

Sanderlings using African–Eurasian flyways: a review of current knowledge

JEROEN RENEERKENS¹, ABDELAZIZ BENOUSSA², HELEN BOLAND³, MARK COLLIER^{4,5},
KIRSTEN GROND¹, KLAUS GÜNTHER⁶, GUNNAR THOR HALLGRIMSSON⁷, JANNIK HANSEN⁸,
WŁODZIMIERZ MEISSNER⁹, BRECHT DE MEULENAER¹⁰, YAA NTIAMOA-BAIDU¹¹,
THEUNIS PIERSMA^{1,12}, MARTIN POOT⁵, MARC VAN ROOMEN¹³, RON W. SUMMERS¹⁴,
PAVEL S. TOMKOVICH¹⁵ & LES G. UNDERHILL¹⁶

¹Animal Ecology Group, Centre for Ecological and Evolutionary Studies,
University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands. J.W.H.Reneerkens@rug.nl

²Département de Biologie, Faculté des Sciences, Université Mohammed V Agdal,
Avenue Ibn Batouta BP 1014, Rabat, Morocco

³Birdwatch Ireland, No. 1 Springmount, Newtownmountkennedy, Co. Wicklow, Eire, Ireland

⁴British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2AD, United Kingdom

⁵Bureau Waardenburg, PO Box 365, 4100 AJ, Culemborg, The Netherlands

⁶Schutzstation Wattenmeer, Nationalparkhaus, Hafestraße 3, D-25813 Husum, Germany

⁷Institute of Biology, University of Iceland, Sturlugata 7, 101 Reykjavík, Iceland

⁸National Environmental Research Institute, Department of Arctic Environment,
University of Aarhus, Frederiksborgvej 399, PO Box 358, DK-4000 Roskilde, Denmark

⁹Avian Ecophysiology Unit, Department of Vertebrate Ecology & Zoology,
University of Gdańsk, Al. Legionów 9, 80-441 Gdańsk, Poland

¹⁰Strodekkeersstraat 4, 9000 Ghent, Belgium

¹¹Centre for African Wetlands/Department of Zoology, University of Ghana, PO Box 67, Legon, Accra, Ghana

¹²Department of Marine Ecology, Royal Netherlands Institute for Sea Research,
PO Box 59, 1790 AB, Den Burg, The Netherlands

¹³SOVON Dutch Centre for Field Ornithology, Rijksstraatweg 178, 6573 DG Beek-Ubbergen, The Netherlands

¹⁴Lismore, Mill Crescent, North Kessock, Inverness, IV1 3XY, Scotland

¹⁵Zoological Museum, Moscow State University, Bolshaya Nikitskaya Str. 6, Moscow 125009, Russia

¹⁶Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch 7701, South Africa

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Despite the worldwide occurrence of Sanderlings *Calidris alba* on popular beaches, strikingly little is known about their biology compared to other common waders. Here we review the limited available knowledge of Sanderlings that use African–Eurasian flyways. The basis for this review was a workshop on Sanderlings, held during the International Wader Study Group conference in Jastrzębia Góra, Poland in 2008. We focus on biogeography, trends, numbers, diet, migration patterns and reproduction. Gaps in our knowledge are identified and we discuss the evidence for a Siberian origin of Sanderlings wintering in NW Europe, and plead for more non-estuarine surveys and collaboration between colour-ring projects both in space and time to get a better understanding of population dynamics and migration phenology.

INTRODUCTION

The Sanderling *Calidris alba* is a long-distance migratory wader that occurs worldwide in coastal areas (particularly on sandy beaches) during the non-breeding season. The breeding range is restricted to the High Arctic tundra of eastern Canada, Greenland and central Siberia (Fig. 1). Despite their presence on sandy beaches visited by people and their appeal to many birdwatchers and biologists, strikingly little is known about Sanderlings compared to many other common wader species. The High Arctic breeding range of Sanderlings is not conducive to studies of breeding biology, so perhaps we

should not be surprised that their breeding system is still not fully understood and that the links between the breeding and non-breeding grounds of different populations are not well established (Langston 2002). Surely, the extensive but scattered non-breeding distribution of Sanderlings makes monitoring of the species difficult.

Yet, there are several good reasons to give the research on Sanderlings a boost. The worldwide non-breeding distribution allows comparisons between wintering populations at different latitudes. The contrast in breeding investments where some Sanderling pairs (presumably) double-clutch and other pairs incubate single clutches together (Parmelee



Fig. 1. Distribution map of Sanderlings in the East Atlantic flyway (dark grey curved line) and the Mediterranean, W-Asia/E African flyway (light grey curved line) based on Scott (in prep.).

