00	0.90	0.00	0.06

& Wilson 1992, Piersma *et al.* 1992, Piersma *et al.* 1993, Piersma 1994, Boyd & Piersma 2001a & b and Nebel *et al.* 2000), since it is presumed to moult in the W-African wintering areas. No other populations than nominate *canutus* and *islandica* were found to occur in the Wadden Sea. An analysis of the catching data of the respective WIWO-expeditions (Ens *et al.* 1988 & 1990a, Wymenga *et al.* 1990, Altenburg *et al.* 1992) in Mauritania and Guinea-Bissau with the NAG-optimization technique showed the sole presence of nominate *canutus* in W-Africa with a predominance of males (Table 38). Male percentages decreased from 10 April onwards, suggesting an earlier spring-departure of males to W-Europe. However, our results (e.g. Table 37) suggest that *canutus* males stage in important proportions in the Wadden Sea with an average predicted presence of 23% *canutus* males among the adults during September and October. Only 2.7% of the adults (*N*= 381) is not moulting its primaries by this time, which implies that many moulting *canutus* must be amongst them. Also, the only two published post-breeding recoveries of adult males belonging to the Taimyr breeding population were collected in W-Europe with one in the Danish Wadden Sea on 26 September 1991 and the other along the coast near Calais in France on 12 September 1993 (Tomkovich & Soloviev 1996). Both these recoveries were not presented in Annex 1, since there was no

direct link with the Netherlands. Finally, Whitfield *et al.* (1996) presented evidence that the estimated wintering population in W-Europe was too large to be explained by *islandica* alone. They argued that 172,000 wintering Red Knots in W-Europe were not *islandica*. These 'extra' wintering birds might be *canutus*. The late occurrence of moulting *canutus* males in the Wadden Sea is probably restricted to the eastern and southern parts. The western part of the Wadden Sea might then be exceptional with a relatively low occurrence of *canutus*.

Dunlins in the Wadden Sea are nearly all *alpina* or *centralis*. *Arctica* and *schinzii* only occur during post-breeding. Their proportional presence decreases from July/ August towards September/ October. *Arctica* seems to occur somewhat more regularly than *schinzii*. Relatively many Bar-tailed Godwits originate from Taimyr immediately after the breeding season and particularly amongst the males. Their relative occurrence decreases during September/ October in favour of the N-European *lapponica*. About 80% of the winter population of the Bar-tailed Godwits in the Wadden Sea are *lapponica* and about 20% *taymyrensis*. In the males, *taymyrensis* was estimated to be strongly dominating during July/August and during May. This is less so amongst the females. Piersma & Jukema (1990) and Drent & Piersma (1990) considered the leap-frog system as a good model to describe the migration system of the Bar-tailed Godwit in the sense that breeding further to the north-east is associated with wintering further to the south. I do not fully agree, because taymyrensis also seems to be present in the Wadden Sea during winter, which makes the system a partial leap-frog system. With respect to the W-African wintering populations, the outcome of the NAG-optimizations is in agreement with the description of the migration system as presented by Piersma & Jukema (1990) and Drent & Piersma (1990), since these populations were nearly always completely classified as *taymyrensis* (Table 39). Also, *taymyrensis* was estimated to predominate strongly amongst the Wadden Sea birds during July - August and May, particularly in the male segment of the population.

Three subspecies of Redshank occur in the Wadden Sea: Fennoscandian breeding *totanus*, W-European *britannica* and Icelandic *robusta*. Both *totanus* and *britannica* mainly occur during post-breeding and spring, whilst the winter flocks are dominated by *robusta*. *Britannica* also includes the local breeding birds, which gather in the Wadden Sea immediately after the breeding season and depart during July/ August to the wintering grounds. The return of the local breeding population takes place during March/April. By mid April *robusta* leaves the Wadden Sea. Half of the birds in the May-flocks concern N-European *totanus* on their way to the breeding grounds.

Since the proportional occurrence, the number of staging birds in the area and the population sizes of the breeding populations (Stroud *et al.* 2004) are approximately known, it is possible

Table 39. Comparing the population composition of Bar-tailed Godwits wintering in the Wadden Sea, on the Banc d'Arguin (Mauritania) and in the Arquipelago dos Bijagos (Guinea-Bissau). Presented are the estimated proportions.

Area	Period	N	N-Fennoscandia	Yamal & Taymyr	Central Siberia	E-Siberia	Alaska
♂♂							
Wadden Sea	1/11 - 30/11	74	1.00	0.00	0.00	0.00	0.00
Wadden Sea	1/12 - 28/2	30	0.58	0.42	0.00	0.00	0.00
Wadden Sea	1/3 - 10/3	24	0.38	0.57	0.00	0.00	0.05
Wadden Sea	11/3 - 20/3	25	0.94	0.00	0.00	0.00	0.06
Wadden Sea	21/3 - 31/3	67	0.89	0.09	0.00	0.02	0.00
Mauritania	< 10 April	29	0.00	0.98	0.02	0.00	0.00
Mauritania	> 10 April	35	0.00	0.99	0.00	0.01	0.00
Mauritania	whole period	64	0.00	0.97	0.03	0.00	0.00
Guinea Bissau	December	40	0.00	0.99	0.01	0.00	0.00
Guinea Bissau	January	40	0.00	1.00	0.00	0.00	0.00
Guinea Bissau	whole period	80	0.00	1.00	0.00	0.00	0.00
♀♀							
Wadden Sea	11/10 - 20/11	35	0.76	0.23	0.00	0.00	0.00
Wadden Sea	21/11 - 20/2	26	0.72	0.16	0.12	0.00	0.00
Wadden Sea	21/2 - 10/3	22	1.00	0.00	0.00	0.00	0.00
Wadden Sea	11/3 - 20/3	31	0.74	0.00	0.00	0.24	0.02
Wadden Sea	21/3 - 31/3	40	1.00	0.00	0.00	0.00	0.00
Mauritania	< 10 April	11	0.00	1.00	0.00	0.00	0.00
Mauritania	> 10 April	12	0.00	1.00	0.00	0.00	0.00
Mauritania	whole period	23	0.00	1.00	0.00	0.00	0.00
Guinea Bissau	December	25	0.80	0.20	0.00	0.00	0.00
Guinea Bissau	January	22	0.00	1.00	0.00	0.00	0.00
Guinea Bissau	whole period	47	0.00	1.00	0.00	0.00	0.00

to estimate the frequencies and proportions of the breeding populations frequenting the Wadden Sea (Table 40 & Fig. 36). The lack of information concerning the breeding origin of first winter birds in the Wadden Sea forced us to focus on the estimates of the adult part of the populations.

At any one moment, more than 10% of the total population size of the following species or breeding populations are estimated to occur in the Wadden Sea: Red Knot subsp. *islandica*, Dunlin subsp. *arctica*, Dunlin subsp. *alpina*, Bar-tailed Godwit nominate *lapponica*, Bar-tailed Godwit subsp. *taymyrensis*, Eurasian Curlew subsp. *arquata*, and Redshank subsp. *robusta*. Percentages between 1 and 10% are found in: Grey Plover, Red Knot nominate *canutus*,

Table 40. Estimated number of waders per subspecies or breeding population in the Wadden Sea. Numbers are rounded per hundred. Population size estimates after Stroud et al. *(2004). A figure between brackets indicates the uncertain character of the estimate.*

Species	Subspecies/ breeding population	July/ August	September October	November February	March/ April	May size	Population Max.	%
			Estimated numbers present in the Wadden Sea					
Ringed Plover	*psammodroma*	(800)	-	-	-	-	190000	0.4
	hiaticula	(200)	(100)	-	(500)	(100)	73000	0.7
	tundrae	(800)	(1700)	-	-	(1100)	200000	0.9
Grey Plover	West of Yamal	7500	17500	6600	7100	16600	247000	9.1
	Yamal & Taymyr	3500	3400	200	-	5900		
	East of Taymyr	200	800	1000	-	5500	90000	6.1
Red Knot	*islandica*	7900	46800	52900	33500	2000	339000	13.8
	canutus	25100	21000	1600	5000	8000	450000	5.6
Curlew Sandpiper	whole population	700	400	-	-	-	740000	0.1
Dunlin	*arctica*	5900	3400	-	-	-	20000-45000	13 - 30
	schinzii	4700	2400	-	-	-	975000-1000000[a]	0.5[d]
	alpina	107300	236000	88300	171600	178000	1331000-1334000	17.7
Bar-tailed Godwit	*lapponica*	6300	14900	15100	21800	3500	120000	18.4
	taymyrensis	30800	19200	3400	8500	88000	520000	16.9
	East of Taymyr	1900	700	300	2300	1900	100000-1000000	0.2-2.3
Eurasian Curlew	*arquata*	66600	94000	69700	48600	6200	420000	22.4
Spotted Redshank	whole population	2100	1700	-	200	2300	69000 -138000	1.7-3.3
Redshank	*totanus*	9400	3300	300	2200	4000	222500	4.2
	britannica	6800	500	200	800	3300	110000	6.2
	robusta	6200	12600	7000	8100	-	64500	19.5
Greenshank	whole population	4500	1800	-	200	1100	200000 -500000	0.9-2.3
Ruddy Turnstone	*interpres*	2500	2100	1700	1400	2500	95000[b]	2.2
							49000-107000[c]	2.3-5.1

Notes:
a Baltic breeding population 6.000, British breeding population 30.000 and Icelandic breeding population 939.000 - 964.000 individuals;
b Nearctic breeding population;
c W-African wintering population;
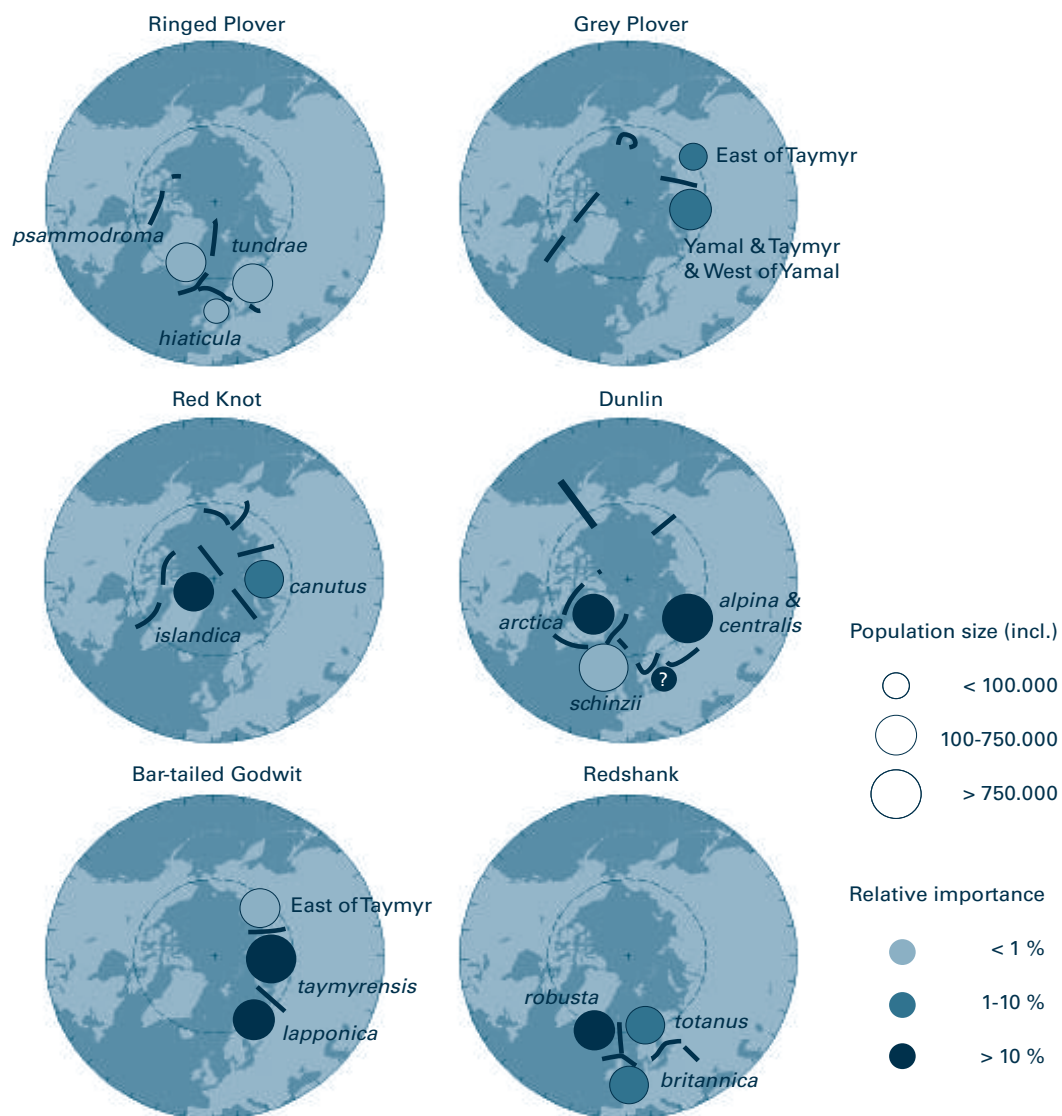d The Wadden Sea might be important for the Baltic population.

Figure 36: Summarizing the proportional significance of the (Dutch part of the) Wadden Sea during the non-breeding season for the breeding populations of six wader species. The percentages are calculated and presented in Table 37. These percentages are minimum estimates since they are only based on the maximum averages being present at one moment in the area without paying attention to the turnover rates.

Bar-tailed Godwit populations breeding east of Taimyr, Spotted Redshank, Redshank nominate *totanus*, Redshank subsp. *britannica*, Greenshank, Ruddy Turnstone Nearctic breeding population, Ruddy Turnstone African wintering population. The obtained percentages concern only the Dutch part of the Wadden Sea and they strongly support the existing knowledge that the Wadden Sea is of utmost importance for most of these populations.

It is unclear whether exclusively Baltic or also some Icelandic breeding Dunlins stage in the Wadden Sea. Even though the Icelandic breeding population is estimated at 270,000 pairs (Thorup 2006) and many recoveries link the Icelandic breeding grounds with the British isles, no recoveries of Icelandic breeding birds were obtained in the Dutch Wadden Sea. But even if only a small proportion of the Icelandic breeding population frequents the Wadden Sea, they might easily outnumber the Baltic population. Baltic breeders are known to follow the W-European coastline on their way to the SW-European wintering grounds (Jönsson 1986). If the Baltic *schinzii* population is the only one involved, nearly 95% of this population can then be staging in the Wadden Sea. However, if only Icelandic *schinzii* stage in the Wadden Sea no more than 0.6% of the breeding population would be involved.

10.4 TURNOVER OF SOUTHWARD BOUND MIGRANTS

In the preceding chapter, the estimates of the proportional occurrence of the different breeding populations frequenting the Wadden Sea excluded the rates of turnover. These estimates can thus only be regarded as the minimal estimates of the real percentages frequenting the Wadden Sea. They represent the situation, that all individuals of a species arrive and depart simultaneously. Such never occurs in the reality of the Wadden Sea. Many waders only stay for a few weeks in the Wadden Sea after the breeding season. They arrive in a large number of flocks from half June through October: it might well concern thousands of flocks, since the flock sizes of migrating waders mostly range between 5 and 100 birds and are nearly never larger than 200 birds (Piersma *et al.* 1990). Many birds only stay as long as needed to build up body reserves in order to continue their migrations to the W-African wintering grounds. Departure from the Wadden Sea is ranging between the end of June towards November (Fig. 26). The rate of turnover can thus be large. It is possible to estimate the proportions of the W-African wintering populations frequenting the Wadden Sea following the approach of Zwarts *et al.* (1990) by estimating the daily proportions of birds ready-to-go amongst the Wadden Sea birds. This was done by calculating the potential

Table 41. Estimated number of long-distance departures from the Wadden Sea during post-breeding compared with the wintering numbers along the Atlantic coast of Africa from Mauritania southwards. Estimated African wintering populations from Stroud et al. *(2004). Percentages can slightly differ from the absolute numbers due to presentation of round numbers. The delineation of the African wintering grounds was based upon the information obtained from our ring recoveries and from Wymenga* et al. *(1990) and Underhill* et al. *(1999).*

Species	wintering numbers Africa	Estimated *N* of departures from Wadden Sea	
		N	%
Ringed Plover[1]	185000	36900	20
Grey Plover[2]	106000	185600	100
Red Knot[1]	330000	445700	100
Curlew Sandpiper[2]	759000	11100	1
Dunlin[2]	951000	24800	2
Bar-tailed Godwit[2]	505000	283300	56
Redshank[2]	196000	179100	91
Ruddy Turnstone[1]	51000	3700	7

Notes:
1 estimates include the Atlantic coast between Mauritania and S-Africa;
2 estimates include the Atlantic coast between Mauritania and Gabon.

maximum flight ranges of the waders involved according to firstly Castro & Myers (1989) and additionally Davidson (1984). Details are given in Chapter 8.3.

Birds with potential flight ranges of 4,000 km or more were considered as the ones ready-to-go in order to reach the African wintering grounds. Estimates of the daily proportions departing per 10-day period during post-breeding were obtained. With these figures the number of long-distance migrants departing from the Wadden Sea can be estimated, when the average staging numbers in the Wadden Sea per 10-day period are known. These numbers were calculated according to Zegers (1985), Zegers & Kwint (1992), Meltofte *et al.* (1994), Koffijberg *et al.* (1999), and De Boer *et al.* (2001). If still information was lacking, the database with local wader counts was used. The numbers of long-distance migrants departing from the Wadden Sea were related to the winter population sizes in W-and NW-Africa (Table 41). This gives insight in the importance of the Wadden Sea for the W-African wintering populations.

The outcome of these calculations gives a quantitative description of the extent of passage through the Wadden Sea. Nearly all birds of the W-African wintering populations of Grey Plover, Red Knot, and Redshank seem to pass through the area. More than half of the W-African wintering population of Bar-tailed Godwit stages in the Wadden Sea prior to their departure to the wintering grounds. Relatively low estimates were obtained for the staging populations of Ringed Plover, Curlew Sandpiper, Dunlin, and Ruddy Turnstone. These findings are generally in line with current knowledge on migration patterns of waders in the E-Atlantic Flyway, since many Ringed Plovers, Dunlins, and Ruddy Turnstones wintering in W-Africa have a Nearctic breeding origin and mainly frequent the British estuaries when in W-Europe during migration (Pienkowski & Dick 1975, Branson *et al.* 1978, Taylor 1980, Ferns 1980, 1981b, 1981c, Wilson 1981, Summers *et al.* 1989, Wymenga *et al.* 1990, Gudmundsson *et al.* 1991). Curlew Sandpipers wintering in W-Africa mostly follow the E-Mediterranean route into Africa (Elliott *et al.* 1976, Wilson *et al.* 1980). The calculations performed do not provide more than a rough approach and might be approved, if (1) the arrival masses of W-African waders in relation to their structural masses were known, (2) the proportions ready-to-go could be estimated per day (instead of using the averages per 10-day period, and (3) the potential flight ranges could be estimated more accurately.

10.5 THE MAINLAND 'HIGHWAY' AND ISLAND 'MOULT RESORTS'

We showed in the results sections, that waders use the various areas in the Wadden Sea differently. There appears to be a coastal 'highway' in contrast to island 'moult resorts' which differ in respect of moult characteristics, staging time, and mass differences. For instance, most waders moult on Vlieland and Schiermonnik-oog during post-breeding, while this is less common along the coast, where more birds prepare for departure. The mainland coast can best be characterized as a 'highway' for Ringed Plover, Grey Plover, Red Knot, Curlew Sandpiper, Dunlin, Bar-tailed Godwit, Redshank, Spotted Redshank, Greenshank, and Ruddy Turnstone with many birds re-fuelling and fewer moulting or moulting less intensely or even delaying moult. It is the highway to the W-African wintering quarters where the post-nuptial moult will be started. Thus, relatively many birds are increasing body mass and are still in full summer plumage during post-breeding. Birds starting primary moult regularly have small gaps in the wing by shedding only few primaries simultaneously. Even birds with moulting primaries appeared to accumulate energy reserves (e.g. Grey Plover).

In contrast, island birds stayed for relatively long periods in order to moult. This is more evident on Vlieland than on Schiermonnikoog. For instance, Schiermonnikoog is both a 'highway' and a 'holiday resort' for Grey Plovers. It has in common with the Frisian coast that relatively many non-moulting, heavy, birds were captured, and that Grey Plovers combined primary moult and mass accumulation during August. On the other hand, Grey Plovers on Schiermonnikoog often had just as large gaps in the wing as the Vlieland birds and relatively many seemed to complete or suspend the process of primary moult.

The causation of such a pattern of spatial variation with respect to primary moult is intriguing. Why are more primaries simultaneously shed on the island sites? Why do the island birds have large gaps and the coastal birds small ones? Do the birds choose the appropriate sites according to their moulting pattern? This study cannot answer these questions, but some hypotheses are as follows:

Breeding origin

Spatial variation might be associated with habitat preferences of distinct geographical populations. For example, Prokosch (1988) stated that the Nearctic population of Red Knots occurs on the sandflats in the Wadden Sea and the Siberian population along the muddy mainland coasts. Also, Scheiffarth (2003) distinguished in the Bar-tailed Godwit the Afro-Siberian population using roosts on the mainland coast and the European population mainly using the island sites for three months during spring. It is then the breeding origin causing the spatial variation of moulters and non-moulters in the Wadden Sea.

Protein requirements

Moulting birds need especially sulfur amino acids in order to replace feathers lost on previous days (Dolnik & Gavrilov 1979, Murphy & King 1984 & 1992). Birds with ample sulphur amino acids enter moult more quickly and moult faster (Wolf *et al.* 2003). Assuming such a difference with respect to the availability of sulphur amino acids is also valid for moulting waders, diet differences between the coastal mudflats and sandflats of the barrier islands can be experimentally tested.

Predation

The habitat differences might be induced by a predation-minimization strategy. Moulting birds with large gaps in the wings and thus reduced flight capacity (manoeuverability, acceleration, flight speed, rate of climb) as well as reduced body masses might experience a lower risk of predation on the island sites. A set of studies was performed on the influence of variations in predation pressure on the spatial distribution of waders (Cresswell & Whitfield

1994, Lissimore *et al.* 1999, Ydenberg *et al.* 2002, Lank & Ydenberg 2003, Lank *et al.* 2003, Dierschke 2003, Whitfield 2003, Ydenberg *et al.* 2004, Nebel & Ydenberg 2005). Ydenberg *et al.* (2002) and Lank *et al.* (2003) stated, that birds with less than maximal flight performance will benefit from using large open sites such as extensive mudflats, providing safety for feeding and roosting, since waders will be less surprised by attacks. Dekker & Ydenberg (2004) showed that Peregrines hunting over the tide zone had a four times higher success rate than when foraging over tidal flats or water.

Pre-migratory restlessness might play a role with the ready-to-go birds flocking together as far southwest in the Wadden Sea area as possible. There might be a parallel with the situation we encountered in some wader species (Avocet, Greenshank, and Oystercatcher) re-assembling in the Mauritanian Baie d'Aouatif during spring migration (Blomert *et al.* 1990). The Baie d'Aouatif appeared to function as a meeting point for Avocets, where they stayed a few hours, and regrouped before they took off on their way northwards. It might result in relatively many non-moulting and heavy birds along the Frisian coast.

What is in this situation cause or effect? There is agreement on the observed pattern, but is a rapidly migrating Bar-tailed Godwit staging along the mainland coast, because it has a Siberian breeding origin? Or is it, because it is functional for fat accumulation? The first explanation suggests a genetic basis and the second a functional one. Here the functional explanation ('highway' versus 'holiday resort') is preferred above the 'genetic' (geographical breeding origin) one and thus differences in breeding origin are effect rather than cause. Future analyses might concentrate on the site choice of individuals from a single geo-graphical breeding population with different migration and moulting strategies. Such might be possible with the Taymyr-populations of Bar-tailed Godwit and Red Knot, since not the whole population migrates rapidly to the W-African wintering quarters, part of them performing their post-nuptial moult in W-Europe.

The analyses required are then only possible if individuals can be assigned trustworthy to their breeding population and such is not the case with using morphometrics based on wing- and culmen lengths.

EPILOGUE

11

11.1 INTRODUCTION

My present-day work centres on using relevant ecological information in policy-making processes. Even when good information is available, implementing it does not always follow. Lawton (2007) listed eleven (partly overlapping) reasons why policy-makers and/or politicians fail to act even though ecologists have clearly demonstrated environmental degradation and the resulting damage to nature: (1) ecologists are not getting the message across clearly enough; (2) policy-makers and politicians do not know where to go for, since there is too much science; (3) the science is ambiguous and there are no clear answers; (4) there is not enough public support for what 'ought' to be done or politicians believe that there is insufficient electoral support; (5) policy has to be formulated to take into account many other legitimate issues and constraints, not least the cost of various options; (6) ecologists and policy-makers work to very different time-scales. The latter often need short-term solutions, whereas ecologists provide long-term and complex advice; (7) policy-makers and politicians are caught between the policy options that emerge from the science, and powerful interest groups with different agendas; (8) there is 'institutional failure' (wrong decision making bodies, poor government, contradictory policies in different parts of government); (9) the solutions require international agreement, while no nation wants to be first off the blocks; (10) scientific advice flies in the face of received political wisdom, dogma or deeply entrenched beliefs; (11) some politicians (or scientists or policy-makers - ME) are corrupt and out to make a fast buck. Lawton presented three examples of the interaction between science and environmental policy: the collapse of global marine fisheries, genetically modified crops and climate change. In the case of marine fisheries not enough could be done due to reasons 3, 5, 6, 7, 8, 9 and 11. The UK government was unable to facilitate genetically modified crops due to reasons 1, 3, 4, 7, and 10. And with respect to climate change Lawton stated, that the proposed policies run far ahead of science.

11.2 SITUATION IN THE CONTEXT OF THE WADDEN SEA

The results of our own studies clearly demonstrate the 6th reason presented by Lawton (2007): ecologists and policy-makers work at very different time-scales. Policy-making involves short time-intervals, and ecological studies a long time-frame. The topics of this thesis on waders illustrate this. This thesis provides information, collected over a time frame of 30 years, on breeding origins, population composition, staging numbers, age ratios, moult patterns and body masses. This information clarifies the function of the

Wadden Sea in the migration system of waders in the East Atlantic Flyway. Much of it is background knowledge. The catching activities presented in this study cannot provide annual results, but the counting activities, presented in Chapter 5, can provide such. With the catching studies, changes per 5- or 10-year intervals can be obtained. If shorter intervals are necessary in order to produce results on a yearly basis, the organization of the catching activities can be intensified. With the counting activities (also organized on a voluntary basis) yearly results can be obtained, which suits better the needs of policy-making. With extra investment in catching activities we might overcome Lawton's 6th reason of the different time-scales.

Some more examples can be collected in the Wadden Sea. One example concerns a study performed by Tromp (2001). She studied the decision-making with respect to nature affairs by the various governmental bodies in the Wadden Sea during the 1990s. Her results are a demonstration of Lawton's reason 8, since she showed that the process of decision-making was mainly directed towards increasing the influence of the 'own' governmental body. Finally, the cockle crisis in the area during (mainly) the 1990s demonstrated Lawton's reasons 2, 3, 5 and 7 (e.g. Van Gils *et al.* 2006, Swart & Van Andel 2007).

In what way are the results in this thesis useful for policy-making? The answer to this question can be approached both from the perspective of decision-making in the Wadden Sea and from the ecological context.

11.3 DECISION-MAKING IN THE WADDEN SEA DURING THE 1990s

Tromp (2001) studied the decision-making process with respect to policies of nature affairs in the northern part of the Netherlands during the 1990s, and one of her case studies concerned decision-making in the Wadden Sea context. She defines decision-making in terms of value- and functional rationalization. Value-rationalized acting is based upon a set of political values in order to judge, whether a goal to be reached is desirable. Functionally rationalized actions were conceived as 'concentrated on managing the proper means in order to reach an earlier defined goal'. According to Tromp value-rationalization is being superseded by functional rationalization in the present-day society. Politicians mostly use value-rationalization, i.e. when they strive for a nice quality landscape or for good living conditions. Tromp analysed the way the three governmental levels (national, provincial, local), co-operating in the 'Coördinatiecollege Waddengebied' (CCW), rationalized their

decision-making with respect to nature management and -development in the 1990s, which ranged from environmental impact assessments to the exploration and exploitation of gas in the area. She concluded that the decision-making was functionally rationalized. However, little functional rationalization was evident with respect to the original goals: natural values of the area. Instead it was mainly re-directed to the influence of the 'own' governmental body. This is hard to accept, since a large majority of the Dutch inhabitants wants to live in a nice, sound and healthy environment. Therefore we should understand how this re-direction in functional rationalization can happen.