Breeding areas are shown in grey, the winter distribution in black. Straight lines link the ringing and recovery locations of six Sanderlings from Russia recovered in Europe or vice versa. The most important locations that are mentioned in the text are indicated with numbers:

- 1: Ellesmere Island, Canada
- 2: Zackenberg, Greenland
- 3: Taimyr peninsula, Russia
- 4: New Siberian islands, Russia
- 5: Kola peninsula, Russia
- 6: Sandgerði, Iceland
- 7: The Wash, Great Britain
- 8: Wadden Sea, the Netherlands, Germany and Denmark
- 9: Brittany, France
- 10: Banc d'Arguin, Mauritania
- 11: Esiama, Ghana
- 12: Barr al Hikman, Oman
- 13: Walvis Bay, Namibia.

& Payne 1973, Reneerkens *et al.* 2008a, but see Pienkowski & Green 1976) is not known in any other wader species, and offers fascinating research possibilities. The complex, but fascinating migration and breeding patterns of Sanderlings require clarification. The site-fidelity of Sanderlings to non-breeding grounds, stopover sites during migration as well as breeding territories, offers opportunities for various studies on survival, migration and reproduction. Furthermore, hardly any other bird species inhabits sandy beaches to the extent that Sanderlings do. Thus, Sanderlings provide an indicator of the ecological state of sandy beaches (cf. Piersma & Lindström 2004), which, like so much other wader habitat, suffer worldwide from increasing human pressure (recreation, habitat destruction, beach nourishment, pollution; Morrison *et al.* 2001, Stroud *et al.* 2004).

In order to bring together all the available knowledge about Sanderlings in Africa and Eurasia, a workshop was held during the International Wader Study Group conference in Jastrzębia Góra, Poland in 2008. Here, we summarise some of the available information as presented during the workshop, supplemented with literature data. Based on this overview, we indicate what we still do not know and which aspects deserve future research.

BIOGEOGRAPHY AND SIZE OF THE FLYWAY POPULATION

For a long time, Sanderlings have been presumed to be monotypic (e.g. Gosbell & Minton 2001), but based on biometri-

cal data and plumage descriptions, Engelmoer & Roselaar (1998) described two subspecies. The nominate subspecies *Calidris alba alba* breeds in Greenland, Jan Mayen, Svalbard and Siberia and winters along the Atlantic coast of Europe and Africa (the E Atlantic Flyway) as well as the east coast of Africa and W and central Asia (the E and S African and SW Asian Flyway). *C. alba rubidus* breeds in the Canadian arctic and Alaska and spends the non-breeding season along the coasts of the Americas. Although Engelmoer & Roselaar (1998) pooled all specimens from Siberia and treated them as one population belonging to *C. alba alba*, they also suggested that Sanderlings from the Lena Delta and New Siberian Islands could possibly belong to the Nearctic *C. alba rubidus*. More study specimens, especially from the eastern part of the Siberian breeding grounds will help to clarify this uncertainty. It remained unclear to which subspecies the Sanderlings from NE Canada (Ellesmere Island) belong, but recent data indicate that at least some of them use the E Atlantic Flyway (Reneerkens *et al.* 2008b; see below) and are therefore likely to belong to the nominate subspecies. In this review on Sanderlings using Eurasian flyways, we only deal with the nominate subspecies.

Sanderlings breed in High Arctic Canada, Greenland and northern Siberia (Engelmoer & Roselaar 1998, Fig. 1). In Greenland, Sanderlings breed along the NE and N Greenland coast (common in Peary Land) and there is a small population on the NW coast (Boertmann 1994). The total Greenlandic breeding population has been estimated to consist of 25,000–50,000 pairs (Meltøfte 2001). The breeding distribution of

the Siberian population is centred on the Taimyr Peninsula, and one (or possibly two, cf. Engelmoer & Roselaar 1998) population occurs more easterly in the Siberian Arctic (Lappo 1998).

The E Atlantic Flyway population was estimated to number 123,000 individuals during the non-breeding season in the 1990s (Stroud *et al.* 2004). It is unknown how many of those belong to the Greenlandic and NE Canadian breeding population and how many to the Siberian breeding population. In this estimate, Sanderlings spending the non-breeding season in southern Africa were excluded because they were believed to be part of the flyway population that uses SW Asia and E and S Africa (Perennou *et al.* 1994, Scott in prep.). Even though several ringing recoveries suggest that Sanderlings with a Greenlandic breeding origin occur as far south as S Africa (Underhill *et al.* 1999, JR unpubl. data), they are presumed to be a minority compared to those from Siberia that reach S Africa via Asia and E Africa (Scott in prep., see below). In this review, we include S Africa because of the apparent mixing of Sanderlings from both flyways in this region. The proportion of Sanderlings in S Africa that uses the E Atlantic Flyway needs to be investigated.

When the S African Sanderlings (53,000) are excluded from the 123,000 flyway estimate of Smit & Piersma (1989), it might be inferred that 70,000 individuals used the flyway in the 1980s. However, the apparent large increase (to 123,000) of the flyway population since the 1980s can largely be explained by an increase in count coverage. The reduced hunting pressure, especially in France since the early 1970s (see below), might also have played a (presumably small) role. Therefore, the population is believed to be “stable or increasing” (Stroud *et al.* 2004).

DISTRIBUTION, NUMBERS AND TRENDS

Africa

An estimated 63% (77,800 of the 123,000) of the Sanderlings of the E Atlantic Flyway spend the non-breeding season along the west coast of Africa, between Morocco and the coast of the Gulf of Guinea (Scott in prep). Given that such a large proportion of the flyway population is estimated to occur in Africa, it is of concern that in most W African countries wader surveys are scarce. Important sites are surveyed irregularly (mostly only in January) or not surveyed at all. This is even more problematic for studies of Sanderlings than for most other waders because their distribution is more scattered over many small beaches rather than concentrated in a few important wetlands that are monitored on a more regular basis. Nevertheless, population trends of Sanderlings at major sites might reflect trends in the flyway population as a whole.

Moroccan beaches were surveyed extensively for Sanderlings and other waders during Jan 1996–2000 (Benhoussa unpubl. data). The total numbers recorded, ignoring different coverage between years, ranged from 2,153 to 9,899. In the 29 sites that were visited in all five years of the survey, there were 2,050 Sanderlings in 1996, around 5,800 in 1997–1999, and 9,800 in 2000 and thus they seemed to have increased. The two main sites for Sanderlings in Morocco were Lagune de Khniffiss and Baie d’Eddakhlha.

The Banc d’Arguin in Mauritania, which supports many Sanderlings, was surveyed in 1980 when the count was 33,850 (Altenburg *et al.* 1982) and in several subsequent years. In 1997, there were 20,156, a decrease of 40% since 1980 (Zwarts *et al.* 1998). This much lower number was confirmed in 2000 when 20,600 Sanderlings were counted

(Hagemeijer *et al.* 2004). In 2006, the Banc d’Arguin population was estimated at 39,840 (31,704 were actually counted), when approximately half the area was surveyed (Diagana & Dodman 2006). The apparent decrease in numbers of Sanderlings on the Banc d’Arguin towards the end of the 20th century is in contrast to the apparent increase of the whole flyway population since the 1980s. This could reflect a redistribution of Sanderlings within the flyway (Stroud *et al.* 2004) or might arise from the difficulties of carrying out complete surveys of large and inaccessible areas, like Banc d’Arguin.

Wetlands in most sub-Saharan African countries are not well monitored, but Ghana is an exception. An impressive long-term dataset of monthly counts has been obtained from all the important wetlands and beaches of Ghana since 1987 (Ntiama-Baidu 1991). Sanderlings are the most abundant species on sandy beaches and the most important site for Sanderlings in Ghana is the beach of Esiamia and adjoining villages (Ntiama-Baidu 1991). During Sep–Feb, an average of 1,200–2,850 Sanderlings was observed there annually. This is 40–70% of the total Sanderling population in Ghana during that period and >1% of the Sanderling population of the E Atlantic Flyway, thereby exceeding the criterion for sites of international importance. Since 1988, the Ghanaian population has grown steadily, both at Esiamia and in the rest of the sites monitored, although the increase was less pronounced at Esiamia compared to the remainder of the coast. The average numbers in the entire country in September–February did not exceed 2,900 in 1987–1995 and was more than 4,000 (up to 6,600) in all but two years in 1996–2006.

In S Africa, most Sanderlings occur on the west coast of South Africa and in Namibia (Harrison *et al.* 1997), especially on sandy and mixed sand and rocky shores (Summers *et al.* 1987). Estimates of total numbers in the 1970s and early 1980s were 36,000 for Namibia and 42,000 for South Africa. Most of these (65,000) occurred on open shores (Summers *et al.* 1987). Counts at Walvis Bay Lagoon, Namibia, since 1977 (annually since 1983) show fluctuations between 3,000 and 14,000 individuals, but in the long term, the population seems to have been stable at approximately 8,000 (K. Wearne unpubl. data). It is suspected that since the 1980s, the species has declined (LGU unpubl. data), but comprehensive surveys of the southern African shoreline are lacking and urgently needed to improve the information on trends.

Apart from Banc d’Arguin in Mauritania, Morocco, Ghana, Namibia and South Africa, information about numbers and distribution of Sanderlings along the west coast of Africa is limited. A recent survey of the most important wetlands in W Africa (which included Banc d’Arguin, the Saloum Delta in Senegal, Cape Verde, ten wetlands (not all coastal) in Gambia, the Bijagos Archipelago and the coast of Guinea-Bissau and several rice fields and mudflat areas in Guinea) resulted in an aggregate count of 38,600 Sanderlings. The majority (31,700, 82%) was recorded at Banc d’Arguin in Mauritania (Diagana & Dodman 2006). A survey in Sierra Leone in Jan–Feb 2005 resulted in a count of 2,000 Sanderlings in or around six key coastal wetlands. However, most sandy beaches in the country were not visited at all (van der Winden *et al.* 2009). Wader surveys in Africa – although very important in themselves – usually cover only a small number of wetlands. Moreover, those that are covered may not be of prime importance for Sanderlings which often occur on sandy beaches that are not part of major wetlands. Indicative of this, are the 1,518 Sanderlings counted in winter 2000 on the beach between Nouakchott and Mamghar (the southernmost limit of Banc d’Arguin) that are not included in the regular wader surveys of Banc d’Arguin (Hagemeijer *et al.* 2004).