Decision-making in the area is a complicated affair, since five governmental levels are involved: European, trilateral, national, provincial and local. On every level four stages of policy-making are involved (Winsemius 1986, Boogerd 2005): (1) the signalling stage, (2) the stage of policy-development, (3) the solution stage, and (4) the control stage. The first stage concerns problem recognition. The second stage starts when the problem is defined and recognized and agreed upon. It continues with formulating an effective policy in order to find the solution. The third stage concentrates on the solution by bringing it into practice, whilst the final stage monitors whether the solution fulfilled the goal. Inherent to nature, this four-stage approach was used for the first time on a national scale in the Dutch Nature Management Plan (Ministry LNV 1990). The various governmental levels have somewhat different roles during these stages, resulting in somewhat different information needs (Winsemius 1986, Boogerd 2005). Whereas Winsemius felt that policy development was primarily a national responsibility, Boogerd concluded that each level inevitably has to cycle through all four stages. These four stages on five governmental levels complicate the decision-making and trigger the re-direction of functional rationalization. When one level has passed the signalling stage, the other still has to start: if one level considers a set of events as problematical, another level still has the option to deny the problematical character.
It will never happen that for instance the European and the local level simultaneously cycle through the four stages of policy-making. This causes frictions between the levels resulting in opposing interests and re-direction in functional rationalization.

11.4 THE ROLES OF ECOLOGICAL SCIENCE

But apart of the decision-making, the ecological science also has its roles in the context of the Wadden Sea. Swart & Van Andel (2007) used the cockle controversy debate in the Wadden Sea to show that not only ecological knowledge, but also societal issues influence conservation research. They conclude on four types of science: autonomous

science, applied science, societal contextualized science and politicizable science. They considered the autonomous and applied science as the classic forms of science. Autonomous science is described as curiosity-driven and applied science as problem- driven. In societal contextualized science is not only the traditional scientific quality important, but also the societal quality, which is reflected by the involvement of stakeholders in the research process. Such a type of science needs so-called 'boundary work'. In the words of Swart & Van Andel (2007): 'Establishing a claim as scientific in such (contextualization - ME) situations requires active efforts of the people involved, which might also imply typifying the opposing claims as political or interest-driven'. So the fourth category, politicizable science, can be described as interest-driven: scientific uncertainties and social interests are both heavily involved. Swart & Van Andel consider it as a radical form of societal contextualization. These developments in both science and society contribute to Lawton's reasons 2, 3 and 7 with too much ambiguous science related to heavy societal disputes, which cannot be followed easily by politicians and/or the general public without knowing the type of science. In the cockle-controversy, the ecological research itself became part of the debate and thus caused frictions resulting in opposing interests and again re-direction in functional rationalization.

11.5 DECISION-MAKING AT THE START OF THE 21ST CENTURY

Since the 1990s several organizational changes have stimulated the functional approach to policy-making among the national, provincial and local governmental levels with respect to the main objective for the area: 'the long-term protection and development of the Wadden Sea as a nature area and the preservation of the unique open landscape' (VROM 2007). Organizational activities include the development of a new management plan for the Wadden Sea: 'Beheer- en Ontwikkelingsplan Waddengebied' including the managements-plans for the EU-Water Directive and Nature 2000, and the 'Uitvoeringsplan Waddenfonds'. This plan will include the first three stages of Winsemius (1986) (signalling, policy development, solution), but not yet systematically the fourth control stage with its relations to the second and third stage.

From the point-of-view of wader studies the long-term protection and development of the Wadden Sea as a nature area requires knowledge on (changes in) population numbers, population composition, mortality, productivity, and body condition in order to serve the various signalling and control stages of the five governmental levels. Important population

declines, poor body conditions or reduced reproduction ought to result in adequate actions of the governmental level best suited for it.

Some of these activities are already organised, for instance, in the context of the trilateral Wadden Sea program TMAP: bird numbers and breeding success of Wadden Sea birds are monitored under this flag (e.g. Essink *et al.* 2005). However, when actions are needed it is not evident how the monitoring results affect the decision-making processes due to a lack of a-priori stated goals. This is changing with the implementation of the European Water Directive: functionally rationalized nature goals are formulated, monitoring these goals is mandatory, and the outcome must result in actions (if needed). Goals and monitoring include both a-biotic and biotic parameters. The biotic part of the program includes phytoplankton, phytobenthos, macrophytes, macrofauna and fishes. Functional rationalization with respect to goals for the higher level organisms is now also developing for the European Natura 2000 and the monitoring needs will follow soon. In other words: there are some locomotives and wagons, and the railway is under construction.

11.6 TOWARDS FUNCTIONAL RATIONALIZATION

Tromp (2001) showed why results of ecological research could not be very useful in the context of decision-making during the 1990s. It might well be a major reason, that even with all the efforts and good intentions of many people in the Dutch Wadden Sea, it has been impossible until recently to organize adequate early-warning systems and distributional and life-history studies in order to prevent major crises with respect to the natural life of the Wadden Sea. When we started the catching of waders in the 1970s, the specific problem was whether or not important parts of the Wadden Sea could be reclaimed. Apart of the reclamation topic, three other major perturbations with respect to birds took place since the 1960s: the dieldrin/ endrin/ telodrin/ DDE-affair in the late 1960s, the PCB-affair in the 1980s, and the over-exploitation by the shell-fisheries in the 1990s. They all had a negative impact on the natural functioning of the system. These events took us by surprise as for instance the poisoning with 'drins' of Sandwich Terns (Koeman in Saris 2007) and the starvation of Oystercatchers and Eider ducks due to too low food stocks (Camphuysen *et al.* 2002, Verhulst *et al.* 2004, Ens *et al.* 2004, Van Gils *et al.* 2006, Kats 2007, Swart & Van Andel 2007). Once the attention was raised by professional and volunteer ecologists, it took some years to take adequate measures. Reparation of the negative effects takes long. Forty years after date the population numbers of the Sandwich Tern are not yet on the levels of the 1950s. It is also expected, that it needs at least 40 years before the Wadden Sea mudflats are recovered from the shell-fisheries affair of the 1990s (Piersma pers. comm.).

The flaw of not having properly functioning early warning systems with respect to the huge public impact of these three crises still needs to be repaired. There is no early warning system including the body condition and reproductive output of species like Eider Duck, Oystercatcher, Red Knot or Sandwich Tern. The organization of such an independent monitoring system in case of the shell fisheries has never been achieved even though permits for harvesting were (and still are) needed and the industrial shellfish fisheries were in a healthy financial state. If a sound monitoring system had already been in place with the involvement of all relevant groups (stakeholders, politicians and biologists) dealing with the shell-fisheries problem, the disputes might well have been less severe resulting in less costly societal processes. Until recently, no functionally rationalized goals with respect to nature in the Wadden Sea were formulated. The ones being formulated invariably originated from the trilateral and European levels (see Chapter 11.5). None of the three national ministries involved (LNV, VROM and VW), none of three provinces (Groningen, Fryslân, Noord-Holland), none of the at least 14 municipalities and none of the inter-governmental commissions have ever had the intention or were able to organize such a monitoring system without the trilateral or European pressure. Until recently, these more than 20 public bodies have denied the necessity of such a monitoring system, failed to organize it or were able to put the responsibility somewhere else. They adopted a surprise-scenario and by doing so they put the ecologists (professionals as well as volunteers) in a signalling position.

11.7 FUTURE OPTIONS FOR WADER CATCHING

The type of wader research, analysed in this thesis, has a strong focus on the method: catching. When used efficiently, it combines different aims directed towards the solution of a set of problems. It may include for instance sampling for avian influenza and DNA-studies as well as catching for survival and population composition estimates. When wader catching adopts a multi-aim approach it can well be integrated with bio-monitoring tasks.

In my view the results of catching activities are especially effective during both the signalling and control stages of policy-making. When Eider Duck, Oystercatcher and Red Knot are involved, attention should be paid to (1) condition and juvenile ratios in the staging populations in November – December, and (2) their body condition prior to their breeding (Eider Duck and Oystercatcher) or to their departure to the breeding grounds (Knot).

The same is true for species like Dunlin, Bar-tailed Godwit and Redshank feeding on worms and shrimps. The abundance of these prey-types is just as well influenced by human activities, while the monitoring is on too small a scale and insufficiently standardized to be adequate. Information on body condition, toxic chemicals, survival and productivity can be collected with a systematically planned international catching program. The present-day organization of at least the wader catching activities is not adequate enough, while it can be re-organized to fulfil specific needs. This type of wader research will be valuable, if (1) it continues to be of scientific interest for ecology, systematics and ornithology, (2) it is more helpful to interpret the results of wader counts, (3) it helps in producing undisputed results when recognizing problems in the signalling stage of policy-making, (4) it is a monitoring activity in the control stage of policy-making for various governmental levels, or (5) it helps these levels to adopt long(er)-term policies with respect to the rationalization of nature goals for the area. Without being comprehensive, the following set of potential goals can be listed:

Goals for (inter)national policies

1. *Monitoring effects of global change on waders in the Wadden Sea.* Boere *et al.* (2006) plea for a continued update of information on population changes, distribution, and the processes involved, since the effects of global change become more and more visible. Global change, either natural or man-made, will affect most breeding grounds because of changes in vegetation patterns, temperature, rainfall, and prey availability. It will also affect most intertidal feeding areas because of higher sea levels or more storms resulting in less exposure of the feeding grounds and changes in the sedimentation processes. It will also affect most wintering grounds because of desertification, changing weather patterns and/or changing temperatures of seawater. Wader populations can thus be expected to be affected in several ways by the processes involved in global change throughout the annual cycle. This explains the plea for a continued update of information. The results are useful for science as well as the international and national level of policy-making. It requires a (partly internationally) organized system for monitoring and research. With respect to wader research organizations like the International Wader Study Group, CHASM, Wetlands International, the Arctic breeding bird survey and EURING have a potential to organize internationally co-ordinated efforts. Changes in population composition will be a major item in these efforts for understanding population changes. Co-ordination of the sampling programs in the arctic breeding regions as well as in the temperate and tropical regions can be reached when qualified organizations join, co-operate and co-ordinate their efforts to obtain collective databases based on standardized sampling.

Goals for (inter)national and provincial Wadden Sea policy-making

2. *Recovery and permanent protection of the Wadden Sea as a nature area and the conservation of the unique open landscape.* This value-rationalized goal is formulated in the 'Derde Nota Waddenzee' as a policy goal of fundamental importance and needs to be operationalized and controlled. With respect to birds it is operationalized as 'the foraging-, breeding- and resting areas of birds have to be protected and preserved'. It thus needs to be clear when and where these areas are protected and preserved and when such is not the case and whether the degree of protection and preservation is adequate. The planning of human activities by the public authorities must take account of these values (amongst several others) according to resp. the 'Flora- en faunawet', the 'Natuurbeschermingswet 1998' and Nature 2000. Especially the European Nature 2000 is based on functional rationalization: numerical targets with respect to wader numbers per (sub) species and site are formulated and must be evaluated. These evaluative results will be useful for the various levels of policy-making, but if numerical targets are not reached, one needs to know cause-and-effect. Otherwise no proper solutions can be developed. This requires (in our situation) insight in population dynamics (yearly survival and productivity rates) and body condition in relation to the seasonal cycle and spatial distribution of waders. Thus, reliable population composition estimates and body condition parameters are required and can only be reached with good science.

3. *Healthy Wadden Sea system.* With value-directed rationalization a healthy Wadden Sea system can be maintained with a high bio-diversity and widely roaming flocks of waders throughout the area. But when is the Wadden Sea ecosystem 'healthy'? It requires knowledge about (1) the numerical fluctuations of the various species throughout the years, (2) population levels, reproduction rates and conditions of the species involved, (3) the spatial distribution of waders throughout the area in order to know whether the Wadden Sea ecosystem is in good or bad health, and (4) the residues of poisonous chemicals. These results are useful for science as well as the various levels of policy-making. The aim of a healthy Wadden Sea system requires the organized monitoring of the status of at least Eider Duck, Oystercatcher and Red Knot in the area in order to serve the control stage of management. However some non-shellfish feeders are required as well in order to avoid the risk of a 'tunnel-vision'. Worm-feeders like Grey Plover, Dunlin, Bar-tailed Godwit and Redshank are good candidates. The first three species were the species being hit the hardest in the Wadden Sea during the shell fisheries crisis of the 1990s (Camphuysen *et al.* 2002, Verhulst *et al.* 2004, Ens *et al.* 2004, Van Gils *et al.* 2006, Kats 2007).

Goals for ecology and ornithology

4. *Improving population composition estimates.* When the attention is focussed on measurements and plumage patterns with more discriminatory power than only wing- and culmen length, it must be possible to obtain better conclusions on population composition. The same is true when DNA-analysis and/or feather sampling for analysing stable isotopes (e.g. Atkinson *et al.* 2005) can be included more frequently. It also requires improvement of the statistical and computational tools, as this thesis showed.

5. *Sex-allocation.* Population composition estimates will become vastly improved once we are able to sex the birds caught. Captured birds can be sexed in a standardized way by using molecular sexing techniques based on blood or feather samples (e.g. Griffiths *et al.* 1998, Robertson *et al.* 1999, Russello & Amato 2001, Eason *et al.* 2001, Blomqvist *et al.* 2002, Lee & Griffiths 2003, Kenward et al 2004, Harvey *et al.* 2006, Lopes *et al.* 2006, Ottvall & Gunnarsson 2007, Rönkä *et al.* 2007). The results obtained are useful for science as well as the international and national level of policy-making.

6. *The collection of good body condition parameters.* Newly developed techniques with blood sampling (haematocrit) in order to obtain condition parameters (Bearhop *et al.* 1999, Verhulst *et al.* 2004, Cuervo *et al.* 2007) will be useful to investigate stress and cumulative effects of human activities in the Wadden Sea.

7. *Analysis of residues of toxic chemicals.* Such analyses might result in knowing the causes of population change due to increased mortality and/or decreasing productivity.

8. *Better information on survival and reproduction rates.* The material collected up to now still has to be analysed with respect to yearly survival and longevity. Several models are already developed (e.g. Lebreton *et al.* 1992). The outcomes obtained with these models will provide (1) species-specific yearly survival estimates during the past 30 years of both adults and first-winter birds, (2) knowledge (together with the recruitment estimates) to understand the population changes of the past 30 years, and (3) insight in the needed quality of sampling. Since most of the Wadden Sea staging populations breed in remote (sub) arctic areas, estimates on reproduction rates could better be collected in areas like the Wadden Sea. Better estimates on juvenile percentages in the Wadden Sea result in better knowledge on breeding performance in the (sub) arctic.

9. *Causation of diversification in numerical patterns.* Several populations are declining in the East Atlantic Flyway (Boere *et al.* 2006) as well as in the international Wadden Sea

(Koffijberg *et al.* 2005), even though most of our studied species appeared to frequent the Dutch Wadden Sea more and more (Chapter 5). These might only be temporary, because of the series of mild winters since 1989, since the numbers present in the Wadden Sea during January are positively related to mean temperatures in the area (Fig. 16). Catching studies might reveal the causation of this discrepancy.

11.8 SUMMARIZING REMARKS

The future catching of waders in the Wadden Sea lies in international co-operation. It then becomes of great value for the signalling and control stages of policy making on the various governmental levels. Problem-oriented research, possibly including catching activities, is needed in the stages of policy development and solution seeking. The future catching of waders in the Wadden Sea will also advance ecological science itself if we succeed to improve: (1) the standardization of sexing procedures of the birds captured, (2) the condition measures of the birds captured, (3) the estimates of yearly survival of populations present, and (4) the reliability of the population composition estimates.

Such needs organization and funding. The British situation might serve as an example. In the British Isles, many efforts of the British Trust for Ornithology concern the combination of -at least- ringing and counting work, which can be used in scenario- as well as cause-and-effect studies. Until recently, bird-ringing activities in the Netherlands have been co-ordinated from the Netherlands' Institute for Ecological Research (NIOO).

The responsibility for the co-ordination of the ringing activities is now being shared with SOVON Bird-research Netherlands, a large organisation with an active volunteer network. This is an excellent opportunity for implementing problem-oriented studies useful both during the various stages of policy-making as well as for the scientific world. It might well result in answers and solutions. Lawton (2007) formulated it as follows: *'Ecologists must be seen not solely as bearers of bad tidings. We face the challenge to function not only in identifying problems but also in suggesting solutions!'*

SUMMARIES

Engelmoer, M. 2007. Breeding origins of wader populations utilizing the Dutch Wadden Sea, as deduced from body dimensions, body mass, and primary moult.

The numerical and functional significance of the Wadden Sea over the past 30 years for twelve wader species is analysed. These species are: Ringed Plover *Charadrius hiaticula*, Grey Plover *Pluvialis squatarola*, Red Knot *Calidris canutus*, Sanderling *Calidris alba*, Curlew Sandpiper *Calidris ferruginea*, Dunlin *Calidris alpina*, Bar-tailed Godwit *Limosa lapponica*, Eurasian Curlew *Numenius arquata*, Spotted Redshank *Tringa erythropus*, Redshank *Tringa totanus*, Greenshank *Tringa nebularia*, and Ruddy Turnstone *Arenaria interpres*. The results of wader counts and wader catching activities are described per species. For every species attention is paid to the spatial distribution within the area, the seasonal changes, and the changes over the past 30 years with respect to the numbers of waders. The population composition is analysed with respect to the geographical breeding origin as deduced from morphometrics, sex ratio and/or age composition, and the changes in primary moult and body mass in the course of the non-breeding season. Findings with respect to the breeding origins were obtained by comparing the wing- and culmen lengths of waders captured in the Wadden Sea with the measurements of skins collected in a series of zoological museums at the northern hemisphere.

Keywords: Wadden Sea - waders - *Charadrius hiaticula* - *Pluvialis squatarola* - *Calidris canutus* - *Calidris alba* - *Calidris ferruginea* - *Calidris alpina* - *Limosa lapponica* - *Numenius arquata* - *Tringa erythropus* - *Tringa totanus* - *Tringa nebularia* - *Arenaria interpres* - morphometrics - population composition - geographical breeding origin - body masses - age composition - sex ratio - primary moult patterns - spatial distribution - seasonal variation - trends.

SAMENVATTING

Het numerieke en functionele belang van de Waddenzee in de afgelopen 30 jaar voor 12 soorten steltlopers wordt behandeld in dit proefschrift. Het betreft de volgende soorten: Bontbekplevier *Charadrius hiaticula*, Zilverplevier *Pluvialis squatarola*, Kanoetstrandloper *Calidris canutus*, Drieteenstrandloper *Calidris alba*, Krombekstrandloper *Calidris ferruginea*, Bonte Strandloper *Calidris alpina*, Rosse Grutto *Limosa lapponica*, Wulp *Numenius arquata*, Zwarte Ruiter *Tringa erythropus*, Tureluur *Tringa totanus*, Groenpootruiter *Tringa nebularia* en Steenloper *Arenaria interpres*. De resultaten van tellingen en vangsten met betrekking tot deze twaalf steltlopersoorten worden behandeld. Bij de tellingen wordt

aandacht gegeven aan zowel veranderingen in tijd als verschillen in ruimtelijke verdeling in het Nederlandse Waddengebied. Deze veranderingen in de tijd spelen zich af tussen jaren, maar ook binnen seizoenen. De analyses richten zich vooral op variatie in populatiesamenstelling met betrekking tot geografische broedherkomst, leeftijdsverhoudingen, ruipatronen en gewichten. Deze schattingen van populatiesamenstelling zijn zoveel mogelijk gerelateerd aan ruimtelijke variatie (eilanden/ kust, oost/west), seizoensveranderingen en veranderingen in de loop van de jaren. Bevindingen met betrekking tot de broedherkomst zijn verkregen door de lichaamsmaten (vleugel- en snavellengtes) van gevangen steltlopers in de Waddenzee te vergelijken met de maten van balgen uit de broedgebieden, welke zijn verzameld in collecties van een groot aantal musea op het noordelijk halfrond.

GEARFETTING

De numerike en funksjonele wichtigens fan de Waadsee foar tolve soarten steltrinners oer de lêste 30 jier wurdt yn dizze dissertaasje behannele. It oanbelanget de folgjende soarten: Bûnte Wilster *Charadrius hiaticula*, Slykwilster *Pluvialis squatarola*, Mients *Calidris canutus*, Sângril *Calidris alba*, Reade Gril *Calidris ferruginea*, Bûnte Gril *Calidris alpina*, Reade Skries *Limosa lapponica*, Wylp *Numenius arquata*, Sewyt *Tringa erythropus*, Tsjirk *Tringa totanus*, Grienskonk *Tringa nebularia* en Stienpikker *Arenaria interpres*. De resultaten fan de heechwettertellingen binne analysearre wer 't it dizze soarten oanbelanget yn it ramt fan (1) feroarings yn de ferrûne 30 jier, (2) feroarings troch it seizoen rinnend tusken oankomst yn de neisimmer en fertrek yn de maitiid en (3) romtlike fariaasje ferspraat oer de eilannen en kust.

De fangstresultaten binne analysearre mei it each op it skatten fan de populaasjegearstalling yn relaasje mei (1) de komôf fan brieden, (2) de prosintuele ferhâldingen tusken ûnfolwoechsen en folwoechsen fûgels, (3) it ferfearjen fan de slachpinnen en (4) feroaringen yn gewichten. Dizze skattingen fan populaasjegearstalling binne safolle as it mar koe yn ferbân brocht mei romtlike fariaasje yn de Waadsee (eilannen/ kust, east/ west), seizoenferoarings en feroarings yn de rin fan de jierren. It skatten fan de populaasjegearstalling yn relaasje mei de komôf fan brieden is dien troch de lichemsmaten fan fongen fûgels yn de Waadsee te fergelykjen mei de maten fan deade fûgels sammele yn in ferskaat fan soölogyske museums op it noardlik healrûn.

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Once on an evening in 1977, Dr. Gerard Boere presented a lecture on wader migration in the Wadden Sea at the Fryske Akademy in Leeuwarden. That lecture grabbed me, since by that time we were struggling to save crucial parts of salt marshes and summer polders of the Frisian mainland coast from being embanked and had started counting waders and waterbirds in the area. I was convinced that solid knowledge of the complex system of wader migration would be helpful for our case. The Netherlands' Youth Organization for Nature study (NJN) and my study of biology at the University of Groningen became the basis for a lifelong interest in waders and mudflats with three major experiences. Firstly, there are the activities of the Wadvogelwerkgroep FFF along the Frisian mainland coast where the ecological functioning of the Wadden Sea was discussed with Klaas van Dijk, Jaap Feddema, Albert Ferwerda, Henk Hiemstra , Klaas Koopman, Robert Kuipers, Johan Taal, and Arend Timmerman, amongst several others. The second experience was that Anne-Marie Blomert, Dolf Logemann and I, inspired by Leo Zwarts, were trying to understand the feeding ecology of the Oystercatcher along the Frisian mainland coast. We were wondering about the functioning of the Wadden Sea and how the area was exploited by Oystercatchers and other waders during the non-breeding season. I was deeply impressed by the way waders cope with the continuously changing feeding conditions. The third experience concerns the venture to the Mauritanian Banc d'Arguin together with Wibe Altenburg, Ron Mes, and Theunis Piersma.

Theunis had read that counts of the waders and waterbirds in that area were necessary. Since it did not seem to be too difficult, we decided to organize an expedition. It succeeded due to the strong support of Gerard Boere. There appeared to be huge numbers of waders in the area and hardly any food for them. So we wondered why on earth they left the food-rich W-European mudflats! When I completed my study under the supervision of Rudi Drent, Gerard Boere was there again offering me a civil service job of one-and-a-half year in order to produce a publication on the breeding origins of waders in the Dutch Wadden Sea. It was also decided to combine his catching results of Vlieland with the ones of Schiermonnikoog, where Ebel Nieboer and his students were also working since the early 1970s. It became a period of more than 20 years of co-operation, both behind the computer and in the mud. During these years several papers and a book were written. I thank Gerard Boere and Ebel Nieboer for having given me this opportunity. Whenever necessary, they were there for advice and for commenting on many pages of text. In combination with the other wader-adventures it has been a real enrichment to learn so much about waders and their migrations.

My would-be promotores Rudi Drent and Willem Schaafsma supported me strongly in composing this PhD thesis. They had the spirit to tackle every new version, which certainly resulted in many improvements. When in May this year, I had finally finished this thesis and

they had given their consent, they were no longer allowed to be promotor: I had really been too slow (even though it did not feel like that). Luckily, Theunis Piersma accepted to continue Rudi's former duties. So then, there was again an approved manuscript with a promotor. Theunis, thanks a lot for helping me out of the fire!

It is often said that writing a thesis is a guarantee for trouble in the relationship. Of course it was tough sometimes. But Joke Bloksma always supported me in writing this thesis or to start again after some period of interruption. Joke, thanks a lot! I have felt and I still feel very priviliged by your continuous encouragement and assistance.
Then there are both our sons: Klaas and Wiebe. In their memory there always has been a father working behind a computer on something what is called a thesis. Well gentlemen, it finally succeeded. I am sure, that I have not been the good example for finishing matters quickly, but, at least, I have been an example - for what it is worth- of stubborn continuance throughout the years.

I am specially indebted my parents. My parents have always supported me in reaching my aims. Since I had decided at my 12th to become a field-biologist, they stimulated me in every possible way to reach that goal. They were always there at the crucial moments of choice and I owe them a lot: Klaas and Yfke thanks for all the back up.

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Due to the efforts of Rob de Bruin and Willem Schaafsma, I found a way out of the statistical mess, which appears when biological information fails to be 'deterministic'. Jaap van der Meer was helpful by developing the calculations to estimate the start and duration of primary moult.
Cees Roselaar, Jan Wattel, and Rudi Drent always supported me to investigate the variability in body dimensions in wader populations by stimulating the visiting of a large number of museum collections throughout the world. It was a great joy to study these collections sometimes accompanied by my travel mates Anne-Marie Blomert, Frieda van Noordwijk†, Theunis Piersma and Cees Roselaar.

But I hope, that they and the field workers mentioned will appreciate that part of the results of their efforts is presented here.

REFERENCES

- Albers, C.J., Schaafsma, W., F., G. de Roos & M. Engelmoer. In preparation. Estimating typicality probabilities by creating distributional inferences with applications to ornithology.
- Alerstam, T. 1990. Bird Migration. Cambridge University Press, Cambridge, U.K.
- Alerstam, T., M. Rosén, J. Bäckman, P.G.P. Ericson, O. Hellgren. 2007. Flight speeds among bird species: allometric and pylogenetic effects. PLoS biology, 8/e197:1656-1992.
- Altenburg, W., E. Wymenga & L. Zwarts (eds.). 1992. Ornithological importance of the coastal wetlands of Guinea-Bissau. WIWO report 26. WIWO Foundation, Zeist.
- American Ornithologists' Union, 1957. Check-list of North American birds. Baltimore.
- Atkinson, P.W. 1996. The origins, moult, movements and changes in numbers of Bar-tailed Godwits *Limosa lapponica* on the Wash, England. Bird Study 43: 60-72.
- Atkinson, P.W., A.J. Baker, R.M. Bevan, N.A. Clark, K.B. Cole, P.M. Gonzalez, J. Newton, L.J. Niles & R.A. Robinson. 2005. Unravelling the migration and moult strategies of a long-distance migrant using stable isotopes: Red Knot *Calidris canutus* movements in the Americas. Ibis 147: 738-749.
- Bainbridge, I.P. & C.D.T. Minton. 1978. The migration and mortality of the Curlew in Britain and Ireland. Bird Study 25: 39-50.
- Balachandran, S., Hussain, S.A. & L.G. Underhill. 2000. Primary moult, biometrics, mass and age composition of Grey Plovers *Pluvialis squatarola* in southeastern India. Bird Study 47: 82-90.
- Baker, A.J., T. Piersma & L. Rosenmeier. 1994. Unravelling the intraspecific phylogeography of Knots *Calidris canutus*: a progress report on the search for genetic markers. Pages 39-45 in T. Piersma. Close to the edge: energetic bottlenecks and the evolution of migratory pathways in Knots. Ph. D. thesis, Univ. of Groningen, The Netherlands.
- Bakken, V., O. Runde & E. Tj rve. 2003. Norsk ringmerkingsatlas. Vol. 1. Stavanger Museum, Stavanger.
- Barrett, J. & C. Barrett. 1986. Notes on the biometrics and egg measurements of breeding Dunlins in Sutherland, Scotland. Wader Study Group Bull. 46: 29-30.
- Barter, M.A. 1985. Sex determination by bill length of live adult Curlew Sandpipers *Calidris ferruginea*. Stilt 7: 8-17.
- Battley, P.F., T. Piersma, M.W. Dietz, S. Tang, A. Dekinga & K. Hulsman. 2000. Empirical evidence for differential organ reductions during trans-oceanic bird flight. Proc. R. Soc. Lond. B 267: 191-195.
- Bearhop, S., R. Griffiths, K. Orr & R.W. Furness. 1999. Mean corpuscular volume (MCV) as a measure of condition in birds. Ecology letters 2: 352-356.
- Belik, V.P. 1998. Current population status of rare and protected waders in south Russia. p. 273-281. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on north Asian, African and European flyways. International Wader Studies 10:273-281.