Europe

Compared to Africa, the non-breeding population in Europe has been monitored more thoroughly, although the intensity of counts in different seasons has varied and coverage differs between countries. In the United Kingdom, Sanderlings are widespread, generally occurring in flocks of up to 100–200 scattered along sandy beaches. A large proportion, 13,560 of the estimated 20,540 Sanderlings in the United Kingdom (16.7% of the E Atlantic Flyway population), occurs on non-estuarine coasts (Rehfishch *et al.* 2003). The largest numbers occur in Scotland, but corrected for kilometres of coastline, England has the greatest densities (Austin *et al.* 2008b). Northern Ireland is of little significance for the species. The Ribble estuary and Carmarthen Bay, both on the west coast of Britain are sites of international importance with peak counts of 2,770 and 1,383 respectively. In addition to these two sites, another 21 locations hold >210 (between 226 and 958) Sanderlings each and are regarded as of national importance (Austin *et al.* 2008a). Winter numbers during the past 30 years seem fairly stable (Austin *et al.* 2008a, Rehfishch *et al.* 2003).

Ireland (excluding Northern Ireland) supported an estimated 6,680 Sanderlings during the non-breeding seasons 1999/2000–2003/04. The majority (64%) occurred in non-estuarine habitats (relatively small sandy beaches). Sanderlings are more or less evenly distributed along the coastline. None of the locations in Ireland were considered to be of international importance in winter (Crowe *et al.* 2008). The species has increased by 4.6 % between 1994/95 and 2003/04 (Crowe *et al.* 2008). During the migration peaks in August and May, no wader counts are conducted in Ireland so it could be that some locations support numbers of international importance for short periods each year.

In the Netherlands, 9,200 Sanderlings occurred in January 2002–2006 of which 52% were on sandy beaches and the others in the mudflat areas of the Zeeuwse Delta and Wadden Sea (van Turnhout & van Roomen 2008). The distribution within the Netherlands changes markedly during spring migration when an average of only 2,100 Sanderlings were counted on sandy beaches but 13,000 on mudflats. Seasonal trends in the use of beaches and intertidal mudflats differ markedly. Generally, the North Sea beaches of the mainland coast are not occupied by Sanderlings before mid October, and in April they are abandoned. This suggests that the beaches are largely avoided during autumn and spring migration (van Turnhout & van Roomen 2008, H. Verkade, unpubl. data). Observations of colour-ringed Sanderlings suggest that some arrive in the Wadden Sea in autumn and stay until mid October or November, before moving to the sandy beaches of the Dutch mainland (JR unpubl. data). Similar post-moult movements occur in Britain (Langston 2002) and France in October and November (JR unpubl. data). Sanderling numbers have increased considerably between 1995 and 2006 both during migration periods and in winter in the Netherlands. However, this increase has only been seen in numbers recorded on intertidal mudflats; counts on the beaches of the Dutch mainland coast and of the Wadden Sea islands have remained stable. The beaches of the mainland coast are only surveyed in January, for which available data indicate little change in numbers between 1977–1978 and 1985–1986 and 2002–2006 (Keijl 1987, Meininger & Becuwe 1979, Platteeuw 1985, van Turnhout & van Roomen 2008).

The majority of Sanderlings that spend the winter in the Wadden Sea occur in the western part (the Netherlands), with decreasing numbers towards the east (Lower Saxony and Schleswig Holstein in Germany, and in Denmark). Dur-

ing northward migration, Sanderlings are more concentrated towards the eastern part of the Wadden Sea and especially in Schleswig Holstein, close to the Elbe River mouth (Meltofte *et al.* 2003). Trends during 1987/88–2006/2007 differ within the Wadden Sea areas, with a large increase in the Netherlands and Denmark; numbers in Schleswig Holstein and Lower Saxony having remained stable (JMJB 2008). Counts from Blåvands Huk, just north of the Danish Wadden Sea between 30 June and 28 September suggest that numbers increased during the 1970s and 1980s, having decreased a little during the 1990s and early 2000s (Meltofte *et al.* 2006).

Belgium has a short coastline and only supports small numbers of Sanderlings. Midwinter numbers during 1972–1997 fluctuated between 180 and 700 without any trend (Becuwe *et al.* 1983, Devos *et al.* 1994, 1996, 1997, 1998, De Putter *et al.* 1993, Voet & Becuwe 1977). The maximum count of 710 was recorded in February 1996 and was thought to represent a response to cold weather (Devos *et al.* 1997). As on the Dutch North Sea beaches, numbers peak between October and March and decrease in spring with no significant peak during northward migration (Becuwe *et al.* 1983).

The French non-breeding Sanderling population is estimated to be about 20,000 (January averages for 2003–2007). Most Sanderlings occur along the Atlantic coast from the Gironde estuary to Brittany and along the Channel coast from Brittany to the Seine estuary. They are found on sandy beaches that are often isolated and difficult to access, and on rocky shores. Since 1977, the total numbers in France have increased (Wetlands International 2006). At most locations significant increases have been reported, and at the rest numbers have been stable. No sites showed declines. Legislation against hunting might have played a role. The species has been protected in France since the early 1970s, which might explain the increase in numbers, and could partly explain the increased numbers counted during migration periods elsewhere in Europe, to the north and east of France.

Overall trend: a growing Sanderling population?

In most countries, the non-breeding Sanderling population is reported to have increased. However, in some parts of the flyway, it is uncertain whether the increase is real or due to increased count coverage, but this effect can be taken into account by focussing the numbers using regularly monitored sites. The establishment of periodic non-estuarine counts in Britain and Ireland has increased our understanding of the non-breeding distribution and numbers of Sanderlings and our knowledge would increase if more such counts were carried out elsewhere (cf. Burton *et al.* 2008) and if they were carried out in other months, especially during the migration periods. Negative trends reported for particular beaches in the Netherlands, Iceland and S Africa may be related to intensified human beach use. In the Netherlands intense beach nourishment probably decreases the availability of food for Sanderlings along some sections of the coast, and this may be compounded by increased recreational activities, especially during the migration periods. Although Sanderlings do not seem to be particularly sensitive to disturbance, the intensity of disturbance can be so high that the birds have insufficient time for foraging (Burger & Gochfeld 1991).

DIET AND FORAGING BEHAVIOUR

Generally the diet of Sanderlings during the non-breeding season consists of small marine invertebrates. Mostly diet has been determined by stomach and faecal analysis, but



Fig. 2. Sanderling eating the flesh of *Ensis subtruncata*, washed up on the shore of the Dutch Wadden Sea island of Schiermonnikoog, 24 December 2008. (Photo: Jeroen Reneerkens.)

the results of such analyses need to be interpreted with care because soft-bodied prey might be underrepresented due to faster and more complete digestion compared to hard-bodied prey (Toshimitsu *et al.* 2005). Furthermore, the identification to species of small prey is often difficult. On the other hand, the availability of prey is usually limited to a few species in the sandy environment, potentially making the reconstruction of the diet relatively straightforward.

The diet in the non-breeding areas mainly consists of polychaetes, molluscs, small crustaceans and insects (e.g. Evans *et al.* 1980) which are searched for and handled in different ways (Kelly 2008). On the breeding grounds, Sanderlings chiefly eat arthropods, although plant material has also been reported to supplement the diet when arthropods were scarce (Johnsen 1953, Løppenthin 1932). After breeding, adult and juvenile Sanderlings forage in muddy river deltas in preparation for the southward journey. The most likely food sources taken in such places are crustaceans (amphipods) and nematodes (Meltofte & Berg 2004, Meltofte & Lahrman 2006). Bird & Bird (1941) found the amphipod *Pseudalibrotus litoralis* and chironomid larvae in stomachs of Sanderlings shot on Greenland breeding grounds.

An important prey item of Sanderlings in NW Europe is the polychaete *Scolecopsis squamata* (Speybroeck *et al.* 2007), but its relative importance changes from place to place. On the North Sea beaches of the Wadden Sea island of Vlieland, *S. squamata* was the most abundant potential Sanderling prey, especially around low tide. Different size classes of *S. squamata* occupy different areas of the beach on Vlieland, making them available to Sanderlings at different times of the tide. The largest individuals (>50 mm long) occurred mainly in the lowest parts of the beach which are accessible only around low tide. On Vlieland, Sanderlings probably also eat the isopod *Haustorium arenarium* (KG & JR unpubl. data and see Evans *et al.* 1980). On Belgian beaches, *S. squamata* only makes up 26% of the prey taken, and is therefore less important (Vanermen *et al.* in press). In contrast to beaches on Vlieland, *S. squamata* occurs in restricted zones of upper intertidal areas in Belgium (Speybroeck *et al.* 2007, Vanermen

et al. in press). In Belgium, Sanderlings only achieved their maximum intake rate of >45 polychaetes h⁻¹ during the two-hour period before high tide. At other times the average consumption rate was around 6 polychaetes h⁻¹.