• Benthem, W. 1981. Geografische herkomst en ruibeschrijving van de Rosse Grutto *Limosa lapponica* L. in de Nederlandse Waddenzee. Student Report, Free University, Amsterdam.

• Berg, Å. 1992. Habitat selection by breeding Curlews *Numenius arquata* on mosaic farmland. Ibis 134:355-360.

• Blew, J. & P. Südbeck (eds.). 2005. Migratory waterbirds in the Wadden Sea 1980-2000. Wadden Sea Ecosystem No. 20. Trilateral Monitoring and Assessment Group, Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

• Blokhin, A.Y. 1998. Breeding wader populations on the marine coasts of north-eastern Sakhalin. p. 221-224. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on north Asian, African and European flyways. International Wader Studies 10: 221-224.

• Blomert, A.-M., M. Engelmoer & Y. Ntiamoa-Baidu. 1990. The Banc d'Arguin, Mauritania, as a meeting point for Avocets during spring migration. Ardea 78: 193-208.

• Blomert, A.-M., B.J. Ens, J.D. Goss-Custard, J.B. Hulscher & L. Zwarts. 1996. Oystercatchers and their estuarine food supplies. Ardea 84A: 1-538.

• Blomqvist, D., M. Andersson, C. Küpper, I.C. Cuthill, J. Kis, R.B. Lanctot, B.K. Sandercock, T, Székely, J. Wallander, B. Kempenaers. 2002. Genetic similarity between mates and extra-pair parentage in three species of shorebirds. Nature 419: 613-615.

• Bock, W.J. 1959. The status of the Semipalmated Plover. Auk 76: 98-100.

• Boer, P. de, B. Koks, M. van Roomen & E. van Winden. 2001. Watervogels in de Nederlandse Waddenzee in 1997/98 en 1998/99. SOVON-monitoringrapport 2001/04. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

• Boere, G.C. 1976. The significance of the Dutch Wadden Sea in the annual life-cycle of arctic, subarctic and boreal waders. Part 1. The function as a moulting area. Ardea 64: 210-291.

• Boere, G.C. & P.M. Zegers. 1974. Wadvogeltelling in het Nederlandse Waddengebied in juli 1972. Limosa 47: 23-28.

• Boere, G.C. & P.M. Zegers. 1975. Wadvogeltellingen in het Nederlandse Waddenzeegebied in april en september 1973. Limosa 48: 74-81.

• Boere, G.C. & P.M. Zegers. 1977. Wadvogeltellingen in het Nederlandse Waddengebied in 1974 en 1975. Watervogels 2: 161-173.

• Boere, G.C., J.W.A. de Bruijne & E. Nieboer. 1973. Onderzoek naar de betekenis van het Nederlandse Waddenzeegebied voor Bonte Strandlopers *Calidris alpina* in nazomer en herfst. Limosa 46: 205-227.

• Boere, G.C., C.S. Roselaar & M. Engelmoer. 1984. The breeding origins of Purple Sandpipers *Calidris maritima* present in The Netherlands. Ardea 72: 101-109.

• Boere, G.C., C.A. Galbraith & D.A. Stroud (eds.). 2006. Waterbirds around the world. The Stationery Office, Edinburgh, UK.

• Boogerd, A. 2005. Van Droge Kennis naar Natte Natuur - de interactie tussen natuurweten-schap en beleid over verdroging. Eburon, Delft.

• Boudewijn, T.J. & B.S. Ebbinge. 1994. General review. In: J. van Nugteren (ed.). Brent Geese in the Wadden Sea. Waddenvereniging, Harlingen.

• Boyd, H. & T. Piersma. 2001a. Changing balance between survival and recruitment explains population trends in Red Knots *Calidris canutus* islandica wintering in Britain, 1969-1995. Ardea 89:301-317.

• Boyd, H. & T. Piersma. 2001b. Why do few Afro-Siberian Knots *Calidris canutus canutus* now visit Britain? Bird Study 48: 147-158.

• Boyd, H. & Æ. Petersen. 2006. Spring arrivals of migrant waders in Iceland in the 20th century. Ringing & Migration 23: 107-115.

• Branson, N.J.B.A. & C.D.T. Minton. 1976. Moult, measurements and migrations of the Grey Plover. Bird Study 23: 257-266.

• Branson, N.J.B.A., E.D. Ponting & C.D.T. Minton. 1978. Turnstone migrations in Britain and Europe. Bird Study 25: 181-187.

• Brenning, U. 1989. Der Zug des Alpenstrandläufers (*Calidris alpina*) auf der Grundlage von Beringungen, Wiederfunden und Kontrollen in der DDR. Ber. Vogelwarte Hiddensee 9: 16-38.

• Browning, M.R. 1977. Geographic variation in Dunlins *Calidris alpina* of North America. Can. Field-Nat. 91:391-393.

• Browning, M.R. 1991. Taxonomic comments on the Dunlin *Calidris alpina* from northern Alaska and eastern Siberia. Bull. Br. Ornithol. Club 111: 140-145.

• Bruin, R. de, W. Schaafsma, A.G.M. Steerneman & G.N. van Vark. 2001. Size and shape as linear combinations of untransformed measurements. Communications in Statistics: Theory and Methods 30: 1695-1714.

• Bruin, R. de, M. Engelmoer, G. de Roos, W. Schaafsma & G.N. van Vark. In prep. Specifying a statistical concept of size and shape such that application is straight forward.

• Butiev, V.T. & E.A. Lebedeva. 1998. Curlew *Numenius arquata* in the Vologda region of North European Russia. p. 299-302. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North -Asian, African and European flyways. International Wader Studies 10.

• Butler, R.W., T.D. Williams, N. Warnock & M.A. Bishop. 1997. Wind assistance: a requirement for migration of shorebirds? Auk 114: 456-466.

• Byrkjedal, I. & D.B.A. Thompson. 1998. Tundra Plovers: the Eurasian, Pacific and American Golden Plovers and Grey Plover. T & AD Poyser, London.

• Camphuysen, C.J. 1998. Olievervuiling en olieslachtoffers in Nederland, 1997/98. Sula 12: 41-72.

• Camphuysen C.J., B.J. Ens, D. Heg, J.B. Hulscher, J. van der Meer & C.J. Smit. 1996. Oyster-catcher winter mortality in The Netherlands: the effect of severe weather and food supply. Ardea 84a: 469-492.

- Camphuysen, C.J., C.M. Berrevoets, H.J.W.M. Cremers, A. Dekinga, R. Dekker, B.J. Ens, T.M. van der Have, R.K.H. Kats, T. Kuiken, M.F. Leopold, J. van der Meer & T. Piersma. 2002. Mass mortality of Common Eiders (*Somateria mollissima*) in the Dutch Wadden Sea. Winter 1999/2000: starvation in a commercially exploited wetland of international importance. Biological Conservation 106: 303-317.
- Castro, G. & J.P. Myers. 1989. Flight range estimates for shorebirds. Auk 106: 474-476.
- Clapham, C. 1978. The Ringed Plover populations of Morecambe Bay. Bird Study 25: 175-180.
- Clark, N.A. 1983. The ecology of Dunlin (*Calidris alpina* L.) wintering on the Severn Estuary. PhD thesis, University of Edinburgh.
- Clark, J.A., S.R. Baillie, N.A. Clark & R.H.W. Langston. 1993. Estuary wader capacity following severe weather mortality. BTO Res. Rep. 103. British Trust for Ornithology, Thetford.
- Clark, J.A., N.A. Clark, R.A. Robinson & P.W. Atkinson. 2003. Using adult/juvenile ratios of waders in winter cannon net catches in Britain & Ireland to measure recruitment. BTO Research Report 344. BTO, Thetford, UK.
- Clark, J.A., R.A. Robinson, N.A. Clark & P.W. Atkinson. 2004. Using the proportion of juveniles in catches to measure recruitment. Wader Study Group Bull. 104: 51-55.
- Collier, M., A. Banks, G. Austin, T. Girling, R. Hearn & A. Musgrove. 2005. The Wetland Bird Survey 2003/04 Wildfowl and Wader Counts. BTO/WWT/RSPB/JNCC, Thetford, UK.
- Cramp, S. & K.E.L. Simmons (eds.). 1983. The birds of the western Palearctic. Vol. III. Oxford Univ. Press, Oxford, UK.
- Cranswick, P., J. Worden, R. Ward, H. Rowell, C. Hall, A. Musgrove, R. Hearn, S. Holloway, A. Bnaks, G. Austin, L. Griffin, B. Hughes, M. Kershaw, M. O'Connell, M. Pollitt, E. Rees & L. Smith. 2005. The Wetland Bird Survey 2001-03 Wildfowl and Wader Counts. BTO/WWT/RSPB/JNCC, Thetford, UK.
- Cresswell, W. & D.P. Whitfield. 1994. The effects of raptor predation on wintering wader populations at the Tyninghame estuary, south-east Scotland. Ibis 136: 223-232.
- Cuervo, J.J., A.P. M ller & F. De Lope. 2007. Haematocrit is weakly related to condition in nestling Barn Swallows Hirundo rustica. Ibis 149: 128-134.
- Currie, D. & J. Valkama. 2000. Population density and the intensity of paternity assurance behaviour in a monogamous wader: the Curlew *Numenius arquata*. Ibis 142: 372-381.
- Currie, D., J. Valkama, Å. Berg, M. Boschert, K. Norddahl, M. Hänninen, E. Korpimäki, V. Pöyri & O. Hemminki. 2001. Sex roles, parental effort and offspring desertion in the monogamous Eurasian Curlew *Numenius arquata*. Ibis 143: 642-650.
- Davidson, N.C. 1983. Formulae for estimating the lean weight and fat reserves of live shorebirds. Ringing & Migration 4:159-167.
- Davidson, N.C. 1984. How valid are flight range estimates for waders? Ringing & Migration 5: 49-64.
- Davidson, N.C. & J.R. Wilson. 1992. The migration system of European-wintering Knots

Calidris canutus islandica. Wader Study Group Bull. 64 Suppl.: 39-52.

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

• Davidson, N.C., J.D. Uttley & P.R. Evans. 1986b. Geographic variation in the lean mass of Dunlins wintering in Britain. Ardea 74:191-198.

• Dekker, D. & R. Ydenberg. 2004. Raptor predation on wintering Dunlins in relation to the tidal cycle. Condor 106: 415-419.

• Delany, S., C. Reyes, E. Hubert, S. Pihl, E. Rees, L. Haanstra & A. van Strien. 1999. Results from the International Waterbird Census in the Western Palearctic and Southwest Asia 1995 and 1996. Wetlands International Publ. 54. Wetlands International, Wageningen.

• Dement'ev, G. 1939. On the Pal arctic Forms of the Grey Plover (*Squatarola squatarola* (L.)). Ibis 14: 352-354.

• Dick, W.J.A. (ed.). 1975. Oxford and Cambridge Mauritanian Expedition 1973-report. University of Cambridge, Cambridge.

• Dick, W.J.A., M.W. Pienkowski, M. Waltner & C.D.T. Minton. 1976. Distribution and geographical origins of Knots *Calidris canutus*, wintering in Europe and Africa. Ardea 64: 22-47.

• Dick, W.J.A., T. Piersma & P.Prokosch. 1987. Spring migration of the Siberian knots *Calidris canutus canutus*: results of co-operative Wader Study Group project. Ornis Scand. 18; 5-16.

• Dierschke, V. 2003. Predation hazard during migratory stopover: are light or heavy birds under risk? J. Avian Biol. 34: 24-29.

• Dodd, S. 2000. Weight loss in Dunlin *Calidris alpina* over the high tide period. Wader Study Group Bull. 91: 28-29.

• Dodman, T., C. de Vaan, E. Hubert & C. Nivet. 1997. African waterfowl census 1997. Les Dénombrements Internationaux d'oiseaux d'eaux en Afrique, 1997. Wetlands International, Wageningen.

• Dolnik, V.R., & V.M. Gavrilov. 1979. Bioenergetics of molt in the Chaffinch (*Fringilla coelebs*). Auk 96: 253-264.

• Drent, R. & T. Piersma. 1990. An exploration of the energetics of leap-frog migration in arctic breeding waders. In: E. Gwinner (ed.) Bird migration: the physiology and ecophysiology. 399-412. Springer-Verlag, Berlin.

• Eades, R.A. & J.D. Okill. 1976. Weight variations of Ringed Plovers on the Dee estuary. Ring. & Migr. 1: 92-97.

• Eason, D., G.D. Millar, A. Cree, J. Halverson, & D.M. Lambert. 2001. A comparison of five methods for assignment of sex in the takahe (*Aves: orphyrio mantelli*). J. Zoology 253: 281-292.

• Ebbinge, B.S. 1992. Population limitation in arctic-breeding geese. Thesis, University of Groningen, Groningen.

• Elkins, N. 1983. Weather and bird behaviour. T & AD Poyser, UK.

- Elliott, C.C.H., M. Waltner, L.G. Underhill, J.S. Pringle & W.J.A. Dick. 1976. The migration system of the Curlew Sandpiper *Calidris ferruginea* in Africa. Ostrich 47: 191-213.
- Engel, S. 2005. Racing the wind. Water economy and energy expenditure in avian endurance flight. PhD thesis University of Groningen.
- Engelen, A.F.V. van, J. Buisman & F. IJnsen. 2001. A millennium of weather, winds and water in the Low Countries. p. 101-124 in: P.D. Jones, A.E.J. Ogilvie, T.D. Davies, K.R. Briffa. History and climate, memories of the future? Kluwer Acad./ Plenum Publ., New York.
- Engelmoer, M. 1995. The application of discriminant analysis to the morphometrics of waders. Pagina 475-490 in: E.J.M. Hagemeijer & T.J. Verstrael (eds.). Bird Numbers 1992. Distribution, monitoring and ecological aspects. Proc. 12th Int. Conf. IBCC & EOAC, Noordwijkerhout, Nederland.
- Engelmoer, M. & C.S. Roselaar. 1998. Geographical Variation in Waders. Kluwer Acad. Publ., Dordrecht, The Netherlands/ Norwell, U.S.A.
- Engelmoer, M., G.C. Boere & E. Nieboer. 2006. Thirty years of arctic wader monitoring in the Dutch part of the Wadden Sea. In: Boere, G.C., C.A. Galbraith & D.A. Stroud (eds.) Waterbirds around the world. The Stationery Office, UK.
- Ens, B.J. 1992. The social prisoner: causes of natural variation in reproductive success of the Oystercatcher. Thesis Univerity of Groningen, Groningen.
- Ens, B.J., T. Piersma, W.J. Wolff, L. Zwarts (eds.). 1988. Report of the Dutch-Mauritanian project Banc d'Arguin 1985-1986. Joint report PNBA/WIWO/RIN/NIOZ, Texel.
- Ens, B.J., T. Piersma, W.J. Wolff & L. Zwarts (eds.). 1990a. Homeward bound: problems waders face when migrating from the Banc d'Arguin to their northern breeding grounds in spring. Special volume Ardea 78.
- Ens, B.J., P. Duiven, C.J. Smit & T.M. van Spanje. 1990b. Spring migration of Turnstones from the Banc d'Arguin in Mauritania. Ardea 78: 301-314.
- Ens, B.J., A.C. Smaal & J. De Vlas. 2004. The effects of shellfish fishery on the ecosystems of the Dutch Wadden Sea and Oosterschelde. Alterra Report 1011/ RIVO report C056-04/ RIKZ 2004-031. Alterra, Wageningen.
- Essink, K., C. Dettmann, H. Farke, K. Laursen, G. Lüerßen, H. Marencic, W. Wiersinga (eds.). 2005. Wadden Sea Quality Status Report 2004. Wadden Sea Ecosystem 19. Common Wadden Sea Secretariat, Wilhelmshaven.
- Etheridge, B. & W.G. Taylor. 1982. Biometrics of breeding Dunlins *Calidris alpina* from South Uist. Wader Study Group Bull. 36: 2-3.
- Exo, K.-M. & S. Wahls. 1996. Origin and movements of Grey Plovers *Pluvialis squatarola* ringed in Germany. Wader Study Group Bull. 81: 42-45.
- Exo, K.-M., O. Stepanova. 2000. Ecology of Grey Plovers *Pluvialis squatarola* breeding in the Lena Delta, The Sakha Republic/ Yakutia in 1997: Report on a pilot study. WIWO-report 69. WIWO Foundation, Zeist.

• Exo, K.-M., O. Stepanova. 20001. Biometrics of adult Grey Plovers *Pluvialis squatarola* breeding in the Lena Delta, NE-Siberia (the Sakha Republic, Yakutia). Ring. & Migr. 20: 303-311.

• Fair, J., S. Whitaker & B. Pearson. Sources of variation in haematocrit in birds. Ibis 149: 535-552.

• Ferns, P.N. 1980. The spring migration of Ringed Plovers through Britain in 1979. Wader Study Group Bull. 29: 10-14.

• Ferns, P.N. 1981a. Identification, subspecific variation, ageing and sexing in European Dunlins. Dutch Birding 3: 85-98.

• Ferns, P.N. 1981b. The spring migration of Dunlins through Britain in 1979. Wader Study Group Bull. 32: 14-19.

• Ferns, P.N. 1981c. The spring passage of Turnstones through Britain in 1979. Wader Study Group Bull. 31: 36-40.

• Ferns, P.N. & G.H. Green. 1979. Observations on the breeding plumage and prenuptial moult of Dunlins *Calidris alpina* captured in Britain. Gerfaut 69: 286-303.

• Figuerola, J. & A. Bertolero. 1998. Sex differences in the stopover ecology of Curlew Sandpipers *Calidris ferruginea* at a refuelling area during autumn migration. Bird Study 45: 313-319.

• Fokker, W. 1991. Analyse van terugvangsten van de Bonte Strandloper (*Calidris alpina*) op Schiermonnikoog. Student report Free University, Amsterdam.

• Gilg, O., R. Sane, D.V. Solovieva, V.I. Pozdnyakov, B. Sabard, D. Tsanos, C. Zöckler, E.G. Lappo, E.E. Syroechkovski & G. Eichhorn. 2000. Birds and mammals of the Lena Delta Nature Reserve, Siberia. Arctic 53: 118-133.

• Gils, A.J. van, T. Piersma, A. Dekinga, B. Spaans & C. Kraan. 2006. Shellfish dredging pushes a flexible avian top predator out of a marine protected area. PLOS Biology | www.plosbiology.org 4(12) - e376: 2399-2404.

• Gilyazov, A.S. 1998. Long-term changes in wader populations at the Lapland Nature Reserve and its surroundings: 1887-1991. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10: 170-174.

• Ginn, H.B. & D.S. Melville. 1983. Moult in Birds. BTO Guide 19. BTO, Tring, U.K.

• Gjerdrum, C., A.M.J. Vallée, C. Cassidy St. Clair, D.F. Bertram, J.L. Ryder, G.S. Blackburn. 2003. Tufted Puffin reproduction reveals ocean climate variability. Proc. Natl. Acad. Sci. U.S.A. 100(16): 9377-9382.

• Glutz von Blotzheim, U.N. (ed.). 1975. Handbuch der Vögel Mitteleuropas. Band 6 - Charadriiformes (1. Teil). Akademisches Verlagsgesellschaft, Wiesbaden.

• Glutz von Blotzheim, U.N. (ed.). 1977. Handbuch der Vögel Mitteleuropas. Band 7 - Charadriiformes (2. Teil). Akademisches Verlagsgesellschaft - Wiesbaden.

• Godfrey, W.E. 1986. The birds of Canada. National Museums of Canada, Ottawa.

- Godfrey, W.E. 1992. Subspecies of the Red Knot *Calidris canutus* in the extreme north-western Canadian arctic islands. W.S.G. Bull. 64, Suppl.: 24-25.
- Goede, A.A. & E. Nieboer. 1983. Weight variation of Dunlins *Calidris alpina* during post-nuptial moult, after application of weight data transformations. Bird Study 30: 157-164.
- Goede, A.A., E. Nieboer & P.M. Zegers. 1990. Body mass increase, migration pattern and breeding grounds of Dunlins, *Calidris* a. *alpina*, staging in the Dutch Wadden Sea in spring. Ardea 78: 135-144.
- Goede, R.G.M. de, J.P. Cronau & J.P.W. Letschert. 1985. Aspecten van de voorjaarsmigratie van de Rosse Grutto *Limosa lapponica* door het oostelijk Waddenzeegebied. Student Report Free University, Amsterdam.
- Goeij. P. de, E. Menkveld & A. Wassink. 2000. Gezenderde Rosse Grutto's op Texel (en over Zweden). Graspieper 20: 57-60.
- Goss-Custard, J.D. (ed.) 1996. The Oystercatcher: from individuals to populations. Oxford University Press, Oxford.
- Goss-Custard, J.D., S.E.A. le V dit Durrell, H. Sitters & R. Swinfen. 1981. Mist nets catch more juvenile Oystercatchers than adults. Wader Study Group Bull. 32: 13.
- Green, G.H. & J.J.D. Greenwood (eds.). 1978. Joint biological expedition to North East Greenland 1974. Dundee.
- Green, M. 2004. Flying with the wind - spring migration of Arctic-breeding waders and geese over South Sweden. Ardea 92: 145-160.
- Green, M., T. Piersma, J. Jukema, P. de Goeij, B. Spaans &J. van Gils. 2002. Radio-telemetry observations of the first 650 km of the migration of Bar-tailed Godwits from the Wadden Sea to the Russian Arctic. Ardea 90: 71-80.
- Greenwood, J.G. 1984. Migration of Dunlin *Calidris alpina*: a worldwide overview. Ringing & Migr. 5: 35-39.
- Greenwood, J.G. 1986. Geographical variation and taxonomy of the Dunlin *Calidris alpina* (L.). Bull. Br. Ornithol. Club 106: 43-56.
- Griffiths, R., M.C. Double, K. Orr, R.J.G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7: 1071–1075.
- Gromadzka, J. 1981. Southeastern autumn migration of Dunlins *Calidris alpina* from the Baltic area. Wader Study Group Bull. 33: 4-5.
- Gromadzka, J. 1983. Results of bird ringing in Poland. Migrations of Dunlin *Calidris alpina*. Acta Orn. 19: 113-136.
- Gromadzka, J. 1985a. Curlew Sandpiper - *Calidris ferruginea* (L.). p. 185-193. In: Ilyichev, V.O., J.A. Viksne & H.A. Micheljson (eds.). [Migrations of birds in eastern Europe and northern Asia.] In Russian. Gruiformes, Charadriiformes. Nauka Press, Moscow.
- Gromadzka, J. 1985b. Dunlin - *Calidris alpina* (L.). p. 193-219. In: Ilyichev, V.O., J.A. Viksne & H.A. Micheljson (eds.). [Migrations of birds in eastern Europe and northern Asia.]

In Russian. Gruiformes, Charadriiformes. Nauka press, Moscow.

- Gromadzka, J. 1985c. Knot - *Calidris canutus* (L.). p. 221-229. In: Ilyichev, V.O., J.A. Viksne & H.A. Micheljson (eds.). [Migrations of birds in eastern Europe and northern Asia.] In Russian. Gruiformes, Charadriiformes. Nauka Press, Moscow.

- Gromadzka, J. 1989. Breeding and wintering areas of Dunlin migrating through southern Baltic. Ornis Scand. 20: 132-144.

- Gromadzka, J. & V.K. Ryabitsev. 1998. Siberian Dunlin *Calidris alpina* migrate to Europe: first evidence from ringing. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10: 88-90.

- Gromadzka, J. & L. Serra. 1998. Differential migration of juvenile and adult Grey Plovers *Pluvialis squatarola* at the mouth of the Vistula River, Poland. Ornis Fennica 75: 193-199.

- Gromadzki, M. 1985. Redshank - *Tringa totanus* (L.). p. 105-123. In: Ilyichev, V.O., J.A. Viksne & H.A. Micheljson (eds.). [Migrations of birds in eastern Europe and northern Asia.] In Russian. Gruiformes, Charadriiformes. Nauka press, Moscow.

- Grosskopf, G. 1963. Weitere Beiträge zur Biologie des Rotschenkels. Vogelwelt 84: 65-83.

- Gudmundsson, G.A. 1994. Spring migration of the Knot *Calidris* c. *canutus* over southern Scandinavia, as recorded by radar. J. Avian Biol. 25: 15-26.

- Gudmundsson, G.A. & Å. Lindström. 1992. Spring migration of Sanderlings *Calidris alba* through SW Iceland: wherefrom and whereto? Ardea 80: 315-326.

- Gudmundsson, G.A., Å. Lindström & T. Alerstam. 1991. Optimal fat loads and long-distance flights by migrating Knots *Calidris canutus*, Sanderlings *C. alba* and Turnstones *Arenaria interpres*. Ibis 133: 140-152.

- Gunnarsson, T.G. 2006. Monitoring wader productivity during autumn passage in Iceland. Wader Study Group Bull. 110: 21-29.

- Haberer, A. 1994. Sandregenpfeifer (*Charadrius hiaticula* L.) im Schleswig-Holsteinischen Wattenmeer: Rastbestände, Zugverlauf und Biometrie. Diplomarbeit Zoologischen Institut Hannover.

- Hagemeijer, E.J.M. & M.J. Blair (eds.). 1997. The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. T&AD Poyser, London.

- Hale, W.G. 1971. A revision of the taxonomy of the Redshank *Tringa totanus*. Zool. J. Linn. Soc. 50: 199-268.

- Hale, W.G. 1973. The distribution of the Redshank *Tringa totanus* in the winter range. Zool. J. Linn. Soc. 53: 177-236.

- Hale, W.G. 1980. Waders. The New Naturalist's Series. Collins, London, U.K.

- Hardy, A.R. & C.D.T. Minton. 1980. Dunlin migration in Britain and Ireland. Bird Study 27: 81-92.

- Hartert, E. 1912-21. Die Vögel der paläarktischen Fauna. Berlin.
- Harvey, M.G., D.N. Bonter, L.M. Stenzler & I.J. Lovette. 2006. A comparison of plucked feathers versus blood samples as DNA sources for molecular sexing. J. Field Ornithol. 77: 136-140.
- Have, T.M. van der, E. Nieboer & G.C. Boere. 1984. Age-related distribution of Dunlin in the Dutch Wadden Sea. In: Evans, P.R., J.D. Goss-Custard, W.G. Hale (eds). Coastal waders and wildfowl in winter. p. 160-176. Cambridge University Press, Cambridge, UK.
- Hayman, P., J. Marchant & T. Prater. 1986. Shorebirds. An identification guide to the waders of the world. Croom Helm, London.
- Heath, M.F. & M.I. Evans. 2000. Important Bird Areas in Europe: Priority sites for conservation. Vol. I: Northern Europe. BirdLife Conservation Series No. 8. Cambridge, UK.
- Heg, D.H. 1999. Life history decisions in Oystercatchers. Thesis University of Groningen, Groningen.
- Heldt, R. 1966. Zur Brutbiologie des Alpenstrandläufers, *Calidris alpina schinzii*. Corax 1: 173-188.
- Helseth, A., Å Lindström & M. Stervander. 2005. Southward migration and fuel deposition of Red Knots *Calidris canutus*. Ardea 93: 213-224.
- Hildén, O. 1975. Breeding system of Temminck's Stint *Calidris temminckii*. Ornis Fenn. 52: 117-144.
- Holmgren, N., H. Ellegren & J. Petterson. 1993a. The adaptation of moult pattern in migratory Dunlin *Calidris alpina*. Ornis Scand. 24: 21-27.
- Holmgren, N., H. Ellegren & J. Petterson. 1993b. Stopover length, body mass and fuel deposition rate in autumn migrating adult Dunlins *Calidris alpina*: evaluating the affects of moulting status and age. Ardea 81: 9-21.
- Holz, R. 1987. Altersmerkmale von Sandregenpfeifern (*Charadrius hiaticula*) der südwestlichen Ostseeküste. Beitr. Vogelkd. 33: 233-243.
- Hørring, R. 1939. 6 og 7 Thule Expedition til Sydostgrønland 1931-33. Medd. Grønland 108: 1-44.
- Hoyo, J. del, A. Elliott & J. Sargatal (eds.). 1996. Handbook of the Birds of the World. Vol. 3: Hoatzin to Auks. Lynx Editions, Barcelona.
- Hulscher, J.B. 1989. Sterfte en overleving van Scholeksters *Haematopus ostralegus* bij strenge vorst. Limosa 62: 177-182.
- Hulscher, J.B. 2000. Winterharde wadvogels: over vorstvluchten en elfstedentochten. In: J.M.Tinbergen, J.P.Bakker, T.Piersma & J.M. Van den Broek (eds). De onvrije natuur. Verkenningen van natuurlijke grenzen p 170-176. KNNV Uitgeverij, Utrecht.
- Hustings, F. & K. van Dijk. 1994. Bird census in the Kizilirmak Delta, Turkey, in spring 1992. WIWO-report 45. WIWO Foundation, Zeist.
- IJnsen, F. 1988. Het karakteriseren van winters. Zenith, February 1988.