The variation in abundance of *S. squamata* at different locations in the Netherlands and Belgium is also reflected in the foraging modes of Sanderlings. *S. squamata* is located by touch (probing), rather than by sight (pecking). During a complete tidal cycle on Vlieland, Sanderlings obtained prey by probing in 8–21% of all recorded captures. In the Voordelta (SW Netherlands), only 2% were captured by probing and on the Belgian beaches <10% and only during low tide. In Sanderling faeces collected at the Voordelta, many copepods were found and only the occasional polychaete; confirming visual observations that *S. squamata* is not a major prey item at this location. The faecal analyses also confirmed that large numbers of insects are occasionally taken in spring when they are washed ashore and become an important prey item. It has been observed that on warm, sunny days, Sanderlings also hunt flying insects (predominantly kelp flies *Ceolopa frigida*) during spring migration in SW Iceland. Second to soft-bodied marine invertebrates (including polychaetes), these are the main prey items taken in spring in Iceland (GTH & JR pers. obs).

Another important, but unpredictable food resource for Sanderlings in NW Europe is the non-native Razorshell *Ensis subtruncata* that occasionally washes ashore in large quantities, especially after strong northerly winds (Kelly 2008, Fig. 2). Sanderlings feed on the dead, opened shellfish. Such massive wrecks often seem to attract many Sanderlings from other areas (Kelly 2008, Langston 2002). On the Wash, Britain, shrimps *Crangon crangon* seem to be a favourite prey species. They are caught during low tide by touch (stitching) or sight (stabbing) (Kelly 2008).

The feeding ecology of Sanderlings on the Banc d'Arguin in Mauritania is difficult to study because the birds feed at a low density on the extensive mudflats, but they are also often observed on the more sandy parts along the gullies (Zwarts *et al.* 1990a, JR pers. obs). On mudflats covered with eelgrass *Zostera* spp., they feed mainly on the abundant polychaetes (Engelmoer 1982, Zwarts *et al.* 1990a). During high tide, a fraction of the Sanderlings gathers in the fishing village of Iwik, where they continue foraging before they start roosting. There the birds forage in dense flocks on small particles of boiled fish remains that are thrown on the beach by the local people (Fig. 3).

Studies of the diet of Sanderlings on the beaches of Esiamia, Ghana, in the late 1990s showed that they fed mainly on soft-bodied marine invertebrates (YN-B and C. Gordon pers. obs.). However, in our studies in 2008 and 2009 Sanderlings were observed to feed primarily on small bivalves (*Donax* sp.) which are (as in Red Knots *Calidris canutus* (Piersma *et al.* 1993, 1999)) swallowed whole and crushed in the birds' gizzards. The bivalves are buried in the sediment just below the surface and with average densities of 5,700–14,300 m⁻², are a very abundant food resource that was available throughout the tidal cycle, except around high tide. Because *Donax* were present in the same high densities and size-classes (6–9 mm long) in two successive years, it seems likely that they are a predictable food source from year to year (JR, YN-B & TP unpubl. data). The high prey availability is reflected in the time budgets of the birds: only 36% of the time was spent foraging, which contrasts with the 79% observed on Vlieland, the Netherlands (KG & JR unpubl. data, Fig. 4). In Belgium, Sanderlings spent a similar amount of time feeding (80%, N. Vanermen & BdM unpubl. data). A similar contrast in time



Fig. 3. Sanderlings, with Ruddy Turnstones *Arenaria interpres* and Slender-billed Gulls *Larus genei*, forage during high tide in dense flocks on fish remains thrown on the beach in Iwik village, Banc d'Arguin, Mauritania. (Photo: Jeroen Reneerkens.)



Fig. 4. A large roost of Sanderlings on the beach near Esiama, Ghana. Sanderlings spend most of their time roosting on this tropical beach, presumably to process their mollusc diet. (Photo: Jeroen Reneerkens.)

spent feeding and resting in daily time budgets of Sanderlings wintering in tropical and temperate locations was observed in the Americas (Castro *et al.* 1992).

It seems likely, however, that the resting periods observed in Ghana were in fact digestive pauses that were necessary to allow the birds to process the hard shell material. Food quality in terms of metabolisable energy intake per shell mass (cf. van Gils *et al.* 2005) is 23 times lower in Esiama compared to Vlieland (KG & JR unpubl. data). Elsewhere in Ghana, the several hundreds of Sanderlings in Songor and Keta Lagoon took a wide variety of prey items. On wet sediments near the dune ridges, birds made deep probes and were likely to be foraging on amphipods. Sanderlings taking polychaetes on mudflats had aggressive interactions with Little Ringed Plovers *Charadrius dubius* suggesting that both species were feeding on the same prey. The Sanderlings also pecked small insects from the water surface and larval fish among beds of Widgeongrass *Ruppia maritima*. Furthermore, Sanderlings were scavenging on fish being dried for human consumption near villages, and droppings showed that some birds even took the seeds of *Ruppia maritima* (Piersma & Ntiamoa-Baidu 1995).

Shubin & Bolshakov (1988) described the territorial behaviour of migrant Sanderlings in autumn on the non-tidal shore of the Caspian Sea. They fed on the amphipod *Niphargoides maoticus* on wet sand. Territorial Sanderlings mostly fed by touch (probing), whereas non-territorial birds mainly fed by sight (pecking).

MIGRATION

The migratory journeys of Sanderlings between their arctic breeding grounds and non-breeding grounds as far as the southern shores of South America, Africa and Australia are among the longest avian migrations known. The migration routes of Sanderlings in the Americas have been fairly well described with information based on intensive colour-ringing and resighting (Myers *et al.* 1990). Nevertheless, the origins of the Sanderlings that winter on the Aleutian Islands (Gibson & Byrd 2007) and the many that migrate through Alaska are unknown.

We have a poorer understanding of the migration patterns of Sanderlings in Eurasia and Africa. In particular, the origin and degree of mixing of birds from different geographic breeding populations (NE Canada, Greenland and northern

Siberia) need clarification (Langston 2002). To date there have been very few ring recoveries that show connectivity between breeding and non-breeding grounds. Sanderlings from different breeding populations cannot be distinguished on the basis of morphology because of the substantial overlap in body measurements of Sanderlings from Nearctic and Palearctic breeding origins, which is further obscured by sex-related differences (Cramp & Simmons 1983, Gosbell & Minton 2001, Gudmundsson & Lindström 1992, Soloviev & Tomkovich 1995, Wymenga *et al.* 1990). Now that birds can be sexed accurately using molecular techniques, it should soon be possible to clarify possible geographical variation. This development, as well as the increased sample size from birds of known rather than presumed breeding origin, should be the focus of future biometric analyses. Meissner & Wlodarczyk (1999) showed that, on average, Sanderlings wintering in Great Britain, presumed to breed in Greenland, had longer wings and shorter bills than Sanderlings, presumed to breed in Siberia, caught on the Baltic coast of Poland during southward migration.

Because satellite transmitters are not yet small enough to be used on Sanderlings and since genetic markers have yet to be developed for distinguishing different populations, currently the most feasible methods for studying Sanderling migration are colour-ringing and observations of departure directions of migrating flocks.

Migration routes and non-breeding distribution of Sanderlings from Greenland and NE Canada

During the breeding seasons of 2007 and 2008, 105 adults and 22 chicks older than five days were colour-ringed in Zackenberg, NE Greenland. This yielded resightings in Denmark, France, Mauritania and Namibia of birds that had reached their final non-breeding destination (i.e. observed between mid October and mid March, in many cases on several dates at the same location; Reneerkens & Koomson 2008, Fig. 5). In addition, observations from Namibia, Cape Verde, Gambia and Morocco of Sanderlings colour-ringed at a spring stop-over site in Iceland, a recent capture in Iceland of a Sanderling ringed in Senegal (JR & GTH, unpubl. data), three resightings in Iceland of Sanderlings colour-ringed in Ghana during the northern hemisphere winter (Gudmundsson & Lindström 1992) and an observation of a colour-ringed Sanderling likely to be from Ghana in Zackenberg (H. Meltofte pers. comm.),