- Innes, J.L. (ed.) 1980. Cambridge Norwegian Expedition 1978 Report. Cambridge, England.
- Insley, H. & L. Young. 1981. Autumn passage of Ringed Plovers through Southampton Water. Ringing & Migr. 3:157-164.
- Insley, H. & B. Etheridge. 1977. Catching bias in cannon and mist netted samples of Redshanks *Tringa totanus* on the Inner Morey Firth. Ringing & Migr. 18: 70-77.
- Johansen, H. 1960. Die Vogelfauna Westsiberiens 10, Limicolae 1. J. Orn. 101: 472-495.
- Johansen, H. 1961. Die Vogelfauna Westsiberiens 11, Limicolae 2. J. Orn. 102: 41-67.
- Johnson, C. 1985. Patterns of seasonal weight variation in waders on the Wash. Ringing & Migration 6:19-32.
- Jönsson, P.E. 1986. The migration and wintering of Baltic Dunlins *Calidris alpina schinzii*. Vår Fågelvärld Suppl. 11: 71-78.
- Jönsson, P.E. 1987. Sexual size dimorphism and disassortative mating in the Dunlin *Calidris alpina schinzii* in southern Sweden. Ornis Scand. 18: 257-264.
- Kam, J. van de, B. Ens, T. Piersma & L. Zwarts. 1999. Ecologische Atlas van de Nederlandse Wadvogels. Schuyt & Co, Haarlem.
- Kania, W. 1990. The primary moult of breeding Dunlins *Calidris alpina* in the central Taymyr in 1989. Wader Study Group Bull. 60: 17-19.
- Kardaun, O.J.W.F, D. Salomé, W. Schaafsma, A.G.M. Steerneman, J.C. Willems & D.R. Cox. 2003. Reflections on some cryptic issues concerning the nature of statistical inference (with discussion). International Statistical Review 71: 277-318.
- Kastepold, T.A. 1985. Curlew - *Numenius arquata* (L.). p. 270-275. In: Ilyichev, V.O., J.A. Viksne & H.A. Micheljson (eds.). [Migrations of birds in eastern Europe and northern Asia.] In Russian. Gruiformes, Charadriiformes. Nauka press, Moscow.
- Kats, R.K.H. 2007. Common Eiders *Somateria mollissima* in the Netherlands: the rise and fall of breeding and wintering populations in relation to the stocks of shellfish. PhD thesis. University of Groningen, Groningen.
- Kenward, B., C. Rutz, A.A.S. Weir, J. Chappell & A. Kacelnik. 2004. Morphology and sexual dimorphism of the New Caledonian Crow *Corvus moneduloides*, with notes on its behaviour and ecology. Ibis 146: 652-660.
- Kersten, M. 1997. Living leisurely should last longer: energetic aspects of reproduction in the Oystercatcher. Thesis University of Groningen, Groningen.
- Khomenko, S., S. Rosenfeld & S. Dyluk. 1999. Birds of Medusa Bay, NW Taimyr, in 1997. WIWO-report 66. WIWO Foundation, Zeist.
- Kleefstra, R., B. Koks, M. van Roomen & E. van Winden. 2002. Watervogels in de Nederlandse Waddenzee in 1999/2000. SOVON-monitoringrapport 2002/01. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Koffijberg, K., B. Koks, M. van Roomen & E. van Winden. 1999. Watervogels in de Nederlandse Waddenzee in 1996/97, met een samenvattend overzicht van integrale tellingen in 1990/91 -

1995/96. SOVON Monitoringrapport 1999/04, IKC coproductie 23. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

- Koffijberg, K., L. Dijksen, B. Hälterlein, K. Laursen, P. Potel, P. Südbeck, J. Blew, K. Eskildsen, K. Günther, H.-U.Rösner & M. Van Roomen. 2005. Birds. In: Essink, K., C. Dettmann, H. Farke, K. Laursen, G. Lüerssen, H. Marencic & W. Wiersinga (eds.). Wadden Sea Quality Status Report 2004. Wadden Sea Ecosystem No. 19. Trilateral Monitoring and Assessment Group, Common Wadden Sea Secretariat, Wilhelmshaven, Germany.
- Koopman, K. 1986. Primary moult and weight changes in Ruffs in The Netherlands in relation to migration. Ardea 74: 69-78.
- Koopman, K. 1987. Vierde verslag van de steltloperringgroep F.F.F. (over 1985 en 1986). Twirre 10(3). Special issue.
- Koopman, K. 1992. IJslandse Tureluurs, wat zijn dat? Op het Vinketouw 66: 16-19.
- Koopman, K. 1993. Een bonte strandloper van Jamal, Aziatisch Rusland in de Waddenzee. NSWG Nieuws 1: 8.
- Koopman, K. 1996. Ringen van steltlopers, meeuwen en sterns in 1995. Twirre 7(3): 9-13.
- Koopman, K. 2001. Ringen van steltlopers, meeuwen en sterns in 1999. Twirre 12: 125-130.
- Koopman, K. 2002. Mass, moult, migration and subspecific status of Red Knot *Calidris canutus* on the Frisian Wadden Sea coast, The Netherlands. Wader Study Group Bull. 97: 30-35.
- Koopman, K. & J.B. Hulscher. 1979. Catching waders with a 'wilsternet'. Wader Study Group Bull. 26: 10-12.
- Koopman, K., T. Piersma, A. Timmerman & M. Engelmoer. 1982. Eerste verslag van de Steltloperringgroep F.F.F. over de periode 1 juli 1980 - 30 december 1981, met speciale aandacht voor kemphaan en tureluur. Twirre special issue may 1982. pp. 38.
- Koopman, K., E. Wymenga, A. Timmerman, M. Engelmoer. 1985. Tweede verslag van de Steltloperringgroep F.F.F., over 1982, met speciale aandacht voor scholekster, Haematopus ostralegus, en grutto, Limosa limosa. Twirre speciaalnummer 1985.
- Koopman, K., A. Timmerman & M. Engelmoer. 1986. Verslag Steltloperringgroep FFF over 1983 en 1984. Twirre 3:1-43.
- Korte, J. de., C.A. Bosman & H. Meltofte. 1981. Observations on waders (Charadriidae) at Scoresby Sund, East Greenland. Medd. Gr nland, Bioscience 7:4-21.
- Krupa, R. 1997. Phenology and dynamics of autumn migration of Grey Plover (*Pluvialis squatarola*) through the Gulf of Gdansk in years 1984 - 1995. Ring 19: 93-104.
- Krupa, M. & R. Krupa. 2002. Biometrics and primary moult of the Grey Plover (*Pluvialis squatarola*) caught during autumn migration through the Puck Bay. Ring 24: 91-103.
- Lank, D.B. & R.C. Ydenberg. 2003. Death and danger at migratory stopovers: problems with "predation risk". J. Avian Biol. 34: 225-228.
- Lank, D.B., R.W. Butler, J. Ireland & R.C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. Oikos 103: 303-319.

- Lappo, E.G. 1998. Mapping breeding range structure of Tundra waders in Russia. p. 145-151. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10: 145-151.
- Lappo, E.G. & P. S. Tomkovich. 1998. Breeding distribution of Dunlin *Calidris alpina* in Russia. p. 152-169. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10.
- Laursen, K. 2005. Curlews in the Wadden Sea - effects of shooting protection in Denmark. In: J. Blew & P. Südbeck (eds.). migratory waterbirds in the Wadden Sea 1980-2000. Wadden Sea Ecosystem 20. TMAP Common Wadden Sea Secretariat, Wilhelmshaven.
- Lawton, J.H. 2007. Ecology, politics and policy. J. Applied Ecol. 44:465-474.
- Lebedeva, E.A. 1998. Waders in agricultural habitats of European Russia. p. 315-324. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10.
- Lee, P.L.M. & R. Griffiths. 2003. Sexing errors among museum skins of a sexually monomorphic bird, the Moorhen *Gallinula chloropus*. Ibis 145: 695-698.
- Leslie, R. & C.M. Lessells. 1978. The migration of Dunlin *Calidris alpina* through northern Scandinavia. Ornis Scand. 9: 84-86.
- Lindström, Å. & T. Piersma. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. Ibis 135: 70-78.
- Lindström, Å., A. Kvist, T. Piersma, A. Dekinga & M.W. Dietz. 2000. Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fuelling. J. Experimental Biology 203: 913-919.
- Lissimore, D., M.J.F. Lemon, D.B. Lank, R.W. Butler & R.C. Ydenberg. 1999. Large and consistent body mass differences of migrant Calidris sandpipers at adjacent stopover sites: phenomenon and possible explanations. Wader Study Group Bull. 88: 55-58.
- Lopes, R.J., J.C. Marques & L. Wennerberg. 2006. Migratory connectivity and temporal segregation of Dunlin *Calidris alpina* in Portugal: evidence from morphology, ringing recoveries and mtDNA. J. Ornithol. 147: 385-394.
- Løvenskiold, H.L. 1954. Studies on the Avifauna of Spitsbergen. Norsk Polarinstitut Skrifter 103: 62-69.
- Low, G.C. 1938. The supposed races of the Grey- or Black-bellied Plover (*Squatarola squatarola*). Ibis 14: 154-158.
- LPO-BirdLife France. 2007. Mid winter count database-International Waterbird Census in France. Ligue pour la Protection des Oiseaux, Rochefort.

- Maclean, S.F. & R.T. Holmes. 1971. Bill lengths, wintering areas and taxonomy of North American Dunlins, *Calidris alpina*. Auk 88: 893-901.
- Madsen, J., G. Cracknell & T. Fox (eds.). 1999. Goose populations of the western Palearctic. A review of status and distribution. Wetlands International Publ. No. 48, Wageningen, The Netherlands. National Environmental Research Institute , Rönde, Denmark.
- Mascher, J.W. 1971. A plumage-painting study of autumn Dunlin *Calidris alpina* migration in the Baltic and North Sea areas. Ornis Scand. 2:27-33.
- Mason, C.F. 1988. Parallel changes in numbers of waders and geese. Bird Study 36: 80-82.
- Meissner, W. 2000. Autumn migration of the Redshank (*Tringa t. totanus*) in the region of the Gulf of Gdánsk (Poland). Vogelwarte 40: 179-188.
- Meissner, W. 2005. Variation in timing of the Siberian Knot *Calidris c. canutus* autumn migration in the Puck Bay region (southern Baltic). Acta Ornithol. 40: 95-101.
- Meissner, W. 2007a. Stopover strategy of adult and juvenile Red Knots *Calidris c. canutus* in the Puck Bay, southern Baltic. Ardea 95: 97-104.
- Meissner, W. 2007b. Different timing of autumn migration of two Ringed Plover *Charadrius hiaticula* subspecies through the southern Baltic revealed by biometric analysis. Ringing & Migration 23: 129-133.
- Meissner, W. & P. Kamont. 2005. Seasonal changes in body size and mass of Red Knots *Calidris canutus* during autumn migration through southern Baltic. Ornis Svecica 15: 97-104.
- Meltofte, H. 1976. Ornithological Observations in southern Peary Land, North Greenland, 1973. Medd. Grønland. 205: 1-57.
- Meltofte, H. 1979. The population of waders, Charadriidae, at Danmarks Havn, Northeast Greenland, 1975. D.O.F.T. 73:69-94.
- Meltofte, H. 1991. The northern Dunlin puzzle. Wader Study Group Bull. 62: 15-17.
- Meltofte, H. 1993. Vadefugletrækket gennem Danmark. D.O.F.T. 87: 1-180.
- Meltofte, H., J. Blew, J. Frikke, H.-U. Rösner & C.J. Smit. 1994. Numbers and distribution of waterbirds in the Wadden Sea. IWRB Publ. 34, Slimbridge/ Wader Study Group Bull. 74 special issue.
- Ministerie van Landbouw, Natuurbeheer en Visserij. 1990. Natuurbeleidsplan. Den Haag.
- Minton, C.D.T. 1971. Wader Ageing Guide. Wader Study Group, Tring.
- Minton, C.D.T. 2003. The importance of long-term monitoring of reproduction rates in waders. Wader Study Group Bull. 100: 178-182.
- Mischenko, A.L. & O.V. Sukhanova. 1998. Waders of the Novgorod region: peculiarities of their distribution and important breeding areas. p. 285-290. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10.
- Morozov, V.V. 1998. Distribution of breeding waders in the Northeast European Russian

tundras. P. 186-194. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10: 186-194.

- Morrison, R.I.G. 1975. Migration and morphometrics of European Knot and Turnstone on Ellesmere Island, Canada. Bird-Banding 46:290-301.
- Morrison, R.I.G. & J.R. Wilson. 1972. Cambridge Iceland Expedition 1971. Cambridge, England.
- Morrison, R.I.G., N.C. Davidson & J.R. Wilson. 2007. Survival of the fattest: body stores on migration and survival in red knots *Calidris canutus islandica*. J. Avian Biol. 38: 479-487.
- Moser, M.E. 1988. Limits to the numbers of Grey Plovers *Pluvialis squatarola* wintering on British estuaries: an analysis of long-term population trends. J. Appl. Ecol. 25: 473-485.
- Moser, M.E. & M. Carrier. 1983. Patterns of population turnover in Ringed Plovers and Turnstones during their spring passage through the Solway Firth in 1983. Wader Study Group Bull. 39:37-41.
- Murphy, M.E. & J.R. King. 1984. Dietary sulfur amino acid availability and molt dynamics in White-crowned Sparrows. Auk 101: 164-167.
- Murphy, M.E. & J.R. King. 1992. Energy and nutrient use during moult by White-crowned Sparrows *Zonotrichia leucophrys gambelii*. Ornis Scand. 23: 304-313.
- Nebel, S., T. Piersma, J. van Gils, A. Dekinga & B. Spaans. 2000. Length of stopover, fuel storage and a sex-bias in the occurrence of two subspecies of Red Knots (*Calidris c. canutus* and *islandica*) in the Dutch Wadden Sea during southward migration. Ardea 88: 165-176.
- Nebel, S. & R.C. Ydenberg. 2005. Differential predator escape performance contributes to a latitudinal sex ratio cline in a migratory shorebird. Behav. Ecol. Sociobiol. 59: 44-50.
- Nechaev, V.A. & P.S. Tomkovich. 1987. Noviy podvid Chyernozobika - *Calidris alpina litoralis* ssp. n. (Aves, Charadriidae) s Sachalina. Zool. Zhurn. 66: 1110-1113.
- Nechaev, V.A. & P.S. Tomkovich. 1988. [A new name for Sakhalin Dunlin (Aves, Charadriidae).] In Russian. Zool. Zhurn. 67: 1596.
- Nicoll, M., R. Rae, R.W. Summers, K.-B. Strann, K. Brockie. 1991. The biometrics of Norwegian and Svalbard Purple Sandpipers Calidris maritima. Ring. & Migr. 12: 67-71.
- Nieboer, E. 1972. Preliminary notes on the primary moult in Dunlins *Calidris alpina*. Ardea 60: 112-119.
- Nieboer, E. 2005. Schiermonnikoog, spil in de jaarcyclus van arctische steltlopers. In: Stuurgroep Avifauna Schiermonnikoog (red.). Vogels van Schiermonnikoog, gezien - geteld - opgetekend. Uniepers, Abcoude.
- Nieboer, E., J. Cronau, R. de Goede, J. Letschert & T. van der Have. 1985. Axillary feathers colour patterns as indicators of breeding origin of Bar-tailed Godwits. Wader Study Group Bull. 45: 34.

- Nikiforov, M.V. 1998. Current distribution and population trends of some rare waders in Belarus. p. 282-284. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10.
- Nikolaev, V.I. 1998. The importance of the peatlands of the Upper Volga area as habitats for breeding waders. p. 291-298. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10.
- Norušis, M.J. 1992a. SPSS/PC+TM Base System User's Guide. Version 5.0. SPSS Inc. Chicago.
- Norušis, M.J. 1992b. SPSS/PC+TM Professional StatisticsTM. Version 5.0. SPSS Inc. Chicago.
- Norušis, M.J. 1992c. SPSS/PC+TM Advanced StatisticsTM. Version 5.0. SPSS Inc. Chicago.
- Norušis, M.J. 1998. SPSS 8.0 Guide to Data Analysis. Prentice Hall. New Jersey.
- Nottrot, F. 1981. Rui, biometrie en herkomst van de zilverplevier *Pluvialis squatarola* L. in het Nederlandse Waddengebied. Student report Free University, Amsterdam.
- Numerical Algorithms Group, 2004. NAG Fortran Library Chapter Introduction E04 - Minimizing or Maximizing a Function. NAG, Oxford, UK. www.nag.co.uk/numeric/fl/manual/pdf/E04/E04_intro.pdf.
- O.A.G. Münster. 1976. Zur Biometrie des Alpenstrandläufers *Calidris alpina* in den Rieselfeldern Münster. Vogelwarte 28: 278-293.
- O.A.G. Münster. 1983. Zur Gewichtsentwicklung und Biometrie des Sichelstrandstrandläufers (*Calidris ferruginea*) in den Rieselfeldern Münster. Vogelwarte 32: 23-32.
- Ogilvie, M.A. 1963. The migrations of European Redshank and Dunlin. Wildfowl Trust 14th Ann. Rep. 1961-62: 142-149.
- Ottvall, R. & G. Gunnarsson. 2007. Morphological and molecular sex identification of Redshanks Tring *totanus*. Bird Study 54: 127-129.
- Parmelee, D.F., H.A. Stephens & R.H. Schmidt. 1967. The birds of Southeastern Victoria Island and adjacent small islands. Natl. Mus. Canada Bull. 222/78. Ottawa, Canada.
- Paulson, D. 1993. Shorebirds of the Pacific Northwest. UBC Press, Vancouver, Canada.
- Peters, J.L. 1934. Check-list of birds of the world 2. Cambridge, Massachusetts, U.S.A.
- Pienkowski, M. W. 1984. Breeding biology and population dynamics of Ringed Plovers *Charadrius hiaticula* in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding. J. Zool., Lond. 202: 83-114.
- Pienkowski, M.W. & W.J.A. Dick. 1975. The migration and wintering of Dunlin *Calidris alpina* in Northwest Africa. Ornis Scand. 6:151-167.
- Pienkowski, M.W. & P. Prokosch. 1982. Wanderungsmuster von Watvögeln zwischen den Küstenvorländern West-Europas - Bericht über ein laufendes Projekt. Seevögel 3: 123-129.

- Pienkowski, M.W., C.S. Lloyd & C.D.T. Minton. 1979. Seasonal and migrational weight changes in Dunlins. Bird Study 26:134-148.
- Piersma, T. 1994. Close to the edge: energetic bottlenecks and the evolution of migratory pathways in Knots. PhD thesis, University of Groningen.
- Piersma, T. & N.E. van Brederode. 1990. The estimation of fat reserves in coastal waders before their departure from Northwest Africa in spring. Ardea 78:221-236.
- Piersma, T. & N.C. Davidson. 1992. The migrations and annual cycles of five subspecies of Knots in perspective. W. S. G. Bull. 64, Suppl.: 187-197.
- Piersma, T., L. Zwarts & J.H. Bruggeman. 1990. Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. Ardea 78: 157-184.
- Piersma, T. & J. Jukema. 1990. Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. Ardea 78: 315-337.
- Piersma, T. & S. van de Sant. 1992. Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. Ornis Svecica 2: 55-66.
- Piersma, T. & J. Jukema. 1993. Red breasts as honest signals of migratory quality in a long-distance migrant, the Bar-tailed Godwit. Condor 95: 163-177.
- Piersma, P. & M. Poot. 1993. Where waders may parallel penguins: spontaneous increase in locomotor activity triggered by fat depletion in a voluntary fasting Knot. Ardea 81: 1-8.
- Piersma, T., P. Prokosch & D. Bredin. 1992. The migration system of Afro-Siberian Knots *Calidris canutus canutus*. W. S. G. Bull. 64 Suppl.: 52-64.
- Piersma, T., R. Hoekstra, A. Dekinga, A. Koolhaas, P. Wolf, P. Battley & P. Wiersma. 1993. Scale and intensity of intertidal habitat use by Knots *Calidris canutus*: in the western Wadden Sea in relation to food, friends and foes. Neth. J. Sea Res. 31: 331-357.
- Pollitt, M., C. Hall, S. Holloway, R. Hearn, P. Marshall, A. Musgrove, J. Robinson & P. Cranswick. 2003. The Wetland Bird Survey 2000-01 Wildfowl and Wader Counts. BTO/ WWT/ RSPB/ JNCC, Slimbridge.
- Post, E. & M.C. Forchhammer. 2001. Pervasive influence of large-scale climate in the dynamics of a terrestrial vertebrate community. BMC Ecology 2001: 1-5. http://www.biomedcentral.com/1472-6785/1/5.
- Post, E. & M.C. Forchhammer. 2004. Synchronization of animal population dynamics by large-scale climate. Nature 427(6976): 697-698.
- Prater, A.J. 1974. The population and migration of Knot in Europe. Proc. I.W.R.B.-symp. Warsaw 1973. p. 99-113.
- Prater, A.J. 1981. Estuary birds of Britain and Ireland. Poyser, Calton, England.
- Prater, A.J., J.H. Marchant & J. Vuorinen. 1977. Guide to the identification and ageing of Holarctic Waders. BTO guide 17. BTO, Thetford.

- Prokosch, P. 1981. Bestand, Jahresrhythmus und traditionelle Nahrungsplatzbindung der Ringelgans (*Branta bernicla*) im nordfriesischen Wattenmeer. Thesis. Christian Albrechts Universität, Kiel.
- Prokosch, P. 1988. Das Schleswig-Holsteinische Wattenmeer als Frühjahrs-Aufenthaltsgebiet arktischer Watvogel-Populationen am Beispiel von Kiebitzregenpfeifer (*Pluvialis squatarola*, L. 1758), Knutt (*Calidris canutus*, L. 1758) und Pfuhlschnepfe (*Limosa lapponica*, L. 1758). Corax 12: 273-442.
- Prokosch, P., E. Nowak & H. Hötker. 1993. Bericht über die Deutsch-Russischen Biologen-Expeditionen zur Taimyr-Halbinsel in den Jahren 1989, 1990 und 1991. W.W.F., Husum.
- Rappoldt, C., M. Kersten & C. Smit. 1985. Errors in large-scale shorebird counts. Ardea 73: 13-24.
- Redfern, C.P.F. 1998. The analysis of primary moult using feather mass. Ringing & Migr. 19: 39-40.
- Reneerkens, J., T. Piersma & B. Spaans. 2005. De Waddenzee als kruispunt van vogeltrekwegen. NIOZ-report 2005 - 4. NIOZ, Texel.
- Robertson, B.C., E.O. Minot & D.M. Lambert. 1999. Molecular sexing of individual kakapo, *Strigops habroptilus* Aves, from faeces. Molecular Ecology 8: 1349-1350.
- Rönkä, A., L. Kvist, J. Karvonen, K. Koivula, V. Pakanen, D. Schamel & D. Tracy. 2007. Population genetic structure in the Temmink's Stint *Calidris temminckii*, with emphasis on the Fennoscandian populations. Conservation Genetics DOI 10.1007/s10592-007-9299-x.
- Roomen, M.W.J. van, E.A.J. van Winden, K. Koffijberg, B. Voslamber, R. Kleefstra, G. Ottens & SOVON Ganzen- en Zwanenwerkgroep. 2002. Watervogels in Nederland in 2000/2001. RIZA-rapport BM02.15/ SOVON-monitoringrapport 2002/04. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Roomen, M. van, E. van Winden, K. Koffijberg, R. Kleefstra, G. Ottens, B. Voslamber & SOVON Ganzen- en Zwanenwerkgroep. 2003. Watervogels in Nederland in 2001/2002. RIZA-rapport BM04.01/ SOVON-monitoringrapport 2004/01. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Roomen, M. van, E. van Winden, K. Koffijberg, A. Boele, F. Hustings, R. Kleefstra, J. Schoppens, C. van Turnhout, SOVON Ganzen- en Zwanenwerkgroep & L. Soldaat. 2004. Watervogels in Nederland in 2002/2003. RIZA-rapport BM04.09/ SOVON-monitoringrapport 2004/02. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Roomen, M. Van, C. Van Turnhout, E. Van Winden, B. Koks, P. Goedhart, M. Leopold & C. Smit. 2005. Trends van benthivore watervogels in de Nederlandse Waddenzee 1975-2002: grote verschillen tussen schelpdiereneters en wormeneters. Limosa 78: 21-38.
- Roomen, M. Van, E. Van Winden, F. Hustings, K. Koffijberg, R. Kleefstra, SOVON Ganzen- en Zwanenwerkgroep & L. Soldaat, 2006a. Watervogels in Nederland in 2003/2004. RIZA-rapport BM05.15/ SOVON-monitoringrapport 2005/03. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

- Roomen, M. Van, E. Van Winden, K. Koffijberg, B. Ens, F. Hustings, R. Kleefstra, J. Schoppers, C. Van Turnhout, SOVON Ganzen- en Zwanenwerkgroep & L. Soldaat, 2006b. Watervogels in Nederland in 2004/2005. RIZA-rapport BM06.14/ SOVON-monitoringrapport 2006/02. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- Rose, P.M. & D.A. Scott. 1997. Waterfowl Population Estimates. Wetlands International, Wageningen.
- Roselaar, C.S. 1979. Fluctuaties in aantallen krombekstrandlopers *Calidris ferruginea*. Watervogels 4: 202-210.
- Roselaar, C.S. 1983. Subspecies recognition in Knot *Calidris canutus* and occurrence of races in Western Europe. Beaufortia 33(7): 97-109.
- Rösner, H.-U. 1990. Sind Zugmuster und Rastplatzansiedlung des Alpenstrandläufers (*Calidris alpina alpina*) abhängig vom Alter? J. Orn. 131: 121-139.
- Rösner, H.-U. 1997. Strategien von Zug und Rast des Alpenstrandläufers (*Calidris alpina*) im Wattenmeer und auf dem Ostatlantischen Zugweg. Shaker Verlag, Aachen.
- Russello, M.A. & G. Amato. 2001. Application of a noninvasive PCR-based test for sex identification in an endangered parrot, Amazona guildingii. Zoo Biology 20: 40-45.
- Ryabitsev, V.K. & N.S. Alekseeva. 1998. Nesting density dynamics and site fidelity of waders on the middle and northern Yamal. p. 195-200. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10: 195-200.
- Rybkin, A.V. 1998. Lemming density in Taimyr tundra and its influence on reproduction of birds. p. 207-213 in: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10.
- Samigullin, G.M. 1998. Migration, breeding and population size of Curlew *Numenius arquata* in Orenburg Region, Russia. p. 325-328 in: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10.
- Saris, F. (ed.) 2007. Een eeuw vogels beschermen. KNNV-Uitgeverij, Zeist.
- Saunders, S.A. & M.A. Katzenberg (eds.) 1992. Skeletal Biology of Past Peoples: Research Methods. Wiley-Liss, New York.
- Scheiffarth, G. 2003. Born to fly - Migratory strategies and stopover ecology in the European Wadden Sea of a long-distance migrant, the Bar-tailed Godwit (*Limosa lapponica*). PhD thesis Christian-Albrechts Universität, Kiel.
- Scheiffarth, G., S. Wahls, C. Ketzenberg & K.-M. Exo. 2002. Spring migration strategies of two

populations of Bar-tailed Godwits (*Limosa lapponica*) in the Wadden Sea: time minimizers or energy minimizers? Oikos 96: 346-354.

• Schekkerman, H. & M. van Roomen. 1995. Breeding waders at Pronchishcheva Lake, northeastern Taimyr, Siberia, in 1991. WIWO-report 55. WIWO Foundation, Zeist.

• Serra, L. 2000. How do Palearctic Grey Plovers adapt primary moult to time constraints? An overview across four continents. Wader Study Group Bull. 93: 11-12.

• Serra, L. 2001. Duration of primary moult affects primary quality in Grey Plovers *Pluvialis squatarola*. J. Avian Biol. 32: 377-380.

• Serra, L. & R. Rusticali. 1998. Biometrics and moult of Grey Plovers (*Pluvialis squatarola*) wintering in norteastern Italy. Vogelwarte 39:281-292.

• Serra, L., Baccetti, N., Cherubini, G. & Zenatello, M. 1998. Migration and moult of Dunlin *Calidris alpina* wintering in the Central Mediterranean. Bird Study 45: 205-218.

• Serra, L., D.A. Whitelaw, A.J. Tree & L.G. Underhill. 1999. Moult, mass and migration of Grey Plovers *Pluvialis squatarola* wintering in South Africa. Ardea 87: 71-81.

• Serra, L, N.A. Clark & J.A. Clark. 2006. Primary moult, body mass and migration of Grey Plovers *Pluvialis squatarola* in Britain. Ibis 148: 292-301.

• Siefke, A. & T.A. Kastepold. 1985. Ringed Plover - *Charadrius hiaticula* L. p. 40-51. In: Ilyichev, V.O., J.A. Viksne & H.A. Micheljson (eds.). [Migrations of birds in eastern Europe and northern Asia.] In Russian. Gruiformes, Charadriiformes. Nauka Press, Moscow.

• Sims, D.W., M.J. Genner, A.J. Southward, S.J. Hawkins. 2001. Timing of squid migration reflects North Atlantic climate variability. Proc. R. Soc. Lond. B. Biol. Sci. 268(1485): 2607-2611.

• Smit, C.J. & T. Piersma. 1989. Numbers, mid-winter distribution and migration of wader populations using the East Atlantic Flyway. p. 24-64. In: Boyd, H. & J.-Y. Pirot (eds.). Flyways and reserve networks for water birds. IWRB Special Publication No. 9. I.W.R.B., Slimbridge.

• Smit, C.J. & W.J. Wolff (eds.). 1981. Birds of the Wadden Sea. Wadden Sea Working Group report 6, Balkema, Rotterdam.

• Smit, C.J. & E. Wymenga. 1989. De toepassing van biometrie voor het bepalen van de herkomst en trekroutes van bontbek- en zilverplevier. In: A.L. Spaans (red.) Wetlands en watervogels. Pudoc, Wageningen.

• Smit, C.J. & P.M. Zegers. 1994. Shorebird counts in the Dutch Wadden Sea, 1980-91: a comparison with the 1965-77 period. In: M. Frederiksen & K. Dahl (eds.). 1994. Birds and their Ecology in the Wadden Sea. Proc. 8th. Internat. Scient. Wadden Sea Symposium, Esbjerg 1993. Ophelia Suppl. 6: 163-170.

• Smith, N. G. 1969. Polymorphism in Ringed Plovers. Ibis 111: 177-188.

• Snow, D.W. 1970. A guide to the moult in British birds. BTO guide, no. 11, B.T.O., Tring.

• Soikkeli, M. 1974. Size variation of breeding Dunlins in Finland. Bird Study 21: 151-154.

• Soloviev, M.Y. & P.S. Tomkovich. 1997. Body mass changes in waders (Charadrii) in a high arctic area at northern Taymyr, Siberia. J. Orn. 139: 271-281.

- SOVON & CBS. 2005. Trends van vogels in het Nederlandse Natura 2000 netwerk. SOVON-informatierapport 2005/09. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- SOVON Ganzen- en Zwanenwerkgroep. 1997. Ganzen- en zwanentellingen in Nederland in 1995/96. SOVON-monitoringrapport 97/05, RIZA-rapport BM 96.20, IKC-Natuurbeheer coproductie 16. SOVON Vogelonderzoek, Beek-Ubbergen.
- SOVON Ganzen- en Zwanenwerkgroep. 1998. Ganzen- en zwanentellingen in Nederland in 1996/97. SOVON-monitoringrapport 98/06/ RIZA-rapport BM 97.17/ IKC Natuurbeheer coproductie 20. SOVON-Vogelonderzoek Nederland, Beek-Ubbergen.
- SOVON Ganzen- en Zwanenwerkgroep. 1999. Ganzen- en zwanentellingen in Nederland in 1997/98. SOVON-monitoringrapport 99/06/ RIZA-rapport BM 98.06/ IKC Natuurbeheer coproductie 24. SOVON-Vogelonderzoek Nederland, Beek-Ubbergen.
- Speek, B.J. & G. Speek. 1984. Thieme's Vogeltrekatlas. Thieme, Zutphen.
- Spiekman, H. & N. Groen. 1993. Breeding performance of arctic waders in relation to lemming densities, Northeast Taimyr, Siberia, 1992. WIWO Report 33. WIWO Foundation, Zeist.
- Stepanyan, L.S. 1990. Konspekt Ornitologicheskoy Fauni CCCP. Nauka Press, Moscow, Russia.
- Stiefel, A. & H. Scheufler. 1989. Der Alpenstrandläufer: *Calidris alpina*.Ziemsen Verlag, Wittenberg Lutherstadt.
- Stishov, M.S., V.I. Pridatko & V.V. Baranyuk. 1991. Ptitsy Ostrova Vrangelya. Nauka Press, Novosibirsk, Russia.
- Stroud, D.A. & N.C. Davidson. 2003. Catching and handling birds, and data: practical papers published in the Wader Study Group Bulletin. Wader Study Group Bull. 69, Special Issue International Wader Studies 6.
- Stroud, D.A., N.C. Davidson, R. West, D.A. Scott, L. Haanstra, O. Thorup, B. Ganter, & S. Delany (compilers) on behalf of the International Wader Study Group. 2004. Status of migratory wader populations in Africa and western Eurasia in the 1990s. International Wader Studies 15: 1-260.
- Summers, R.W. 1980. On the rate of change of moult scores in waders. Wader Study Group Bull. 28: 24.
- Summers, R.W. & L.G. Underhill. 1987. Factors related to breeding production of Brent Geese *Brenta b. bernicla* and waders (Charadrii) on the Taimyr peninsula. Bird Study 34: 161-173.
- Summers, R.W. & L.G. Underhill. 1991. The relationship between body size and time of breeding in Icelandic Redshanks *Tringa t. robusta*. Ibis 133: 134-139.
- Summers, R.W., C.J. Corse, D.P. Whitfield. 1987a. Purple Sandpiper studies in North Iceland 1986. Report Tay, Orkney and Grampian Ringing Groups, Orkney, Scotland.
- Summers, R.W., C.J. Corse, M. Nicoll, R. Smith & D.P. Whitfield. 1988a. The biometrics and wintering area of Icelandic Purple Sandpipers. Ring. & Migr. 9: 133-138.
- Summers, R.W. , M. Nicoll, L.G. Underhill & A. Petersen. 1988b. Methods for estimating the proportions of Icelandic and British Redshanks *Tringa totanus* in mixed populations wintering

on British coasts. Bird Study 35: 169-180.

• Summers, R.W., L.G. Underhill, C.F. Clinning & M. Nicoll. 1989. Populations, migrations, biometrics and moult of the Turnstone *Arenaria i. interpres* on the East Atlantic coastline, with special reference to the Siberian population. Ardea 77: 145-168.

• Suschkin, P.P., 1925. Spisok i raspredelenie ptits russkogo Altaya. Akad. Nauk SSSR, Moscow, Russia.

• Sutton, G.M. & D.F. Parmelee. 1955. Breeding of the Semipalmated Plover on Baffin Island. Bird-Banding 26: 137-47.

• Swart, J.A.A. & J. Van Andel. 2007. Rethinking the interface between ecology and society. The case of the cockle controversy in the Dutch Wadden Sea. Journ. Applied Ecol. In print

• Swennen, C.S. 1984. Differences in quality of roosting flocks of Oystercatchers. In: Evans, P.R., J.D. Goss-Custard & W.G. Hale (eds.). Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge.

• Sybex. 1996. Werken met SPSS 7.0 voor Windows 95. Sybex Uitgeverij, Soest.

• Tamis, W. 1980. Een vergelijking van de populaties van de Tureluur *Tringa totanus* L. van Vlieland en Schiermonnikoog. Student Report, Free University, Amsterdam.

• Taylor, R.C. 1980. Migration of the Ringed Plover *Charadrius hiaticula*. Ornis Scand. 11: 30-42.

• Tempel, R. van den, E.R. Osieck. 1994. Belangrijke Vogelgebieden in Nederland. Technical Report Vogelbescherming Nederland 13. Vogelbescherming Nederland.

• Thayer, H. & O. Bangs. 1914. Notes on the birds of the arctic coast of East Siberia. Proc. N. Engl. Zool. Club 9: 1-66.

• Thomas, D.G. & A.J. Dartnall. 1970. Differences in size between the sexes of the Curlew Sandpiper. Emu 70: 89.

• Thompson, P.M. & J.S. Ollason. 2001. Lagged effects of ocean climate change on fulmar population dynamics. Nature 413(6854): 417-420.

• Thorup, O. 1998. Ynglefuglene på Tipperne 1928-1992. Dansk Orn. Foren. Tidsskrift 92: 1-192.

• Tjørve, E. & K.M.C. Tjørve. 2007. Movements of Dunlins *Calidris alpina* ringed along the Norwegian coast. Wader Study Group Bull. 112: 37-44.

• Tomkovich, P.S. 1985. K biologii morskogo pesochnyika na Zemlya Frantsa-Iosifa. Ornitologiya 20: 3-17.

• Tomkovich, P.S. 1986. Geograficheskai izmyenchivoste chernozobikov dalenyego vostoka. Biul. Moskv. 91: 3-15.

• Tomkovich, P.S. 1990. analys Geografichesko izmenchivostii Yslandskogo Pesochnika *Calidris canutus* (L.). Byull. Mosk. Biol. 95/5: 59-72.

• Tomkovich, P.S. 1992. An analysis of the geographic variability in Knots *Calidris canutus* based on museum skins. Wader Study Group Bull. 64, Suppl.: 17-23.

• Tomkovich, P.S. 2001. A new subspecies of Red Knot *Calidris canutus* from the New Siberian Islands. British Ornithologists' Club Bulletin 121: 257-263.

• Tomkovich, P.S. & L. Serra. 1999. Morphometrics and prediction of breeding origin in some holarctic waders. Ardea 87: 289-300.

• Tomkovich, P.S. & M.Y. Soloviev. 1996. Distribution, migrations and biometrics of Knots *Calidris canutus canutus* on Taimyr, Siberia. Ardea 84: 85-98.

• Tomkovich, P.S. & M.Y. Soloviev. 2000. Review of bird breeding conditions in the Arctic in 1999. Arctic birds 2: 12-15.

• Tomkovich, P.S. & M.Y. Soloviev. 2001. Bird breeding conditions in the Arctic in 2000. Arctic birds 6: 17-20. http://www.arcticbirds.ru.

• Tomkovich, P.S. & M.Y. Soloviev. 2002. Bird breeding conditions in the Arctic in 2001. Arctic birds 6. http://www.arcticbirds.ru.

• Tomkovich, P.S. & M.Y. Soloviev. 2003. Bird breeding conditions in the Arctic in 2002. Arctic birds 5. http://www.arcticbirds.ru.

• Tomkovich, P.S. & M.Y. Soloviev. 2004. Bird breeding conditions in the Arctic in 2003. Arctic birds 6. http://www.arcticbirds.ru.

• Tomkovich, P.S., E.G. Lappo & E.E. Syroechkovski jr. 2000. Ringing and migratory links of Taimyr waders. In: Ebbinge B.S., Y.L. Mazourov & P.S. Tomkovich. Heritage of the Russian Arctic - reseach, conservation and international co-operation. Proc. Int. Sci. Willem Barents Memorial Arctic Cons. Symp., Moscow March 1998. Ecopros Publ., 2000.

• Townshend, D.J. 1982. The Lazarus syndrome in Grey Plovers. W.S.G. Bull. 34: 11-12.

• Tromp, G. 2001. Politiek door de Staten: doel- of waarderationeel handelen in het besloten overleg over de Wadden en het openbaar beraad over de ecologische hoofdstructuur. Proefschrift Rijksuniversiteit Groningen.

• Tubbs, C.R. 1991. The population history of Grey Plovers *Pluvialis squatarola* in the Solent, southern England. W.S.G. Bull.61: 15-21.

• Tulp, I.Y.M. 2007. The arctic pulse: timing of breeding in long-distance migrant shorebirds. Thesis, University of Groningen.

• Tulp, I., L. Bruinzeel, J. Jukema & O. Stepanova. 1997. Breeding waders at Medusa Bay, western Taimyr, in 1996. WIWO-report 61. WIWO Foundation, Zeist.

• Tulp, I., H. Schekkerman, T. Piersma, J. Jukema, P. de Goeij & J. van de Kam. 1998. Breeding waders at Cape Sterlegova, northern Taimyr, in 1994. WIWO-report 61. WIWO Foundation, Zeist.

• Underhill, L.G. & A. Joubert. 1995. Relative masses of primary feathers. Ringing & Migr. 16: 109-116.

• Underhill, L.G. & R.W. Summers. 1993. Relative masses of primary feathers in waders. Wader Study Group Bull.71: 29-31.

• Underhill, L.G. & W. Zucchini. 1988. A model for avian primary moult. Ibis 130: 358-372.

• Underhill, L. G., M. Waltner & R. W. Summers. 1989. Three-year cycles in breeding productivity of Knots *Calidris canutus* wintering in southern Africa suggest Taimyr Peninsula provenance. Bird Study 36: 83-88.

- Underhill, L.G., R.P. Pr s-Jones, E. E. Syroechkovski jr., N.M. Groen, V. Karpov, H.G. Lappo, M.W.J. van Roomen, A. Rybkin, H. Schekkerman, H. Spiekman & R.W. Summers. 1993. Breeding of waders (Charadrii) and Brent Geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. Ibis 135: 277-292.
- Underhill, L.G., A.J. Tree, H.D. Oschadleus & V. Parker. 1999. Review of ring recoveries of waterbirds in southern Africa. Cape Town: Avian Demography Unit, University of Cape Town.
- Underhill , L.G., P.S. Tomkovich & J.A. Harrison (eds.). 2006. The annual cycle of the Curlew Sandpiper *Calidris ferruginea*. International Wader Studies 19. Wader Study Group, U.K.
- Uttley, J.D., C.J. Thomas, N.C. Davidson, K.-B. Stramm & P.R. Evans. 1987. The spring migration system of Nearctic Knots *Calidris canutus* islandica: a re-appraisal. Wader Study Group Bull. 49, Suppl.: 80-84.
- Vähätalo, A.V., K. Rainio, A. Lehikoinen & E. Lehikoinen. 2004. Spring arrival of birds depends on the North Atlantic Oscillation. J. Avian Biol. 35: 210-216.
- Väisänen, R.A. 1969. Evolution of the Ringed Plover (*Charadrius hiaticula* L.) during the last hundred years in Europe. Ann. Ac. Scient. Fenn. Series A. IV. Biol. 149.
- Valle, R. & F. Scarton. 1996. Status and distribution of Redshank *Tringa totanus* breeding along Mediterranean coasts. Wader Study Group Bull. 81: 66-70.
- Vark, G.N. van & W.W. Howells (eds.) 1984. Multivariate Statistical Methods in Physical Anthropology. Reidel, Dordrecht.
- Vaurie, C. 1964. Systematic notes in Palearctic birds. No. 53. Charadriidae: the genera Charadrius and Pluvialis. Am. Mus. Novit. 2177: 1-22.
- Vaurie, C. 1965. The birds of the Palaearctic fauna; non-passeriformes. Witherby, London, U.K.
- Verhulst, S., K. Oosterbeek, A.L. Rutten & B.J. Ens. 2004. Shellfish fishery severely reduces condition and survival of oystercatchers despite creation of large marine protected areas. Ecology and Society 9(1): art. 17.
- Vik, J.O., N.C. Stenseth, G. Tavecchia, A. Mysterud & O.C. Lingjaerde. 2002. Ecology: living in synchrony on Greenland coasts? Nature 427(6976):697-698.
- Visser, H. 2002. Detectie van Milieuveranderingen. Een toepassing van structurele tijdreeks-modellen en het Kalmanfilter. RIVM rapport 550002002/2002. RIVM, Bilthoven NL.
- Weber, T.P. & A.J. Houston. 1997. Flight costs, flight range and the stopover ecology of migrating birds. J. Anim. Ecol. 66: 297-306.
- Wenink, P.W., A.J. Baker & M.G.J. Tilanus. 1993. Hypervariable control region sequences reveal global population structuring in a long-distance migrant shorebird, the Dunlin (*Calidris alpina*). Proc. Natl. Acad. Sci. USA. 90: 94-98.
- Wenink, P.W., A.J. Baker, H.-U. Rösner & M.G.J. Tilanus. 1996. Global mitochondrial DNA phylogeography of holarctic breeding Dunlin (*Calidris alpina*). Evolution 50: 318-330.
- Wennerberg, L., N.M.A. Holgren, P.-E. Jönsson & T. von Schantz. 1999. Genetic and morphological variation in Dunlin *Calidris alpina* breeding in the Palearctic tundra. Ibis 141: 391-398.

• Wernham, C., M. Toms, J. Marchant, J. Clark, G. Siriwardena & S. Baillie (eds.). 2002. The Migration Atlas: movements of the birds of Britain and Ireland. T. & A.D. Poyser, London.

• Wetlands International. 2006. Waterbird population estimates - fourth edition. Wetlands International, Wageningen, The Netherlands.

• Whitfield, D.P. 2003. Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to Sparrowhawk Accipiter nisus predation. J. Avian Biol. 34: 163-169.

• Whitfield, D.P., J.J. Brade, R.W. Burton, K.W. Hankinson & S. Young. 1996. The abundance of breeding Knot *Calidris canutus* islandica. Bird Study 43: 290-299.

• Winsemius, P. 1986. Gast in eigen huis - beschouwingen over milieumanagement. Samsom H.D. Tjeenk Willink, Alphen aan de Rijn.

• Wilson, J.R. 1981. The migration of high arctic shorebirds through Iceland. Bird Study 28: 21-32.

• Wilson, J.R., M.A. Czajkowski, M.W. Pienkowski. 1980. The migration through Europe and wintering in West Africa of the Curlew Sandpiper. Wildfowl 31: 107-122.

• Witts, B.F. 1982. Waders. In: Report of the Joint Services Expedition to Princess Marie Bay, Ellesmere Island, 1980.

• Wolf, P., N. Rabehl & J. Kamphues. 2003. Investigations on feathering, feather growth and potential influences of nutrient supply on feathers' regrowth in small pet birds (canaries, budgerigars and lovebirds). J. Anim. Physiol. Nutrition (Berlin) 87: 134-141

• Wymenga, E., M. Engelmoer, C.J. Smit & T.M. van Spanje. 1990. Geographical breeding origin and migration of waders wintering in West Africa. Ardea 78: 83-113.

• Wynne-Edwards, V.C. 1952. Zoology of the Baird Expedition (1950) I. The birds observed in Central and South-East Baffin Island. Auk 69: 353-391.

• Ydenberg, R.C., R.W. Butler, D.B. Lank, C.G. Guglielmo, M. Lemon & N. Wolf. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. J. Avian Biol. 33: 47-55.

• Ydenberg, R.C., R.W. Butler, D.B. Lank, B.D. Smith & J. Ireland. 2004. Western Sandpipers have altered migration tactics as Peregrine falcon populations have recovered. Proc. R. Soc. Lond. B 271: 1263-1269.

• Yesou, P., I.I. Chupin, V.I. Grabovsky. 1992. Notes on the breeding biology of the Bar-tailed Godwit *Limosa lapponica* in Taimyr. Wader Study Group Bull. 66: 45-47.

• Zegers, P.M. 1985. Vogeltellingen in het Nederlandse deel van de Waddenzee 1976-1979. Report National Forest Service 85-10, Utrecht, The Netherlands.

• Zegers, P.M. & N.D. Kwint. 1992. Vogeltellingen in het Nederlandse deel van het Waddengebied 1979-90. SOVON-report 1992/14. SOVON, Beek-Ubbergen.

• Zeiske, O. 1992. Die Rastbestände des Sichelstrandläufers *Calidris ferruginea* (Pont.) in den Nördlichen Küstenvorländern des Elbe-ästuars. Zoologischen Institut und Zoologischen Museum der Universität Hamburg.

- Zekhuis, M.J. & D. Tempelman (eds.) 1998. Breeding birds of the Albanian wetlands, spring 1996. WIWO-report 64. WIWO Foundation, Zeist.
- Zubakin, V.A., Sviridova, T.V., Kontorschikov, V.V., Grinchenko, O.S., Smirnova, E.V., Volkov, S.V., Krasnova, E.D. & Kreindlin, M.L. 1998. Rare breeding waders of the Moscow region: distribution and numbers. p. 303-308. In: Hötker, H., E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud & R.B. West (eds.). Migration and international conservation of waders. Research and conservation on North Asian, African and European flyways. International Wader Studies 10.
- Zwarts, L., B.J. Ens, M. Kersten & T. Piersma. 1990. Moult, mass and flight range of waders ready to take off for long-distance migrations. Ardea 78: 339-364.
- Zwarts, L., J.B. Hulscher, K. Koopman & P.M. Zegers. 1996a. Discriminating the sex of Oystercatchers *Haematopus ostralegus*. Ardea 84A: 1-12.
- Zwarts, L., J.B. Hulscher, K. Koopman & P.M. Zegers. 1996b. Body weight in relation to variation in body size of Oystercatchers *Haematopus ostralegus*. Ardea 84A: 21-28.
- Zwarts, L., J.B. Hulscher, K. Koopman, T. Piersma & P.M. Zegers. 1996c. Seasonal and annual variation in body weight, nutrient stores and mortality of Oystercatchers *Haematopus ostralegus*. Ardea 84A: 327-356.
- Zwarts, L., J.B. Hulscher, K. Koopman & P.M. Zegers. 1996d. Short-term variation in the body weight of Oystercatchers *Haematopus ostralegus*: effect of exposure time by day and night, temperature and wind force. Ardea 84A: 357-373.

SELECTED RECOVERIES AND CONTROLS

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annex 1

This study resulted in a large number of ring recoveries. Most recoveries deal with movements within W Europe during the non-breeding period. In this annex four categories of recoveries are selected and presented:

1. *Known breeding locations.* These recoveries include ringed pulli and certainly breeding adults. From the data it was clear that these birds had been raised or were breeding at the location of trapping or recovery. They include the local breeding populations of Ringed Plover, Eurasian Curlew and Redshank from the northern part of the Netherlands (N of 53°N).

2. *Recoveries N of 62°N.* Birds were also recovered during the breeding period or from regions N of the Wadden Sea without sure knowledge on the status of these birds. They might have been still on migration or they might have been breeding. Nearly all efforts to distinguish these recoveries according to 'breeding' or 'migration' persisted in some degree of subjectiveness or not-knowing. Therefore it was decided to present all recoveries N of 62°N. This table thus includes probable breeders as well as probable migrants.

3. *Recoveries connecting the African continent with the Dutch part of the Wadden Sea.*

The following sources were used: (1) all recoveries gathered at the Dutch Ringing Centre prior to 1981; (2) all recoveries collected with the catching activities of the authors, (3) all recoveries collected with the catching activities of the Wader Ringing Group 'Calidris' on Schiermonnikoog (Engelmoer *et al.* 2001) and (4) Ens *et al.* (1988), Ruiters & Fokker (1998), Underhill *et al.* (1999), Tomkovich *et al.* (2000) and Engelmoer *et al.* (2001).

The recoveries are sorted according to the date (month/ day) present on the non-breeding grounds. Symbols: '●' ringing details; ' ○' recovery details.

Table 1. Recoveries of waders ringed as pulli or ringed/ recovered when breeding

Ring	Age at trapping	Details
Ringed Plover ssp. hiaticula - first winter or younger when recovered		
K.192900	pull.	● 22-06-1963 NL Vlieland 53.18N 05.00E
		○ 01-08-1963 NL Vlieland 53.18N 04.54E; found
B.104182	pull.	● 12-07-1967 NL Workumerwaard 53.00N 05.24E
		○ 08-08-1967 FRANCE Calvados 49.18N 00.12W; freshly dead - shot
80303942 Helgoland	pull.	● 17-06-1971 GERMANY Amrum 54.42N 08.24E
		○ 29-08-1971 NL Texel 53.12N 04.54E; dead for > 1 week - found
H.136244	pull.	● 15-06-1978 NL Bandpolder 53.24N 06.09E
		○ 12-09-1978 NL Bandpolder 53.24N 06.09E; taken by owl or raptor
A...9291	pull.	● 25-06-1932 NL Vlieland 53.18N 05.00E
		○ 29-09-1932 PORTUGAL Minho 41.42N 08.48W; freshly dead - shot
.741697 Helgoland	pull.	● 14-06-1968 GERMANY Amrum 54.42N 08.24E
		○ 20-03-1969 NL Harlingen 53.12N 05.24E; freshly dead - found
H.100906	pull.	● 22-05-1971 NL Peazemerlânnen 53.24N 06.06E
		○ 30-04-1972 GERMANY Osterhever 54.24N 08.48E; captured, not shot
Ringed Plover ssp. hiaticula - older than first winter when recovered		
B..91604	pull.	● 07-06-1962 NL Texel 53.00N 04.48E
		○ 02-06-1966 NL Texel 53.00N 04.54E; dead for > 1 week - found
K..79886	pull.	● 30-05-1961 NL Vlieland 53.18N 05.00E
		○ 10-10-1962 NL Texel 53.12N 04.54E; found
K.192905	pull.	● 25-06-1963 NL Vlieland 53.12N 04.54E
		○ 29-03-1969 NL Texel 53.00N 04.42E; found dead
B..91608	pull.	● 06-06-1963 NL Texel 53.00N 04.48E
		○ 17-10-1965 GREAT BRITAIN Devon 50.36N 03.24W; found dead
Dunlin		
H.119353	> 1 c.y.	● 24-07-1973 NL Vlieland 53.16N 04.59E
		○ 20-05-1983 SWEDEN Arlovs Angar 55.38N 13.04E; with clutch - *schinzii*
H.133283	> 1 c.y.	● 18-09-1977 NL Vlieland 53.16N 04.59E
		○ 25&26-05-1985 FINLAND Hoytiaisen Suisto 62.37N 29.41E; inland - control
H.161449	> 2 c.y.	● 17-04-1987 NL East-Holwerd 53.24N 05.54E
		○ 19-06-1993 RUSSIA Yamal, Tyumen 71.18N 72.02E: control, breeding bird
		○ 02-08-1996 NL East-Holwerd 53.24N 05.54E
Eurasian Curlew W. European breeding population - first winter birds or younger when recovered		
.5153003	pull.	● 11-05-1980 NL Texel 53.04N 04.44E
		○ 14-05-1980 NL Texel 53.04N 04.44E; freshly dead - taken by other species of bird
.5126946	pull.	● 19-05-1978 NL Texel 53.04N 04.44E
		○ 25-06-1978 NL Texel 53.03N 04.44E; found dead
.4019245	pull.	● 25-05-1964 NL Vlieland 53.18N 05.00E
		○ 26-06-1964 NL Vlieland 53.18N 05.00E; dead for > 1 week - found
.4029131	pull.	● 19-05-1966 NL Vlieland 53.18N 05.00E
		○ 30-06-1966 NL Vlieland 53.18N 05.00E; freshly dead - found
.5054554	pull.	● 16-05-1972 NL Texel 53.06N 04.48E
		○ 02-07-1972 NL Texel 53.06N 04.48E; found dead
...61793	pull.	● 24-05-1931 NL Texel 53.00N 04.48E
		○ 05-07-1931 NL Texel 53.06N 04.48E; taken by owl or raptor
.5160064	pull.	● 04-05-1981 NL Texel 53.04N 04.44E
		○ 10-07-1981 NL Texel 53.02N 04.45E; only ring found

.514306	pull.	● 11-05-1979 NL Texel 53.04N 04.44E
		○ 11-07-1979 NL Texel 53.04N 04.44E; dead for > 1 week - found
.515783	pull.	● 20-06-1981 NL Schiermonnikoog 53.29N 06.12E
		○ 12-07-1981 NL Schiermonnikoog 53.29N 06.12E; dead for > 1 week - found
.401822	pull.	● 03-07-1963 NL Vlieland 53.18N 05.00E
		○ 15-07-1963 NL Vlieland 53.18N 05.00E
.5143065	pull.	● 16-05-1979 NL Texel 53.04N 04.44E
		○ 20-07-1979 NL Texel 53.01N 04.44E; found dead
.5114023	pull.	● 16-06-1978 NL Steggerda 52.52N 06.05E
		○ 23-07-1978 FRANCE Manche 49.14N 01.36W; freshly dead - shot
.3007932	pull.	● 24-05-1962 NL Ameland 53.30N 05.48E
		○ 26-07-1962 NL Ameland 53.24N 05.36E; dead for > 1 week - found
.4026734	pull.	● 20-06-1967 NL Vlieland 53.18N 05.00E
		○ 26-07-1967 NL Vlieland 53.18N 05.00E; freshly dead - found
.5126949	pull.	● 19-05-1978 NL Texel 53.04N 04.44E
		○ 27-07-1978 NL Texel 53.04N 04.44E; found dead
..168542	pull.	● 23-06-1937 NL Vlieland 53.18N 05.00E
		○ 28-07-1937 NL Vlieland 53.18N 05.00E; dead for > 1 week - found
.5126942	pull.	● 16-05-1978 NL Texel 53.04N 04.44E
		○ 31-07-1978 NL Texel 53.04N 04.44E; found dead
.5114401	pull.	● 19-05-1977 NL Texel 53.06N 04.48E
		○ 10-08-1977 NL Texel 53.06N 04.48E; dead for > 1 week through owl or raptor
.4010102	pull.	● 30-05-1961 NL Texel 53.12N 04.48E
		○ 12-08-1961 NL Texel 53.06N 04.48E; found dead
..157551	pull.	● 21-05-1935 NL Texel 53.12N 04.48E
		○ 14-08-1935 FRANCE Finistère 48.36N 04.30W; freshly dead - shot
..383820	pull.	● 08-07-1958 NL Vlieland 53.18N 05.00E
		○ 17-08-1958 NL Vlieland 53.18N 05.00E; found dead
.4019291	pull.	● 05-07-1964 NL Hoornsterzwaag 53.00N 06.12E
		○ 01-09-1964 GREAT BRITAIN Cornwall 50.30N 04.54W; freshly dead - shot
.401925	pull.	● 01-06-1964 NL Vlieland 53.18N 05.00E
		○ 01-09-1964 NL Vlieland 53.18N 05.00E; dead for > 1 week - found
.5042303	pull.	● 29-05-1970 NL Terschelling 53.24N 05.12E
		○ 06-09-1970 GREAT BRITAIN Lincoln 52.54N 00.00W; freshly dead - shot
..382529	pull.	● 03-06-1962 NL Terschelling 53.24N 05.30E
		○ 08-09-1962 PORTUGAL Beira Litoral 40.36N 08.48W; freshly dead - shot
.4048081	pull.	● 22-05-1973 NL Texel 53.06N 04.48E
		○ 15-09-1973 FRANCE Loire-Atlantique 47.24N 02.24W; freshly dead - shot
.4005698	pull.	● 21-06-1964 NL Bunnerveen 53.06N 06.30E
		○ 20-09-1964 PORTUGAL Beira Litoral 40.42N 08.36W; freshly dead - shot
....2050	pull.	● 09-06-1912 NL Assen 53.00N 06.36E
		○ 24-09-1912 NL Assen 53.00N 06.36E; dead for > 1 week - found
.5109265	pull.	● 09-06-1976 NL Luxwoude 53.00N 06.00E
		○ 02-10-1976 GREAT BRITAIN Essex 51.48N 00.48E; dead for > 1 week, washed ashore
..349346	pull.	● 07-07-1956 NL Ameland 53.24N 05.42E
		○ 07-10-1956 FRANCE Morbihan 47.42N 02.42W; freshly dead - shot
.5114404	pull.	● 19-05-1977 NL Texel 53.06N 04.48E
		○ 14-10-1977 NL Texel 53.06N 04.48E; ring and leg found

.5051759	pull.	● 21-06-1975 NL Jubbega 53.00N 06.06E
		○ 22-10-1975 GREAT BRITAIN Essex 51.30N 00.36E; freshly dead - shot
.4045905	pull.	● 29-05-1969 NL Texel 53.06N 04.42E
		○ 26-10-1969 SPAIN Pontevedra 42.12N 08.42W; freshly dead - shot
.4006762	pull.	● 18-05-1961 NL Noord-Holland 52.54N 04.42E
		○ 10-11-1961 FRANCE Manche 49.30N 01.48W; freshly dead - shot
.4048085	pull.	● 26-05-1973 NL Texel 53.06N 04.48E
		○ 15-11-1973 NL Texel 53.06N 04.48E dead for > 1 week - drowned
.5051651	pull.	● 02-06-1971 NL Terschelling 53.24N 05.30E
		○ 07-12-1971 FRANCE Côtes-du-Nord 48.54 03.00W; freshly dead - shot
.4017851	pull.	● 25-05-1963 NL Vlieland 53.18N 05.00E
		○ 24-12-1963 NL Zeeland, Brouwershaven 51.42N 03.54E; found dead
..250064	pull.	● 24-07-1951 NL Vlieland 53.18N 05.00E
		○ 25-12-1951 NL Vlieland 53.18N 05.00E; found dead
..250814	pull.	● 11-06-1953 NL Jubbega 53.00N 06.06E
		○ 25-12-1953 FRANCE Finistère 48.36N 04.06W; freshly dead - shot
.5124219	pull.	● 01-06-1978 NL De Hege Warren 53.06N 05.56E
		○ 01-01-1979 FRANCE Pas-de-Calais 50.24N 01.34E
.5142137	pull.	● 08-06-1981 NL Texel 53.10N 05.58E
		○ 03-01-1982 NL Noord-Holland 52.24N 04.40E; dead for > 1 week - found
.4011625	pull.	● 23-06-1963 NL Terschelling 53.24N 05.24E
		○ 17-01-1964 FRANCE Somme 50.12N 01.36E; freshly dead - shot
.4047904	pull.	● 16-06-1974 NL Texel 53.06N 04.48E
		○ 08-03-1975 NL Texel 53.06N 04.48E; dead for > 1 week - found

Eurasian Curlew W. Europe - (sub)adults when recovered

.400676	pull.	● 17-05-1961 NL Texel 53.00N 04.42E
		○ 15-07-1977 GREAT BRITAIN Cornwall 50.12N 04.48W; ring and leg found in tide line
..121437	pull.	● 01-06-1936 NL Oosterwolde 53.00N 06.18E
		○ 18-07-1946 NL Oosterwolde 53.00N 06.18E; found dead
.4014801	pull.	● 21-05-1962 NL Vlieland 53.18N 05.00E
		○ 31-08-1964 NL Vlieland 53.18N 05.00E
.4047956	pull.	● 08-06-1975 NL Texel 53.06N 04.48E
		○ 19-09-1976 NL Texel 53.06N 04.48E; ring and leg found
.4018123	pull.	● 14-05-1965 NL Drente 53.06N 06.42E
		○ 21-10-1966 GREAT BRITAIN Scilly Isles 49.54N 06.18W; shot
.510536	pull.	● 19-05-1976 NL Texel 53.04N 04.44E
		○ 08-12-1979 NL Texel 53.04N 04.44E; only ring found
.4005694	pull.	● 09-06-1964 NL Bunnerveen 53.06N 06.30E
		○ 15-12-1970 FRANCE Morbihan 47.36N 02.48W; freshly dead - shot
..165028	pull.	● 11-06-1938 NL Texel 53.12N 04.48E
		○ 25-01-1940 GREAT BRITAIN Devon 50.42N 03.30W
...87954	pull.	● 19-05-1931 NL Texel 53.12N 04.54E
		○ 25-01-1939 IRELAND Dublin 53.24N 06.06W; freshly dead - shot
..198204	pull.	● 04-06-1946 NL Texel 53.00N 04.48E
		○ 02-02-1954 FRANCE Manche 48.54N 01.30W; freshly dead - shot
.4048026	pull.	● 18-06-1976 NL Texel 53.06N 04.48E
		○ 01-03-1978 NL Texel 53.06N 04.48E; ring and leg found
..250811	pull.	● 17-05-1953 NL Gorredijk 53.01N 06.06E
		○ 15-03-1981 NL Wynjeterp 53.03N 06.09E; freshly dead - found

.4048083	pull.	● 22-05-1973 NL Texel 53.06N 04.48E
		○ 03-04-1975 NL Texel 53.06N 04.48E; freshly dead - found
..400321 Hiddensee	pull.	● 30-05-1965 GERMANY Wustrow 54.18N 12.24E
		○ 15-04-1969 NL Zurich 53.06N 05.24E; dead for > 1 week - found
..165022	pull.	● 18-06-1936 NL Texel 53.12N 04.48E
		○ 22-04-1938 NL Terschelling 53.24N 05.24E; found dead
.4022518	pull.	● 20-06-1967 NL Drente 53.06N 06.30E
		○ 15-05-1969 NL Drente 53.06N 06.30E; ring and leg found
.4016316	pull.	● 23-05-1964 NL Texel 53.06N 04.48E
		○ 19-05-1976 NL Noord-Holland Bergen 52.42N 04.42E; freshly dead - found
.4011162	pull.	● 20-05-1962 NL Texel 53.06N 04.48E
		○ 24-06-1964 NL Vlieland 53.18N 05.00E; freshly dead - found
Eurasian Curlew Fennoscandia - first winter birds or younger when recovered		
C..68020 Helsinki	pull.	● 06-06-1958 FINLAND Kaskö 62.18N 21.30E
		○ 24-01-1959 NL Noord-Holland 52.54N 04.48E; freshly dead - shot
Eurasian Curlew Fennoscandia - (sub)adults when recovered		
D..23837 Göteborg	pull.	● 29-06-1944 SWEDEN Öland 56.30N 16.31E
		○ 15-07-1947 NL Ameland; found dead
C..44024 Helsinki	pull.	● 04-06-1954 FINLAND Häme, Valkeakoski 61.18 24.12E
		○ 23-08-1955 NL Groningen 53.12N 06.36E; found dead
CT039107 Helsinki	pull.	● 07-07-1983 FINLAND Kuopio 63.32N 26.35E
		○ 17-10-1985 NL East-Holwerd 53.24N 05.54E: control
D....882 Göteborg	pull.	● 25-06-1924 SWEDEN Öland 56.12N 16.24E
		○ 23-11-1925 NL Groningen 53.24N 06.30E; found dead
Redshank N. part Netherlands - first winter birds or younger when recovered		
.115545	pull.	● 25-05-1981 NL Grou 53.06N 05.50E
		○ 07-06-1981 NL Idaerd 53.07N 05.50E; dead through traffic
.2002556	pull.	● 07-05-1959 NL Damwoude 53.18N 06.00E
		○ 10-06-1959 NL Damwoude 53.18N 06.00E; freshly dead - found
.1153764	pull.	● 03-06-1977 NL Achter de Zwarten 53.24N 06.12E
		○ 14-06-1977 NL Achter de Zwarten 53.24N 06.12E; taken by owl or raptor
.1102458	pull.	● 01-06-1973 NL Achter de Zwarten 53.24N 06.12E
		○ 15-06-1973 NL Peazemerlânnen 53.24N 06.06E; dead for > 1 week - found
.1153765	pull.	● 03-06-1977 NL Achter de Zwarten 53.24N 06.12E
		○ 18-06-1977 NL Achter de Zwarten 53.24N 06.12E; taken by owl or raptor
.1178531	pull.	● 18-06-1981 NL Bandpolder 53.24N 06.09E
		○ 19-06-1981 NL Bandpolder 53.24N 06.09E freshly dead - taken by mammal
.1178529	pull.	● 18-06-1981 NL Bandpolder 53.24N 06.09E
		○ 19-06-1981 NL Bandpolder 53.24N 06.09E; freshly dead - taken by mammal
.2021505	pull.	● 11-06-1965 NL Vlieland 53.18N 05.00E
		○ 24-06-1965 NL Vlieland 53.18N 05.00E; freshly dead - dead through traffic
.1178475	pull.	● 11-06-1981 NL Bandpolder 53.24N 06.09E
		○ 27-06-1981 NL Bandpolder 53.24N 06.09E; taken by owl or raptor
.1178532	pull.	● 18-06-1981 NL Bandpolder 53.24N 06.09E
		○ 27-06-1981 NL Bandpolder 53.24N 06.09E; taken by owl or raptor
.1184185	pull.	● 13-06-1981 NL Bandpolder 53.24N 06.09E
		○ 27-06-1981 NL Bandpolder 53.24N 06.09E; taken by owl or raptor
.1184158	pull.	● 01-06-1981 NL Bandpolder 53.24N 06.09E
		○ 27-06-1981 NL Bandpolder 53.24N 06.09E; taken by owl or raptor

.1163589	pull.	● 17-06-1978 NL Ezumazijl 53.22N 06.09E
		○ 29-06-1978 NL Ezumazij 53.21N 06.09E; taken by owl or raptor
.2016853	pull.	● 11-06-1963 NL Vlieland 53.18N 05.00E
		○ 01-07-1963 NL Vlieland 53.18N 05.00E; freshly dead - found
.2044784	pull.	● 22-05-1971 NL Jubbega 53.00N 06.06E
		○ 01-07-1971 NL Drachten 53.06N 06.06E; not freshly dead - found
.2016851	pull.	● 10-06-1963 NL Vlieland 53.18N 05.00E
		○ 07-07-1963 NL Vlieland 53.18N 05.00E; found dead
..290411	pull.	● 24-06-1958 NL Vlieland 53.18N 05.00E
		○ 09-07-1958 NL Vlieland 53.18N 05.00E; found dead
.2009561	pull.	● 28-06-1964 NL Vlieland 53.18N 05.06E
		○ 14-07-1964 NL Vlieland 53.18N 05.00E; found dead
.2023339	pull.	● 17-05-1968 NL Jubbega 53.00N 06.06E
		○ 14-07-1968 FRANCE Manche 49.18N 01.12W; freshly dead - shot
.1162743	pull.	● 20-05-1978 NL Gorredijk 53.00N 06.02E
		○ 15-07-1978 NL Van Oordt's Mersken 53.02N 06.03E; taken by owl or raptor
.1320667	pull.	● 03-06-1994 NL Ameland 53.27N 05.51E
		○ 16-07-1994 NL East-Holwerd 53.24N 05.54E: control
.200191	pull.	● 29-05-1967 NL Grote Veenpolder 53.06N 06.00E
		○ 18-07-1967 NL Haskerdijken 53.00N 05.54E; found dead
K.152018	pull.	● 30-06-1961 NL Texel 53.06N 04.54E
		○ 18-07-1961 NL Texel 53.06N 04.54E; freshly dead - taken by animal
.1132658	pull.	● 30-05-1977 NL Twellingea 53.00N 05.42E
		○ 24-07-1977 FRANCE Manche 48.36N 01.30W; freshly dead - shot
.1153775	pull.	● 04-06-1977 NL De Hoge Warren 53.06N 05.54E
		○ 24-07-1977 FRANCE Pas-de-Calais 50.30N 01.42E; freshly dead - shot
.115286	pull.	● 21-05-1977 NL Jubbega 53.00N 06.06E
		○ 24-07-1977 FRANCE Somme 50.12N 01.36E; freshly dead - shot
..152681	pull.	● 23-06-1934 NL Friens 53.06N 05.48E
		○ 25-07-1934 NL Twellingea 53.00N 05.42E; found sick - fate unknown
..218950	pull.	● 17-06-1948 NL Vlieland 53.18N 05.00E
		○ 25-07-1948 FRANCE Somme 50.12N 01.36E; freshly dead - shot
.1118359	pull.	● 16-06-1975 NL Terschelling 53.24N 05.24E
		○ 26-07-1975 NL Vlieland 53.18N 05.00E; control
.11629	pull.	● 22-05-1979 NL Gorredijk 53.00N 06.04E
		○ 30-07-1979 FRANCE Calvados 49.17N 00.15W; freshly dead - shot
.1169416	pull.	● 31-05-1979 NL Bandpolder 53.24N 06.08E
		○ 30-07-1979 MOROCCO Essaouira 31.31N 09.46W; freshly dead - killed by man not shot
.1163258	pull.	● 10-06-1978 NL Oudega 53.07N 06.00E
		○ 01-08-1978 FRANCE Gironde 44.46N 01.08W; freshly dead - shot
.1167468	pull.	● 03-06-1980 NL Peazemerlânnen 53.25N 06.06E
		○ 01-08-1980 NL Peazemerlânnen 53.24N 06.05E; not freshly dead
.2040356	pull.	● 21-06-1969 NL Drachten 53.06N 06.06E
		○ 04-08-1969 FRANCE Calvados 49.18N 00.18W; freshly dead - shot
.114352	pull.	● 09-06-1977 NL Giekerk 53.15N 05.54E
		○ 06-08-1977 NL East-Holwerd 53.24N 05.54E: control
.20036	pull.	● 25-06-1962 NL Workumerwaard 53.00N 05.24E
		○ 09-08-1962 FRANCE Pas-de-Calais 50.36N 01.36E; freshly dead - shot

..290419	pull.	● 31-07-1958 NL Vlieland 53.18N 05.00E
		○ 11-08-1958 NL Vlieland 53.18N 05.00E; control
.1325054	pull.	● 03-06-1995 NL Garijp 53.10N 05.57E
		○ 12-08-1995 NL East-Holwerd 53.24N 05.54E: control
.2021591	pull.	● 05-06-1966 NL Vlieland 53.18N 05.00E
		○ 13-08-1966 NL Hallum 53.18N 05.48E; control
.111544	pull.	● 20-06-1973 NL Ameland 53.30N 05.42E
		○ 15-08-1973 NL Ameland 53.24N 05.42E; dead for > 1 week - found
.1090403	pull.	● 03-06-1971 NL Terschelling 53.24N 05.18E
		○ 15-08-1971 FRANCE Gironde 45.36N 01.06W; freshly dead - shot
.1360745	pull.	● 27-05-1998 NL Akkerwoude 53.19N 05.59E
		○ 15-08-1998 NL East-Holwerd 53.24N 05.54E: control
.1153886	pull.	● 13-06-1977 NL Westergeest 53.18N 06.06E
		○ 16-08-1977 FRANCE Manche 49.24N 01.12W; found shot and wounded - fate unknown
.1121028	pull.	● 09-06-1974 NL Rotstergaast 52.54N 05.54E
		○ 17-08-1974 PORTUGAL Algarve 37.00N 08.00W; freshly dead - shot
.1173333	pull.	● 29-06-1979 NL Veenwouden 53.14N 05.59E
		○ 19-08-1979 FRANCE Calvados 49.17N 00.15W; freshly dead - shot
.1172096	pull.	● 18-06-1979 NL Bandpolder 53.24N 06.09E
		○ 21-08-1979 NL Schiermonnikoog 53.29N 06.12E; control
.2003436	pull.	● 05-06-1961 NL Workumerwaard 53.00N 05.24E
		○ 27-08-1961 FRANCE Charente-Maritime 46.18N 01.06W; freshly dead - shot
.108988	pull.	● 12-06-1971 NL Drogeham 53.12N 06.06E
		○ 08-09-1971 NL Drogeham 53.12N 06.06E; freshly dead - entangled
...12267	pull.	● 22-06-1912 NL Texel 53.06N 04.48E
		○ 20-09-1912 PORTUGAL Beira Litoral 40.12N 08.54W; freshly dead - shot
..289194	pull.	● 28-06-1958 NL Frieschepalen 53.06N 06.12E
		○ 21-09-1958 FRANCE Gironde 44.42N 01.12W; freshly dead - shot
...20112	pull.	● 13-06-1914 NL Texel 53.06N 04.48E
		○ 04-10-1914 SPAIN Huelva 37.18N 07.00W; freshly dead - shot
.1142206	pull.	● 18-05-1976 NL Jubbega 53.00N 06.06E
		○ 21-10-1976 FRANCE Bouches-de-Rhône 46.24N 04.42E; freshly dead - shot
.115799	pull.	● 09-06-1980 NL Peebos 53.12N 06.14E
		○ 01-11-1980 SENEGAL Dakar 14.45N 17.31W; freshly dead - found
..404930	pull.	● 14-06-1960 NL Luxwoude 53.00N 06.00E
		○ 13-11-1960 FRANCE Charente-Maritime 45.54N 01.12W; freshly dead - shot
.1154995	pull.	● 14-06-1980 NL Grou 53.06N 05.50E
		○ 20-11-1980 PORTUGAL Ribatejo 38.54N 08.53W; freshly dead - shot
D..57338	pull.	● 18-07-1945 NL Hallum 53.18N 05.48E
		○ 09-12-1945 FRANCE Pas-de-Calais 51.00N 01.48E; freshly dead - shot
..225755	pull.	● 04-07-1953 NL Ameland 53.30N 05.42E
		○ 13-01-1954 SPAIN Cádiz 36.42N 06.06W; freshly dead - shot
...16003	pull.	● 21-06-1913 NL Texel 53.06N 04.48E
		○ 25-03-1914 PORTUGAL Algarve 37.06N 08.42W; freshly dead - shot
.2017592	pull.	● 05-06-1964 NL Vlieland 53.18N 05.00E
		○ 31-03-1965 FRANCE Somme 50.18N 01.36E; freshly dead - shot
..107207	pull.	● 19-06-1933 NL Vlieland 53.18N 05.00E
		○ 08-04-1934 SENEGAL Sine-Saloum 14.00N 16.48W; freshly dead - shot

.1124725	pull.	● 21-07-1974 NL East-Holwerd 53.24N 05.54E
		○ 18-04-1975 DENMARK Jylland 56.48N 08.18E; control
.116593	pull.	● 31-05-1979 NL Hoptille 53.10N 05.41E
		○ 21-04-1980 NL Hijlaard 53.10N 05.43E; dead through traffic
Redshank N part Netherlands - older than first winter when recovered		
.1153848	pull.	● 08-06-1977 NL Anjum 53.23N 06.08E
		○ 06-07-1981 NL Paesens 53.25N 06.05E; freshly dead - found
.1153858	pull.	● 09-06-1977 NL Jouswier 53.21N 06.05E
		○ 14-07-1979 FRANCE Gironde 44.40N 01.03W; freshly dead - shot
.111008	pull.	● 07-07-1973 NL Terschelling 53.22N 05.13E
		○ 22-07-1978 FRANCE Pas-de-Calais 50.57N 01.57E; freshly dead - shot
.1288025	> 2 c.y.	● 03-04-1992 NL De Valom 53.16N 06.02E; breeding bird
		○ 28-07-1998 NL East-Holwerd 53.24N 05.54E: control
.1354653	> 2 c.y.	● 27-04-1998 NL Zwagermieden 53.16N 06.02E; breeding bird
		○ 01-08-2000 NL East-Holwerd 53.24N 05.54E: control
.1309016	pull.	● 20-05-1993 NL Roodkerk 53.15N 05.56E
		○ 15-08-1995 NL East-Holwerd 53.24N 05.54E: control
.2039378	pull.	● 07-06-1969 NL Nijesyl 53.00N 05.36E
		○ 16-08-1970 PORTUGAL Algarve 37.06N 07.42W; freshly dead - shot
.1172061	pull.	● 13-06-1979 NL Peazemerlânnen 53.24N 06.06E
		○ 18-08-1980 NL Peazemerlânnen 53.24N 06.06E: control
...33712	pull.	● 06-06-1924 NL Texel 53.06N 04.54E
		○ 15-10-1927 FRANCE Somme 50.12N 01.36E; freshly dead - shot
..223721	pull.	● 23-06-1952 NL Tjeukemeer 52.54N 05.48E
		○ 02-12-1953 FRANCE Vendée 46.24N 01.06W
.2007801	pull.	● 22-06-1961 NL Frieschepalen 53.06N 06.12E
		○ 05-12-1963 FRANCE Charente-Maritime 46.12N 01.30W; freshly dead - shot
.2012365	pull.	● 12-06-1968 NL Molkwar 52.54N 05.24E
		○ 06-12-1970 MOROCCO Agadir 30.24N 09.18W; freshly dead - shot
.200913	pull.	● 02-06-1965 NL De Hoge Warren 53.06N 05.54E
		○ 13-12-1968 PORTUGAL Estremadura 38.30N 08.54W; shot
.1115448	pull.	● 22-06-1973 NL Ameland 53.27N 05.41E
		○ 30-12-1976 FRANCE Manche 49.04N 01.35W; freshly dead - shot
.2001906	pull.	● 06-06-1966 NL Grote Veenpolder 53.06N 06.00E
		○ 20-01-1969 SENEGAL Casamance 12.36N 16.36W; freshly dead - shot
.1124343	pull.	● 28-06-1974 NL Toppenhuzen 53.01N 05.42E
		○ 24-01-1981 SPAIN Sevilla 37.18N 06.15W; freshly dead - shot
..201210	pull.	● 03-07-1949 NL Westergeest 53.18N 06.06E
		○ 20-02-1956 PORTUGAL Beira Litoral 40.36N 08.42W; freshly dead - shot
.202141	pull.	● 19-06-1976 NL Langweer 52.58N 05.43E
		○ 22-02-1979 FRANCE Loire-Atlantique 47.18N 02.31W; freshly dead - shot
.2017593	pull.	● 05-06-1964 NL Vlieland 53.18N 05.00E
		○ 13-03-1966 MOROCCO Casablanca 33.42N 07.36W
.2019354	pull.	● 13-06-1964 NL Vlieland 53.18N 05.00E
		○ 23-03-1969 FRANCE Pas-de-Calais 50.30N 01.36E; freshly dead - shot
.2023321	pull.	● 20-05-1967 NL Jubbega 53.00N 06.06E
		○ 29-03-1971 FRANCE Charente-Maritime 45.48N 01.00W
..166003	pull.	● 12-06-1938 NL Vlieland 53.18N 05.00E
		○ 07-04-1947 FRANCE Aude 43.12N 03.06E; freshly dead - shot

.1316648	> 1 c.y.	● 09-07-1997 NL East-Holwerd 53.24N 05.54E
		○ 11-04-2000 NL Grootegast 53.13N 06.16E: ring read with binoculars
..289060	pull.	● 24-06-1961 NL Ameland 53.30N 05.42E
		○ 16-04-1963 FRANCE Hérault 43.36N 03.54E; freshly dead - shot
.2017564	pull.	● 31-05-1964 NL Vlieland 53.18N 05.00E
		○ 19-04-1972 NL Vlieland; found dead
..201236	pull.	● 19-06-1951 NL Westergeest 53.18N 06.06E
		○ 21-04-1954 FRANCE Pas-de-Calais 50.48N 01.36E; freshly dead - shot
.1314403	> 1 c.y.	● 17-09-1993 NL East-Holwerd 53.24N 05.54E
		○ 25-04-1997 NL Zwagermieden 53.16N 06.02E; breeding bird - control
		○ 01-05-2000 NL Wouterswoude 53.18N 06.01E; freshly dead
..218958	pull.	● 27-06-1948 NL Noord-Holland 52.54N 04.48E
		○ 26-04-1953 FRANCE Somme 50.12N 01.30E; freshly dead - shot
.2027477	pull.	● 19-06-1966 NL Vlieland 53.18N 05.00E
		○ 28-04-1969 NL Terschelling 53.24N 05.24E; freshly dead - found
.2003631	pull.	● 21-06-1960 NL Zurich 53.06N 05.24E
		○ 29-04-1962 FRANCE Gironde 44.42N 01.12W; freshly dead - shot
..218520	pull.	● 08-06-1958 NL Molkwar 52.54N 05.24E
		○ 05-05-1961 FRANCE Gironde 44.42N 01.00W; freshly dead - shot
..218516	pull.	● 29-05-1957 NL Friens 53.06N 05.48E
		○ 11-05-1961 FRANCE Gironde 44.42N 01.06W; freshly dead - shot
.2017561	pull.	● 27-05-1964 NL Vlieland 53.18N 05.00E
		○ 24-05-1973 NL Vlieland 53.18N 05.00E; dead for > 1 week - found
.1172146	pull.	● 11-06-1979 NL Bandpolder 53.24N 06.08E
		○ 25-05-1982 NL Peazemerlânnen 53.24N 06.06E; control
.2007806	pull.	● 09-06-1963 NL Bunnerveen 53.06N 06.30E
		○ 02-06-1965 FRANCE Eure-et-Loire 48.12N 01.36E; found dead
.1169381	pull.	● 26-05-1979 NL Leeuwarden 53.12N 05.48E
		○ 03-06-1980 NL Leeuwarden 53.12N 05.48E; dead for > 1 week through traffic
...55460	pull.	● 16-06-1927 NL Vlieland 53.18N 05.00E
		○ 05-06-1933 FRANCE Somme 50.12N 01.36E; freshly dead - shot
.1165936	pull.	● 31-05-1979 NL Baijum 53.10N 05.38E
		○ 24-06-1981 NL lens 53.08N 05.37E; freshly dead - dead through traffic
.2016559	pull.	● 29-05-1963 NL Vlieland 53.18N 05.00E
		○ 25-06-1965 SPAIN Cádiz 36.48N 06.24W; freshly dead - shot
Redshank Fennoscandia - first winter birds or younger when recovered		
AT162038 Helsinki	pull.	● 10-07-1997 FINLAND Vehkalati, Kymy, 60.25N 27.26E
		○ 05-09-1997 NL Schiermonnikoog 53.29N 06.12E; control
Redshank Fennoscandia - older than first winter when recovered		
A.268564 Helsinki	pull.	● 04-07-1966 FINLAND Vaasa, Kristinestad 62.12N 21.18E
		○ 03-07-1973 NL Vlieland 53.18N 05.00E; control
Redshank Denmark & Germany - first winter birds or younger when recovered		
Redshank Denmark & Germany - older than first winter when recovered		
Redshank British isles - first winter birds or younger when recovered		
DR.13674 London	pull.	● 03-06-1974 GREAT BRITAIN Aberdeen 57.06N 02.36W
		○ 12-08-1974 NL Vlieland 53.18N 05.00E; control
DA..5939 London	pull.	● 15-06-1975 GREAT BRITAIN Northumberland 55.24N 01.48W
		○ 05-02-1976 NL Groningen 53.24N 06.42E; freshly dead - frost victim

Redshank British isles - older than first winter when recovered		
Redshank Iceland - first winter birds or younger when recovered		
..747092 Reykjavik	pull.	● 21-06-1993 ICELAND Miklavatn 66.04N 19.08W ○ 22-09-1993 NL East-Holwerd 53.24N 05.54E: control
Redshank Iceland - older than first winter when recovered		
..734065 Reykjavik	> 1 c.y.	● 17-06-1981 ICELAND Borgarnes 64.32N 21.48W; breeding bird ○ 03-11-1981 NL Schiermonnikoog 53.29N 06.12E; control
742830 Reykjavik	pull.	● 02-07-1986 ICELAND Blikalon 66.29N 16.15W ○ 09-04-1989 NL East-Holwerd 53.24N 05.54E: control
Turnstone - Nearctic population		
K. 225015	> 1 c.y.	● 10-09-1964 NL Vlieland 53.16N 04.59E ○ 27-06-1966 NE CANADA Hazen meer 81.49N 71.18W; shot - with brood patches
Turnstone - Fennoscandian population		
AT..2000 Helsinki	pull.	● 24-06-1970 FINLAND Uusima, Helsinki 60.12N 25.12E ○ 31-07-1973 NL Schiermonnikoog 53.30N 06.12E; control ○ 17-07-1981 FINLAND Uusima, Helsinki 60.07N 25.25E; control - breeding male
SV.. 6478 Vollebekk	pull.	● 21-07-1971 NORWAY Tranöy 69.09N 17.25E ○ 09-10-1971 NL Westplaat, Brielse Gat 51.56N 04.02E; killed by raptor
A. 338289 Helsinki	pull.	● 13-07-1968 FINLAND Majholm Nauvo 60.16N 22.02E ○ 07-12-1968 NL De Hors, Texel 53.00N 04.45E; not freshly dead

Table 2. Recoveries of waders, which were ringed/ recovered in or near the Dutch part of the Wadden Sea and ringed/ recovered north of 62°N.

Ring	Age	Details										Distance	Direction	Days
					Ringed Plover									
H.155366	> 1 c.y.	●	30	8	79	NL		12	53.29	N	6.12	E	male		
		○	11	8	80	NORWAY		23	70.09	N	28.52	E	control	2183	32	346
					Grey Plover									
.1155434	> 2 c.y.	●	9	5	81	NL		05	53.22	N	5.54	E			
		○	31	5	81	RUSSIA		15	67.34	N	53.11	E	freshly dead - shot	2992	58	22
					Red Knot									
..290348	> 1 c.y.	●	16	7	64	NL		02	53.18	N	5.18	E			
		○	7	6	66	GREENLAND	2-		77.30	N	69.18	W		4150	310	692
..724076 Reykjavik	> 1 c.y.	●	23	5	72	ICELAND	1-		64.18	N	21.42	W			
		○	30	7	75	NL		01	53.18	N	5.00	E	control	1952	129	1164
..725809 Reykjavik	> 1 c.y.	●	9	8	72	ICELAND	1-		64.48	N	22.36	W			
		○	2	9	73	NL		01	53.18	N	5.00	E	control	2017	129	389
..725159 Reykjavik	> 1 c.y.	●	28	7	72	ICELAND	1-		64.30	N	22.24	W			
		○	2	9	73	NL		01	53.18	N	5.00	E	control	1993	129	401
..725968 Reykjavik	> 1 c.y.	●	10	8	72	ICELAND	1-		64.47	N	22.36	W			
		○	8	9	79	NL		13	53.33	N	6.28	E	dead for > 1 week, found	2060	127	2586
..744552 Reykjavik	> 1 c.y.	●	28	5	87	ICELAND			65.31	N	23.10	W			
		○	23	9	98	NL		12	53.30	N	6.12	E		2116	129	4136

Ring / Station	Age		d	m	y	Place		Lat		Long		Notes			
..725254 Reykjavik	> 1 c.y.	●	28	7	72	ICELAND	1-	64.48	N	22.36	W				
		○	24	9	73	NL	12	53.30	N	6.12	E	control	2053	128	423
..720536 Reykjavik	> 1 c.y.	●	12	8	70	ICELAND	1-	64.24	N	21.36	W				
		○	24	9	73	NL	12	53.30	N	6.12	E	control	1989	128	1138
	1 c.y.	●	28	9	76	NL	5	53.16	N	5.33	E				
		○	12	5	85	NORWAY		69.20	N	19.20	E	control	1927		3149
	1 c.y.	●	10	11	78	NL	5	53.16	N	5.33	E				
		○	26	5	87	ICELAND		65.31	N	23.10	W	control	2106		119
..721182 Reykjavik	> 1 c.y.	●	28	7	72	ICELAND	1-	64.48	N	22.36	W				
		○	18	11	72	NL	17	53.06	N	5.18	E	found dead	2047	129	113
...78296 Reykjavik	full gr.	●	21	5	57	ICELAND	1-	64.06	N	22.42	W				
		○	29	11	58	NL	03	53.24	N	5.12	E	found dead	1988	127	558
..724794 Reykjavik	> 1 c.y.	●	15	5	70	ICELAND	1-	64.18	N	21.42	W				
		○	10	12	72	NL	03	53.24	N	5.12	E	freshly dead - attracted by light	1953	128	39
..724224 Reykjavik	> 1 c.y.	●	23	5	72	ICELAND	1-	64.18	N	21.42	W				
		○	13	12	74	NL	05	53.18	N	5.36	E	control	1979	128	935
K.388037	full gr.	●	6	1	73	NL	14								
		○	23	6	74	CANADA	4-	80.06	N	86.00	W	finding date ± 3 days, found dead			534
K.215359	> 1 c.y.	●	13	1	65	NL	02	53.18	N	5.18	E				
		○	15	6	74	GREENLAND	2-	77.30	N	69.18	W	finding date ± 2 weeks, freshly shot	4150	310	3441
..724997 Reykjavik	> 1 c.y.	●	28	7	72	ICELAND	1-	64.36	N	22.24	W				
		○	1	6	73	NL	00	53.12	N	4.54	E	found dead	2002	129	308
Sanderling															
..894259 Stavanger	1 c.y.	●	30	8	71	NORWAY	26	62.30	N	6.00	E				
		○	21	8	74	NL	1	53.12	N	4.54	E	control	1036	184	1087
Dunlin															
.8114259 Stavanger	full gr.	●	25	8	71	NORWAY	23	70.06	N	29.48	E				
		○	2	8	72	NL	01	53.18	N	5.00	E	control	2258	214	342
.8158687 Stavanger	1 c.y.	●	22	9	75	NORWAY	26	62.30	N	6.02	E				
		○	11	8	78	NL	12	53.29	N	6.12	E	control	1002	179	1054
..201209 Moskwa	1 c.y.	●	12	8	88	RUSSIA		69.50	N	31.35	E				
		○	14	8	91	NL	12	53.29	N	6.12	E	control			1183
H.116377	> 1 c.y	●	17	8	74	NL	05	53.19	N	5.40	E				
		○	28	8	78	NORWAY	23	70.09	N	28.52	E	control	2215	32	1472
.8522991	1 c.y	●	14	8	91	NORWAY	26	62.30	N	6.02	E				
		○	19	8	93	NL	12	53.29	N	6.12	E		1002	179	1090
.8112037 Stavanger	1 c.y.	●	9	9	72	NORWAY	26	62.30	N	6.00	E				
		○	21	8	74	NL	01	53.18	N	5.00	E	control	1024	183	712
.8243648 Stavanger	1 c.y.	●	3	9	89	NORWAY		62.58	N	7.03	E				
		○	21	8	96	NL	1	53.18	N	5.00	E	control	1024	183	2543
KT.18256 Helsinki	>2 c.y.	●	18	7	93	FINLAND		63.09	N	27.42	E				
		○	21	8	93	NL	12	53.29	N	6.12	E	control			
.8112112 Stavanger	1 c.y.	●	11	9	72	NORWAY	26	62.30	N	6.00	E				
		○	23	8	74	NL	01	53.18	N	5.00	E	control	1024	183	712

Ring no. / Scheme	Age		day	mo	yr	Country		Lat	N	Lon	E	Notes			
.8158249	1 c.y.	●	14	9	75	NORWAY	26	62.30	N	6.02	E				
Stavanger		○	26	8	84	NL	12	53.29	N	6.12	E	control	1002	179	3266
.8101257	1 c.y.	●	23	9	70	NORWAY	26	62.30	N	6.00	E				
Stavanger		○	27	8	71	NL	12	53.30	N	6.12	E	control	1000	179	338
..892649	1 c.y.	●	15	9	70	NORWAY	26	62.30	N	6.00	E				
Stavanger		○	27	8	71	NL	12	53.30	N	6.12	E	freshly dead - captured not shot	1000	179	346
.892649	1 c.y.	●	15	9	70	NORWAY	26	62.30	N	6.02	E				
Stavanger		○	27	8	71	NL	12	53.29	N	6.12	E	control	1002	179	314
.8101257	1 c.y.	●	23	9	70	NORWAY	26	62.30	N	6.02	E				
Stavanger		○	27	8	71	NL	12	53.29	N	6.12	E	control	1002	179	306
..892649	1 c.y.	●	15	9	70	NORWAY	26	62.30	N	6.00	E				
Stavanger		○	27	8	71	NL	12	53.30	N	6.12	E	freshly dead - captured not shot	1000	179	346
DA.01778	1 c.y.	●	31	8	77	NORWAY	23	70.09	N	28.52	E				
Oslo		○	30	8	79	NL	12	53.29	N	6.12	E	found dead in tide line	2183	212	730
.8152038	1 c.y.	●	31	7	74	NORWAY	23	70.06	N	30.12	E				
Stavanger		○	4	9	75	NL	12	53.30	N	6.12	E	finding date ± 3 days, control	2214	214	400
H.188538	> 1 c.y.	●	16	9	93	NL	12	53.29	N	6.12	E				
		○	18	7	99	FINLAND		63.09	N	27.40	E	control	1643	49	2131
H.133283	> 1 c.y.	●	18	9	77	NL	1	53.16	N	4.59	E				
		○	25	5	85	FINLAND		62.37	N	29.40	E	control	1782	54	2806
		○	26	5	85	FINLAND		62.37	N	29.40	E	control	1782	54	2807
PT.10386	1 c.y.	●	18	9	76	FINLAND	85	64.48	N	24.36	E				
Helsinki		○	20	9	77	NL	12	53.30	N	6.12	E	control	1629	220	367
DA.02967	1 c.y.	●	21	8	78	NORWAY	23	70.09	N	28.52	E				
Oslo		○	24	9	79	NL	12	53.29	N	6.12	E	control	2183	212	399
..886375	full gr.	●	29	8	68	NORWAY	23	70.06	N	29.48	E				
Stavanger		○	1	10	73	NL	01	53.18	N	5.00	E	control	2258	214	1859
PT.10233	1 c.y.	●	2	9	76	FINLAND	85	64.48	N	24.36	E				
Helsinki		○	24	9	76	NL	05	53.18	N	5.36	E	control	1669	220	22
.8112032	1 c.y.	●	9	9	72	NORWAY	26	62.30	N	6.00	E				
Stavanger		○	8	10	72	NL	01	53.18	N	5.00	E	control	1024	183	29
..8372119	1 c.y.	●	19	8	90	NORWAY	26	62.30	N	6.02	E				
Stavanger		○	12	10	91	NL	5	53.24	N	5.54	E	control	1002	179	426
.8155019	1 c.y.	●	12	8	76	NORWAY	23	70.04	N	29.45	E				
Stavanger		○	3	11	81	NL	12	53.29	N	6.12	E	control	2201	213	1909
.8150161	1 c.y.	●	10	8	73	NORWAY	23	70.09	N	28.52	E				
Stavanger		○	9	11	78	NL	12	53.29	N	6.12	E	control	2183	212	1918
DA.02580	1 c.y.	●	17	8	78	NORWAY	23	70.09	N	28.52	E				
Oslo		○	19	11	79	NL	05	53.25	N	6.06	E	control	2193	212	459
P.243902	> 1 c.y.	●	18	5	69	FINLAND	81	62.36	N	29.42	E				
Helsinki		○	29	1	75	NL	1	53.18	N	5.06	E	control	1773	234	2083
Arnhem	2 c.y.	●	17	4	87	NL	12	53.23	N	5.54	E				
		○	19	6	93	RUSSIA	36	71.18	N	72.07	E	male breeding on 4 eggs			

.8147199	full gr.	○	16	8	73	NORWAY	23	70.06	N	29.48	E				
Stavanger		○	30	5	74	NL	12	53.30	N	6.12	E	ring in pellet	2203	213	288
..050811	1 c.y.	●	13	8	83	RUSSIA	36	69.50	N	31.34	E				
Moskwa		○	31	5	84	NL	12	53.30	N	6.12	E	control			

Bar-tailed Godwit

.1113635	> 1 c.y.	●	9	8	74	NL	01	53.18	N	5.00	E				
		○	4	6	76	RUSSIA	36	69.18	N	88.06	E	found dead	4674	68	664
.1300713	>2 c.y.	●	9	8	94	NL	12	53.30	N	6.12	E				
		○	5	6	98	RUSSIA		72.57	N	94.59	E	shot			
.1135114	> 1 c.y.	●	13	8	79	NL	01	53.16	N	4.59	E				
		○	2	6	80	RUSSIA	29	65.34	N	72.44	E	freshly dead - shot	4021	70	293
.1224792	>1 c.y.	●	16	10	85	NL	12	53.30	N	6.12	E				
		○	12	5	86	RUSSIA		66.21	N	42.43	E	shot			208
.1224126	>2 c.y.	●	5	5	91	NL		52.33	N	04.37	E	female			
		○	0	6	95	RUSSIA		c. 72.00	N	102.15	E	shot			
.1286126	>2 c.y.	●	10	5	93	NL	12	53.30	N	6.12	E				
		○		7	97	RUSSIA		73.05	N	113.50	E	shot			
.71032	1 c.y.	●	12	9	80	NORWAY		62.30	N	6.02	E				
Stavanger		○	18	5	98	NL	1	53.04	N	4.47	E	control	1047		6457
.1225934	> 2 c.y.	●	18	5	85	NL	01	53.24	N	6.06	E	male			
		○	4	6	89	RUSSIA		66.00	N	68.00	E	shot	4141		1478
.1321087	>2 c.y.	●	27	5	95	NL		53.02	N	4.46	E	female			
		○	0	8	96	RUSSIA		68.20	N	88.56	E	found dead			
.1014326	full gr.	●	1	6	62	NL	05	53.18	N	5.48	E				
		○	6	6	68	RUSSIA	33	67.30	N	86.36	E	freshly dead - shot	4630	70	2196

Eurasian Curlew

.5254393	> 1 c.y.	●	26	7	90	NL	5	53.24	N	5.54	E				
		○	8	8	98	SWEDEN		65.51	N	22.17	E	found dead			
.4028939	> 1 c.y.	●	31	8	65	NL	01	53.18	N	5.00	E				
		○	3	5	67	RUSSIA	10	62.36	N	40.36	E	freshly dead - shot	2328	64	611
.4028540	full gr.	●	7	9	67	NL	01	53.18	N	5.00	E				
		○	15	9	70	RUSSIA	13	63.30	N	48.54	E	finding date ± 2 weeks, freshly shot	2777	66	1104
.5131226	> 1 c.y.	●	10	9	77	NL	05	53.25	N	6.06	E				
		○	21	10	80	FINLAND	81	63.22	N	27.45	E	finding date ± 6 weeks, shot	1670	49	1137
.4028801	full gr.	●	19	9	66	NL	01	53.17	N	5.01	E				
		○	18	8	78	RUSSIA	13	63.27	N	49.30	E	freshly dead - shot	2809	66	4351
.5058453	> 1 c.y.	●	26	9	72	NL	01	53.18	N	5.00	E				
		○	6	7	76	FINLAND	81	62.48	N	26.42	E	shot	1649	50	1379
.5058566	> 1 c.y.	●	6	10	72	NL	01	53.18	N	5.00	E				
		○	1	7	75	FINLAND	85	64.18	N	27.24	E	dead for > 1 week, found	1768	46	999
CT039107	pull.	●	7	7	83	FINLAND		63.32	N	26.35	E				
		○	17	10	85	NL	5	53.22	N	5.54	E	controlled; female			
C..68020	pull.	●	6	6	58	FINLAND	88	62.18	N	21.30	E				
Helsinki		○	24	1	59	NL	14	52.54	N	4.48	E	freshly dead - shot	1438	223	232

Spotted Redshank															
	full gr.	●	7	5	81	NL	5	52.59	N	5.26	E				
		○	20	6	82	SWEDEN		65.19	N	18.00		ring read	1544		409
Common Redshank															
A.268564 Helsinki	pull.	●	4	7	66	FINLAND	88	62.12	N	21.18	E				
		○	3	7	73	NL	01	53.18	N	5.00	E	control	1379	224	2555
.1193976	>1 c.y.	●	15	8	83	NL	12	53.29	N	6.12	E				
		○	15	10	88	ICELAND		65.41	N	18.05	W	found dead			
.2012187	> 1 c.y.	●	2	9	65	NL	01	53.18	N	5.00	E				
		○	5	7	68	ICELAND	1-	65.30	N	21.54	W	finding date ± 1 week, found dead	2024	312	1037
.2022385	> 1 c.y.	●	10	9	64	NL	01	53.18	N	5.00	E				
		○	31	5	67	ICELAND	1-	65.36	N	17.06	W	found dead	1840	318	994
.1159113	> 1 c.y.	●	17	9	77	NL	5	53.21	N	5.49	E				
		○	15	7	85	ICELAND		64.50	N	23.00	W	ring found			
..734065 Reykjavik	> 1 c.y.	●	17	6	81	ICELAND	1-	64.32	N	21.48	W	breeding			
		○	3	11	81	NL	12	53.29	N	6.12	E	control	2006	128	139
1159173	full gr.	●	15	12	77	NL	5	53.24	N	6.06	E				
		○	2	7	81	ICELAND		65.43	N	18.20	W	not freshly dead			
.1314847	> 2 c.y.	●	6	4	96	NL	5	53.24	N	6.06	E				
		○	21	6	99	ICELAND		65.38	N	17.00	W	ring read with binoculars			
.1192752	> 2 c.y.	●	19	4	83	NL	5	53.24	N	6.06	E				
		○	15	6	83	ICELAND		66.11	N	18.50	W	leg and ring found			
.1155414	> 2 c.y.	●	8	5	81	NL	5	53.24	N	5.54	E				
		○	28	5	83	NORWAY		63.59	N	12.06	E	killed by raptor			
Common Greenshank															
.1083435	> 1 c.y.	●	11	8	78	NL	12	53.29	N	6.12	E				
		○	4	5	83	FINLAND		62.41	N	6.12	E	freshly dead			
Ruddy Turnstone															
K.196778	> 1 c.y.	●	8	9	64	NL	01	53.18	N	5.06	E	male			
		○	5	6	65	GREENLAND	2-	68.42	N	52.42	W	freshly dead - shot	3491	299	270
K.225015	> 1 c.y.	●	10	9	64	NL	01	53.18	N	5.00	E				
		○	27	6	66	CANADA	4-	81.48	N	71.18	W	breeding bird; freshly dead - shot	4197	319	656

Table 3. Recoveries of waders connecting the Dutch part of the Wadden Sea with the staging grounds in Africa

Ring	Age	Details	Distance	Direction	Days
Ringed Plover					
BX.14201	1 c.y.	● 7 9 72 MOROCCO 4 32.42 N 9.00 W			
London		○ 5 8 75 NL 01 53.18 N 5.00 E control	2549	26	1063
H.110335	> 1 c.y.	● 17 8 72 NL 01 53.18 N 5.00 E			
		○ 24 4 77 MOROCCO 04 33.18 N 7.48 W freshly dead - shot	2446	205	1711
Grey Plover					
.1172273	> 1 c.y.	● 11 8 80 NL 5 53.24 N 5.54 E			
		○ 12 1 85 GUINEA BISSAU 11.15 N 15.40 W freshly dead - shot			
.1316918	> 2 c.y.	● 30 8 98 NL 5 53.24 N 5.54 E			
		○ 20 4 0 MOROCCO 33.00 N 8.50 E control			
.1166819	> 1 c.y.	● 5 9 78 NL 12 53.29 N 6.12 E			
		○ 31 10 81 MOROCCO 04 32.55 N 8.50 W captured alive and released	2582	208	1151
.1212943	1 c.y.	● 28 10 84 NL 5 53.24 N 5.54 E			
		○ 16 4 93 GUINEA BISSAU 11.22 N 16.07 W control			
.1174893	?	● 24 11 79 NL 12 53.29 N 6.12 E			
		○ 25 5 85 MOROCCO 33.37 N 7.35 W found dead			
Red Knot					
K.398698	> 1 c.y.	● 30 7 73 NL 12 53.29 N 6.12 E 5084			
		○ 20 12 86 GUINEA BISSAU 11.23 N 15.58 W control			
..419340	1 c.y.	● 4 3 73 SOUTH AFRICA 33.06 S 18.00 E	9689		6790
		○ 10 10 91 NL 12 53.29 N 6.12 E control; moulting primaries			
Sanderling					
yellow1		● 4 85 MAURITANIA 16 19.40 N 16.21 W			
		○ 11 6 85 NL 5 53.24 N 6.06 E sighting yellow underwings			
Curlew Sandpiper					
B.127484	1 c.y.	● 1 10 70 NL 01 53.18 N 5.00 E			
		○ 25 8 72 WEST SAHARA 17 28.00 N 12.18 W control	3154	207	693
Dunlin					
B.127611	> 1 c.y.	● 9 8 72 NL 12 53.30 N 6.12 E			
		○ 2 4 73 MOROCCO 04 32.18 N 9.12 W freshly dead - found in tide line	2660	208	236
H.207419	>1 c.y.	● 11 8 91 NL 12 53.30 N 6.12 E			
		○ MOROCCO 4 33.16 N 7.35 W dead			
JA155734	> 1 c.y.	● 4 3 69 TUNISIA 05 36.54 N 10.18 E			
	> 1 c.y.	○ 17 8 72 NL 12 53.30 N 6.12 E control	1872	350	1262
		○ 15 2 74 TUNISIA 05 36.54 N 10.18 E control	1872	170	1809
JY..3974	> 1 c.y.	● 22 9 69 TUNISIA 05 36.54 N 10.18 E			
Paris		○ 7 9 72 NL 12 53.30 N 6.12 E finding date ± 3 days, control	1872	350	1081
H.128237	>1 c.y.	● 11 9 75 NL 12 53.30 N 6.12 E			
		○ 15 1 76 TUNISIA 5 35.31 N 10.58 E freshly dead - shot	2036	169	126
H.125941	> 1 c.y.	● 19 9 74 NL 01 53.16 N 4.59 E			
		○ 24 10 81 MOROCCO 04 32.55 N 8.50 W captured alive and released	2517	206	2591

Ring / Place	Age	●/○	Day	Mon	Yr	Country	Reg	Lat	N/S	Long	E/W	Notes			
SA696359 Paris	>1 c.y.	●	10	3	81	MOROCCO		32.50	N	8.46	W				
		○	25	10	87	NL	12	53.30	N	6.12	E	control			
SA696025 Paris	> 1 c.y.	●	1	3	81	MOROCCO	04	32.50	N	8.46	W				
		○	29	10	81	NL	12	53.29	N	6.12	E	control	2588	28	242
		○	26	8	84	NL	12	53.29	N	6.12	E	control	2588	28	1272
H.151755	> 1 c.y.	●	9	11	78	NL	12	53.29	N	6.12	E				
		○	5	1	80	MOROCCO	04	32.33	N	9.05	W	freshly dead - shot	2628	208	422
Bar-tailed Godwit															
.1264435	> 1 c.y.	●	10	8	89	NL	12	53.29	N	6.12	E				
		○	25	4	93	GUINEA BISSAU		11.22	N	16.07	W				
FT.60038 Paris	> 1 c.y.	●	16	11	73	MAURITANIA	16	19.40	N	16.21	W	female			
		○	14	8	80	NL	5	53.24	N	5.55	E	control	4215	27	2463
.1213259	> 2 c.y.	●	5	5	88	NL	5	53.24	N	5.12	E	male			
		○	15	8	98	GUINEA BISSAU		11.15	N	15.52	W	found			
.1257135	> 1 c.y.	●	5	5	88	NL	5	53.20	N	5.45	E				
		○	14	3	93	GUINEA BISSAU		11.32	N	15.55	W	found			
yellow1		●		4	85	MAURITANIA	16	19.40	N	16.21	W				
		○	9	5	85	NL	5	53.24	N	6.06	E	sighting yellow underwings			
		○	18	5	85	NL	5	53.24	N	6.06	E	sighting yellow underwings			
FT.92333	> 1 c.y.	●	20	12	86	MAURITANIA	16	19.40	N	16.21	W				
		○	16	5	87	NL	5	53.20	N	5.45	E	control			
.1281730	> 2 c.y.	●	22	5	92	NL	5	53.02	N	4.45	E	female			
		○	10	9	92	GUINEA BISSAU		11.50	N	16.25	W	shot	4999		339
.1218465	full gr.	●	24	5	84	NL	5	53.24	N	6.08	E	male			
		○	10	9	92	GUINEA BISSAU		11.50	N	16.25	W	shot	5031		3031
Spotted Redshank															
.1169658	full gr.	●	22	9	79	NL	05	53.20	N	5.45	E				
		○	31	3	80	MOROCCO	04	32.38	N	8.42	W	freshly dead - shot	2575	207	190
Common Redshank															
.1109322	> 1 c.y.	●	3	7	73	NL	01	53.18	N	5.00	E				
		○	30	3	76	MOROCCO	04	34.18	N	6.36	W	freshly dead - taken by raptor	2303	204	1001
.1125570	> 1 c.y.	●	5	7	75	NL	01	53.18	N	5.00	E				
		○	27	1	78	MOROCCO	04	32.36	N	9.06	W	freshly dead - shot	2563	206	936
.1234843	> 1 c.y.	●	27	7	90	NL	5	53.24	N	5.54	E				
		○	27	11	91	IVORY COAST		5.17	N	3.55	W	found dead			
.1167504	> 1 c.y.	●	19	8	80	NL	05	53.25	N	6.06	E				
		○	10	1	81	SENEGAL	18	14.55	N	17.07	W	freshly dead - shot	4747	206	144
.1268235	1 c.y.	●	21	8	92	NL	5	53.24	N	5.54	E				
		○	22	11	94	SIERRA LEONE		9.30	N	12.10	W	captured and released			
.1271237	1 c.y.	●	23	8	90	NL	12	53.30	N	6.12	E				
		○	26	7	96	MOROCCO		33.37	N	7.35	E				
.1314365	> 1 c.y.	●	7	9	93	NL	5	53.24	N	5.54	E				
		○	26	3	97	GUINEA BISSAU		9.20	N	13.24	W	freshly dead - shot			
.1177310	> 1 c.y.	●	4	4	81	NL	5	53.19	N	5.57	E				
			23	3	82	MOROCCO		33.00	N	8.50	W				

Ring	Age		Day	Mo	Yr	Country		Lat		N	Long			Notes			
.1169416	pull.	●	31	5	79	NL	5	53.24		N	6.08		E				
		○	30	7	79	MOROCCO	04	31.31		N	9.46		E	freshly dead - captured not shot	2450	173	60
.2017593	pull.	●	5	6	64	NL	01	53.18		N	5.00		E				
		○	13	3	66	MOROCCO	04	33.42		N	7.36		W		2398	205	647
.2001906	pull.	●	6	6	66	NL	05	53.06		N	6.00		E				
		○	20	1	69	SENEGAL	18	12.36		N	16.40		W	freshly dead - shot	4937	204	958
.1157990	pull.	●	9	6	80	NL	07	53.12		N	6.14		E				
		○	1	11	80	SENEGAL	18	14.45		N	17.30		W	freshly dead - found	4765	206	145
.2012365	pull.	●	12	6	68	NL	05	52.54		N	5.24		E				
		○	6	12	70	MOROCCO	04	30.24		N	9.18		W	freshly dead - shot	2774	206	908
..107207	pull.	●	19	6	33	NL	01	53.18		N	5.00		E				
		○	8	4	34	SENEGAL	18	14.00		N	16.48		W	freshly dead - shot	4779	204	294

Common Greenshank

Ring	Age		Day	Mo	Yr	Country		Lat		N	Long			Notes			
.1109413	> 1 c.y.	●	15	7	73	NL	01	53.18		N	5.00		E				
		○	19	4	75	MOROCCO	04	32.18		N	9.12		W	freshly dead - shot	2598	206	644
.1124638	> 1 c.y.	●	29	6	74	NL	01	53.18		N	5.00		E				
		○	11	9	75	NIGERIA	26	4.18		N	6.06		E	freshly dead - shot	5447	179	439

Ruddy Turnstone

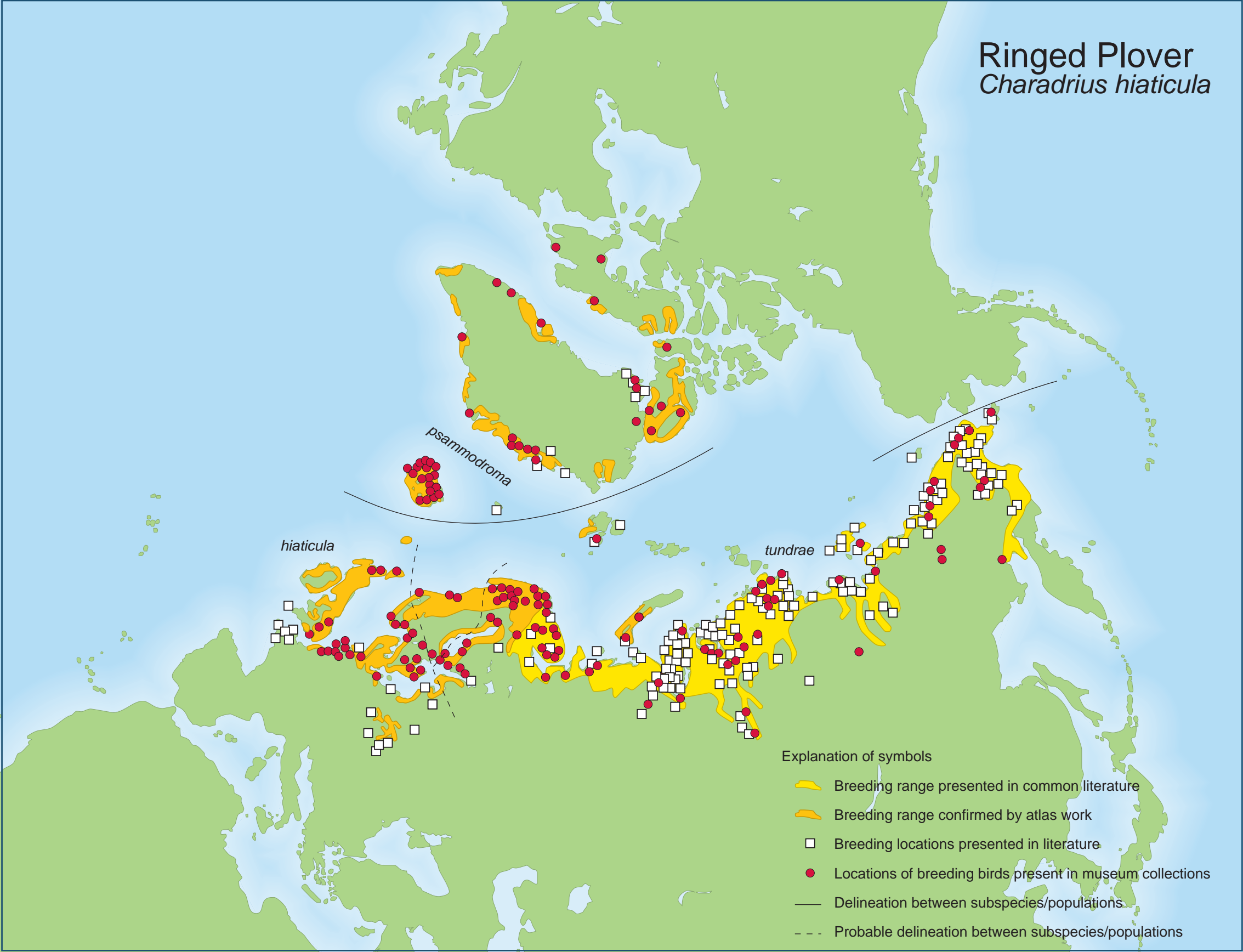| Ring	Age		Day	Mo	Yr	Country		Lat		N	Long			Notes			
K.445348	> 1 c.y.	●	18	7	72	NL	01	53.18		N	5.00		E				
		○	1	5	75	MOROCCO	04	33.18		N	8.30		W	freshly dead - shot	2470	206	1018
K.571481	> 2 c.y.	●	4	5	84	NL	5	53.22		N	5.54		E				
		○	26	2	86	MAURITANIA		19.52		N	16.20		W	control			

EXPLANATION OF THE BREEDING DISTRIBUTION MAPS

Breeding range presented in common literature. General breeding ranges are given a light-yellow colour. Breeding distribution based on ornithological Atlas-work. When breeding was confirmed by recent Atlas-work a yellow-ochre colour was used. Breeding sites as reported from literature. White squares symbolize breeding sites with evidence of breeding from literature.

Locations of breeding birds present in museum collections. Museum specimens with brood patches or birds reported with nests and/or young are presented as red circles. In some cases birds with brood patches were collected outside their known breeding range: these might be waders on the return migration to southerly areas, but it might also indicate a breeding area not yet reported. Therefore, these dots were shown as well.
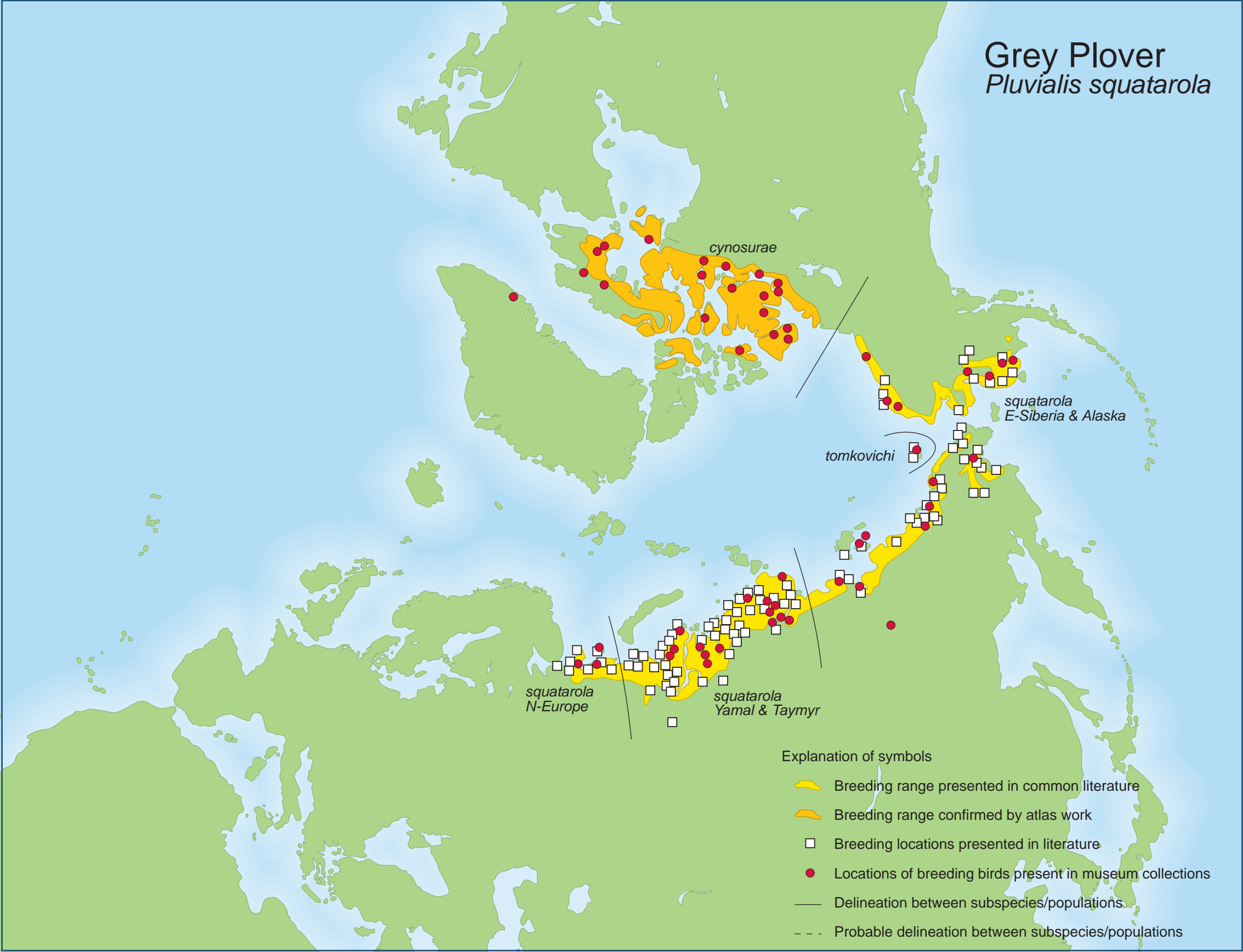
Black lines delineate the boundaries between subspecies or populations. Evident boundaries are presented as drawn black lines, probable boundaries as interrupted black lines. Zones of intermixing between subspecies can be recognized by the bordering interrupted black lines, showing the boundary most likely between the zone of intermixing and the single-subspecies region.
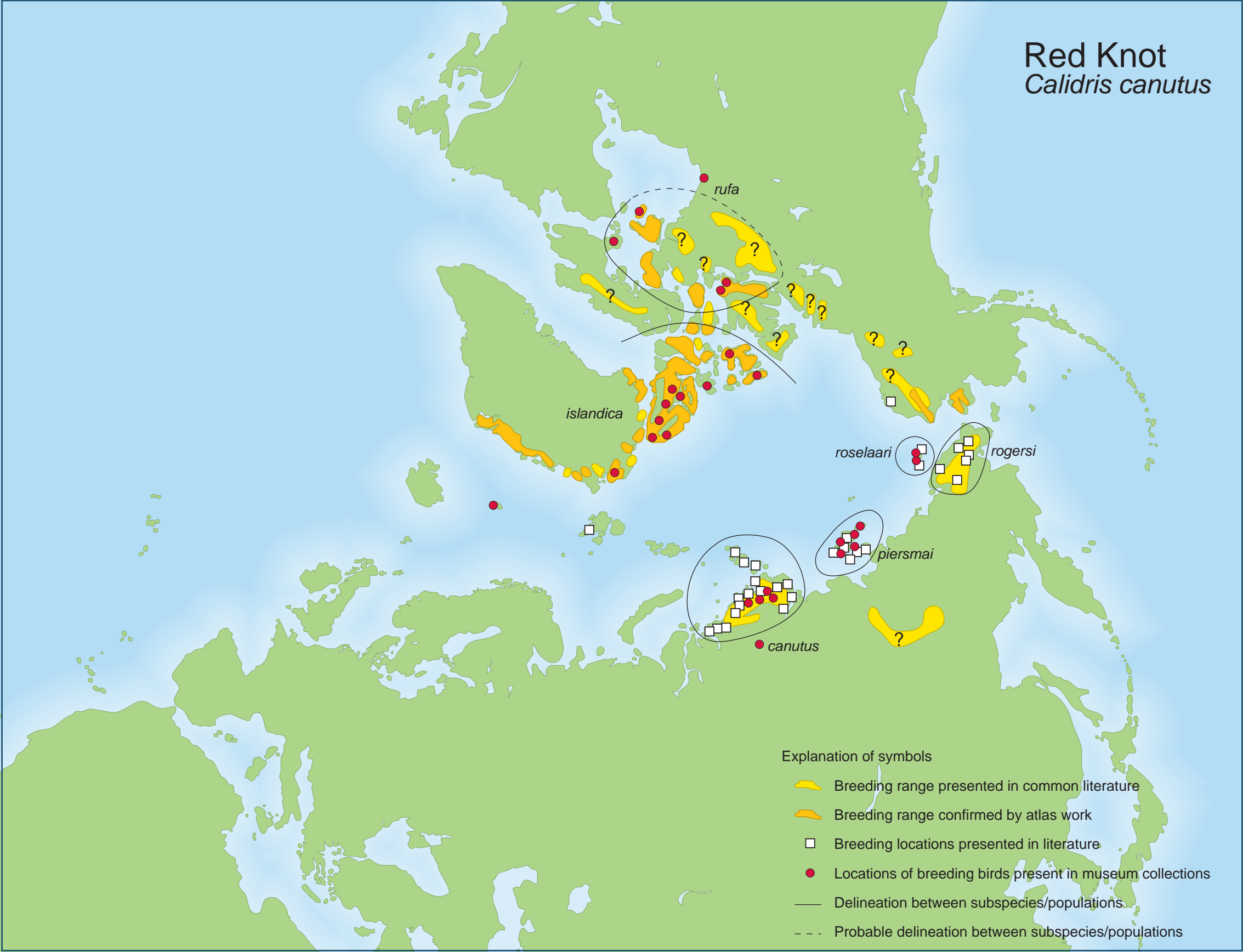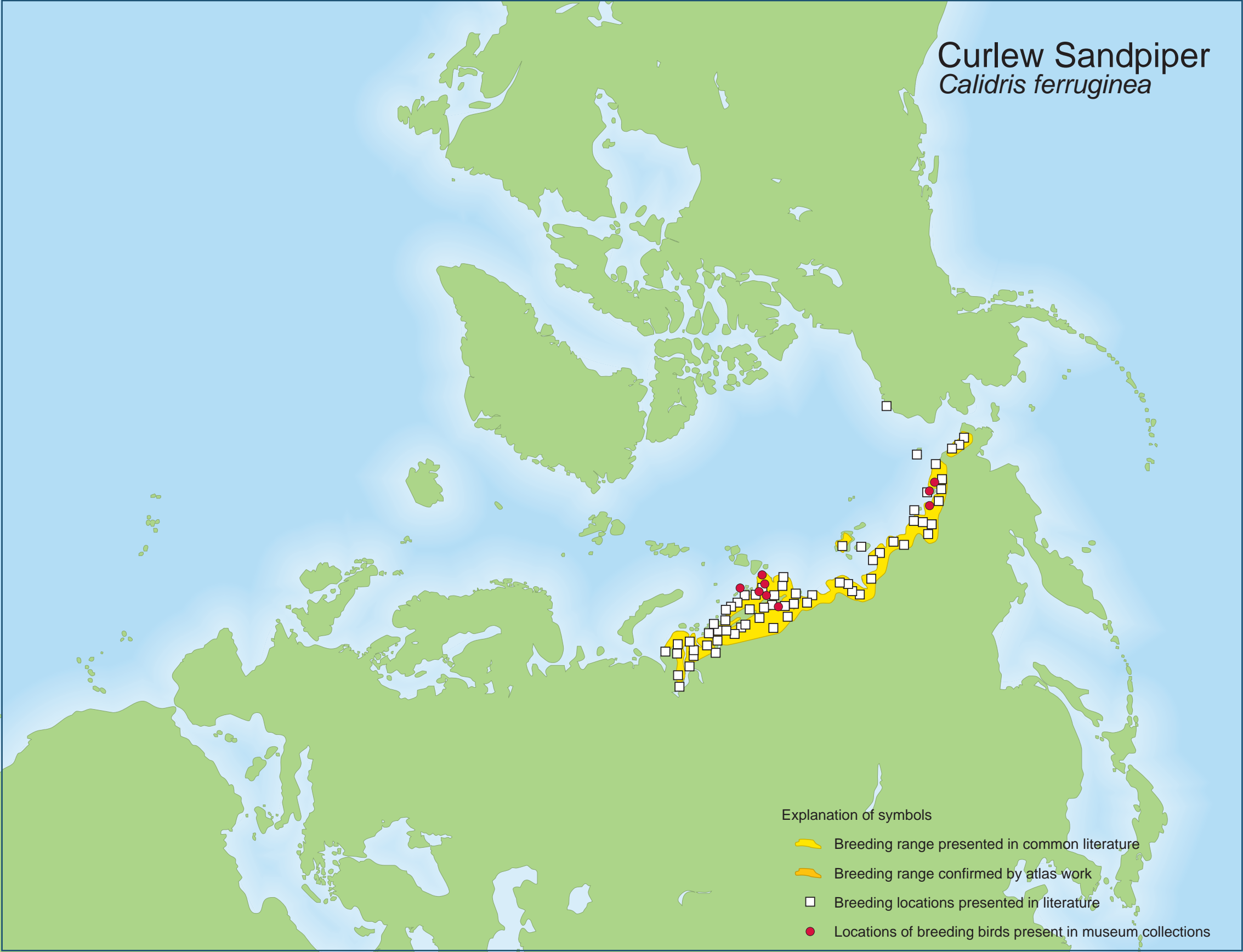
Ringed Plover
Charadrius hiaticula

psammodroma

hiaticula

tundrae

Explanation of symbols

Breeding range presented in common literature

Breeding range confirmed by atlas work

☐ Breeding locations presented in literature

⬤ Locations of breeding birds present in museum collections

—— Delineation between subspecies/populations

- - - Probable delineation between subspecies/populations

Grey Plover
Pluvialis squatarola

cynosurae

squatarola
E-Siberia & Alaska

tomkovichi

squatarola
N-Europe

squatarola
Yamal & Taymyr

Explanation of symbols

Breeding range presented in common literature

Breeding range confirmed by atlas work

☐ Breeding locations presented in literature

● Locations of breeding birds present in museum collections

— Delineation between subspecies/populations

- - - Probable delineation between subspecies/populations

Red Knot
Calidris canutus

rufa

islandica

roselaari

rogersi

piersmai

canutus

Explanation of symbols

- Breeding range presented in common literature
- Breeding range confirmed by atlas work
- □ Breeding locations presented in literature
- ● Locations of breeding birds present in museum collections
- — Delineation between subspecies/populations
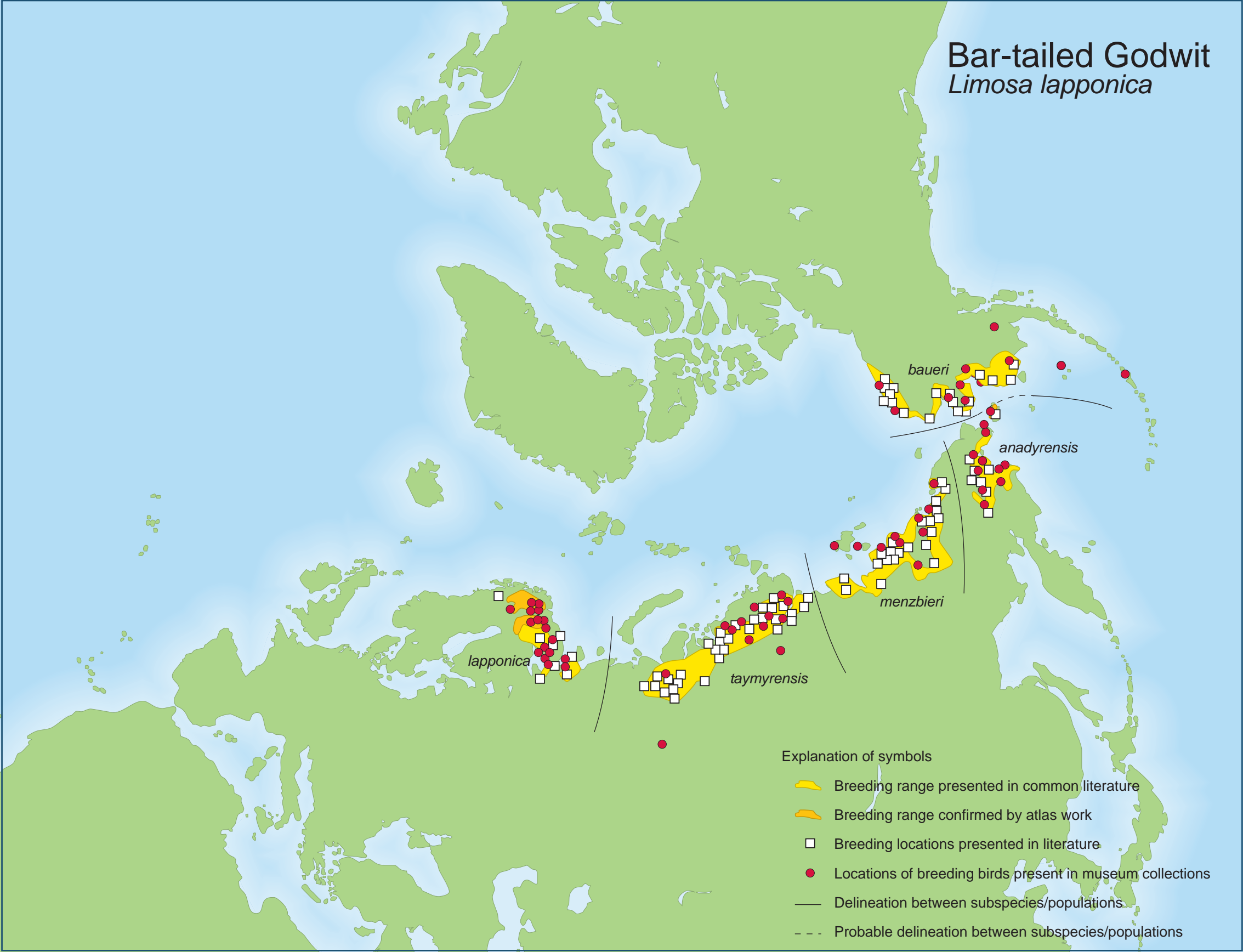- – – Probable delineation between subspecies/populations

Curlew Sandpiper
Calidris ferruginea

Explanation of symbols

- Breeding range presented in common literature
- Breeding range confirmed by atlas work
- □ Breeding locations presented in literature
- ● Locations of breeding birds present in museum collections

Dunlin
Calidris alpina

hudsonia

arcticola

arctica

pacifica

sakhalina

schinzii

kistchinski

alpina

centralis

actites

Explanation of symbols

Breeding range presented in common literature

Breeding range confirmed by atlas work

Breeding locations presented in literature

Locations of breeding birds present in museum collections

Delineation between subspecies/populations

Probable delineation between subspecies/populations

Bar-tailed Godwit
Limosa lapponica

baueri

anadyrensis

menzbieri

lapponica

taymyrensis

Explanation of symbols

Breeding range presented in common literature

Breeding range confirmed by atlas work

□ Breeding locations presented in literature

● Locations of breeding birds present in museum collections

— Delineation between subspecies/populations

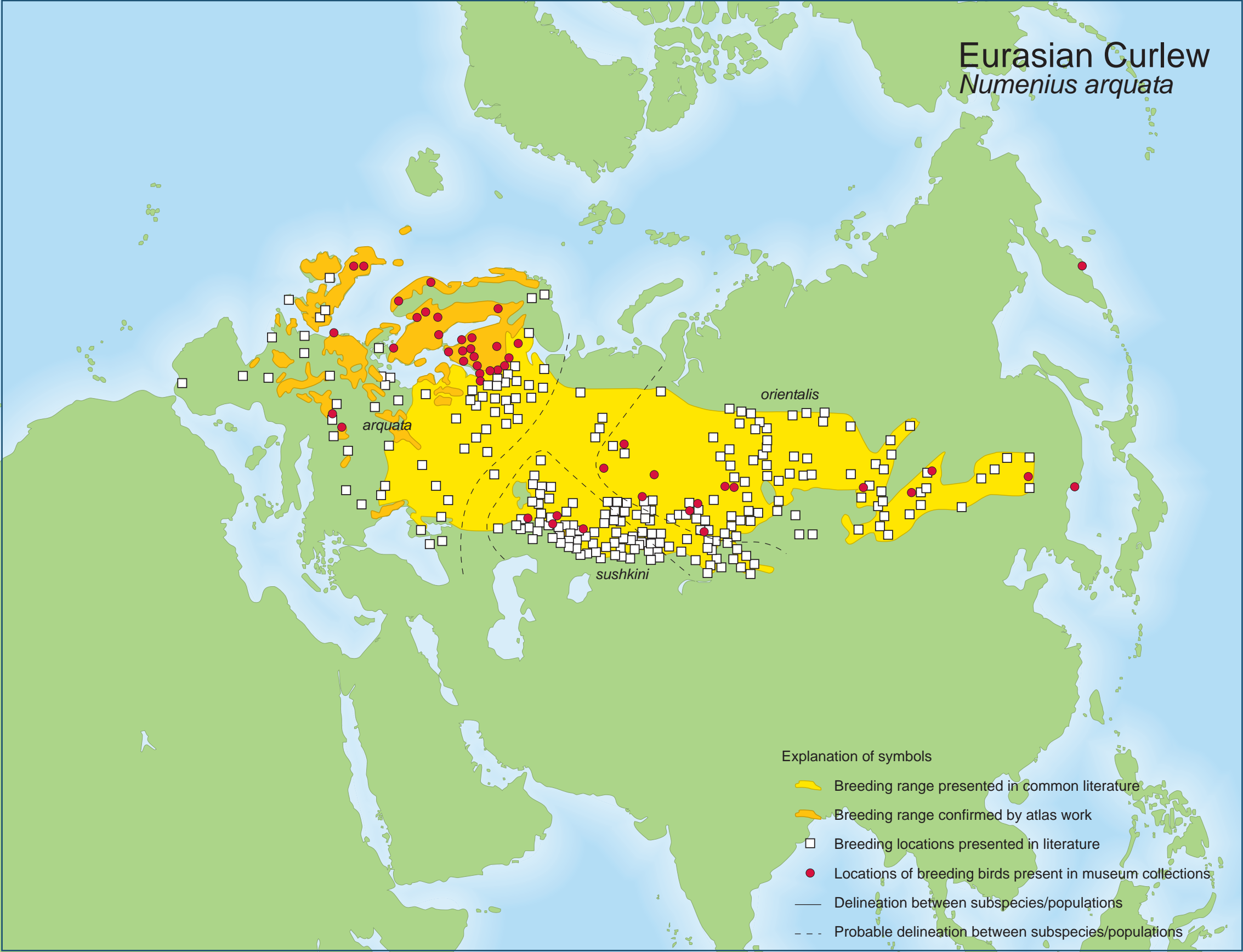- - - Probable delineation between subspecies/populations

Eurasian Curlew
Numenius arquata

orientalis

arquata

sushkini

Explanation of symbols

Breeding range presented in common literature

Breeding range confirmed by atlas work

Breeding locations presented in literature

Locations of breeding birds present in museum collections

Delineation between subspecies/populations

Probable delineation between subspecies/populations

Redshank
Tringa totanus

robusta

totanus

britannica

ussuriensis

terrignotae

?

?

?

?

?

craggi?

eurhinus

Explanation of symbols

Breeding range presented in common literature

Breeding range confirmed by atlas work

☐ Breeding locations presented in literature

● Locations of breeding birds present in museum collections

Delineation between subspecies/populations

Probable delineation between subspecies/populations