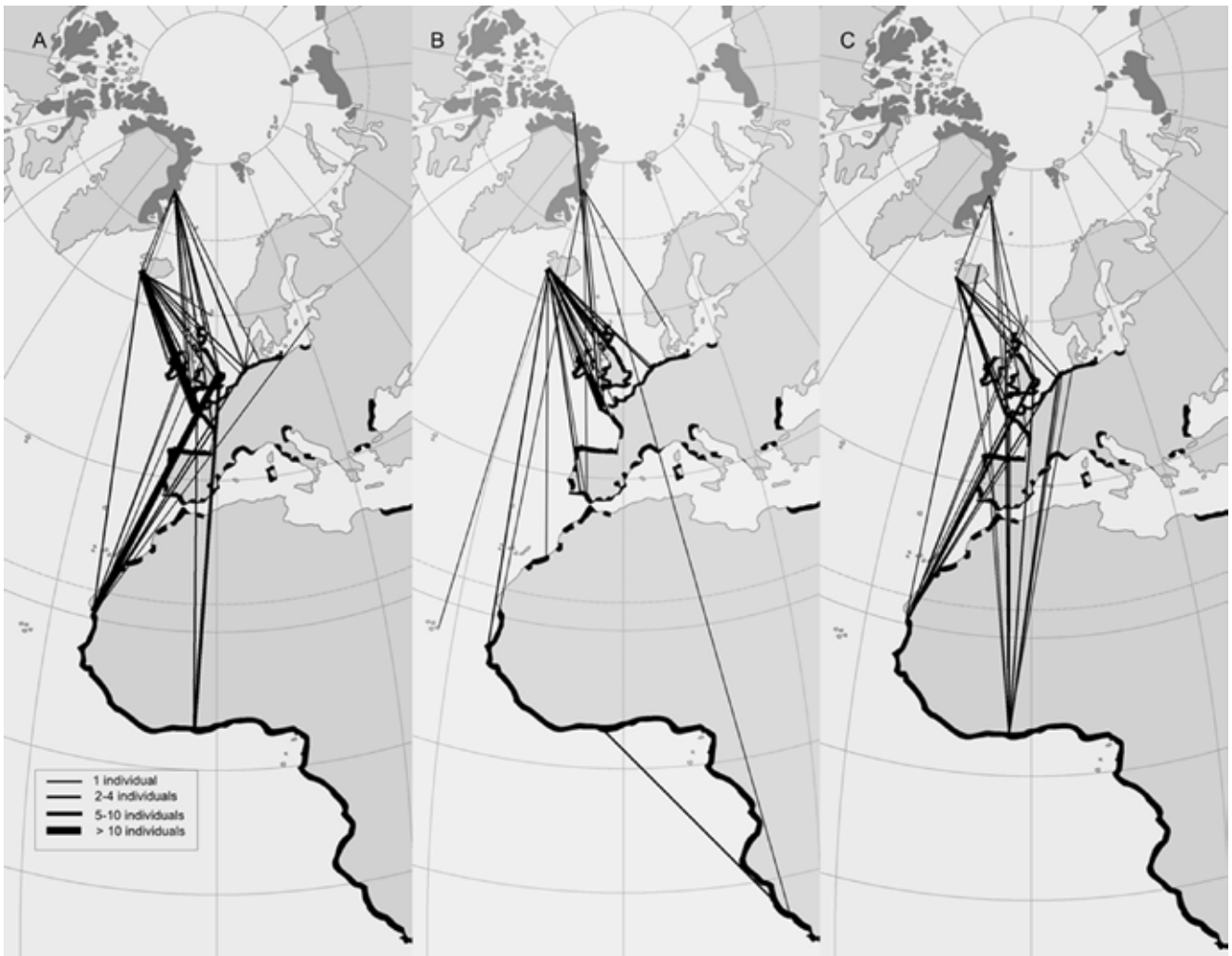


Fig. 5. Observations of colour-ringed Sanderlings in Africa, Europe and part of Asia during (A) southward migration, 15 Jul to 15 Oct, (B) the northern winter, 15 Oct to 15 Mar and (C) northward migration, 15 Mar to 1 Jul. The straight lines connect locations of ringing with locations of resighting. The thicker the line the more individuals it represents.

show that Sanderlings from Greenland indeed winter in W and S Africa. This confirms the conclusions of Gudmundsson & Lindström (1992) that Sanderlings breeding in Greenland (based on those that stop over in Iceland) have an extensive wintering range along the west coasts of Europe and Africa.

For a long time, it has been questioned whether the relatively small breeding populations in NE Canada and NW Greenland winter along the west coasts of Europe and Africa or in North or South America (e.g. Lyngs 2003). Recent resightings of two colour-ringed Sanderlings from Ellesmere Island that spent the winter in Brittany, France, suggests that birds from the E Atlantic Flyway population also breed in Ellesmere Island (Reneerkens *et al.* 2008b, R.I.G. Morrison unpubl. data).

The importance of Iceland during northwards and southwards migration

Sanderlings occur in Iceland on passage to and from the breeding grounds in Greenland and NE Canada. In Iceland, they occur mainly on sandy beaches, but also in muddy and rocky areas (Gudmundsson & Gardarsson 1993). Gudmundsson & Gardarsson (1993) surveyed most of the coasts of Iceland from the air in May 1990 during the peak spring passage of arctic-breeding waders. A minimum of 8,000 Sanderlings was estimated to occur. This was based on single

counts at each location without taking turnover into account, and based largely on the count near Akrar, Myrar on the west coast. This location and Sandgerði in the south-west (Fig. 1) are the sites that annually hold some hundreds or thousands of Sanderlings during northwards passage (Gudmundsson & Gardarsson 1993, G.A. Gudmundsson & GTH unpubl. data). There were no indications of large numbers of Sanderling away from the west coast. The count of 8,000 corresponds to only 8–16% of the Greenland breeding population, which was estimated at 25,000–50,000 pairs (Meltofte 1985). This suggests that, on passage northwards, only a small part of the Greenland birds stop in Iceland (cf. Wilson 1981), or that there is high turnover, or that the estimates of the population size are inaccurate. Based on estimated flight ranges, Scott *et al.* (2004) calculated that Sanderlings wintering in Great Britain obtain large enough fuel loads to fly non-stop to the breeding grounds, but many nevertheless stopover in Iceland. Recent studies with colour-marked Sanderlings show that they stopped over for on average 3.0 days in 1996 (based on the dilution of non-individually marked Sanderlings over the stop-over period, $n = 35$ and 112; Scott *et al.* 2004) and 6.6 days in Sandgerði in 2008 (based on first and last observations of birds marked at the same location the year before, $n = 70$; JR & GTH unpubl. data) and maximally for 19 days and 21 days, respectively. Many Sanderlings stopping over in Iceland during northwards migration spend the winter in

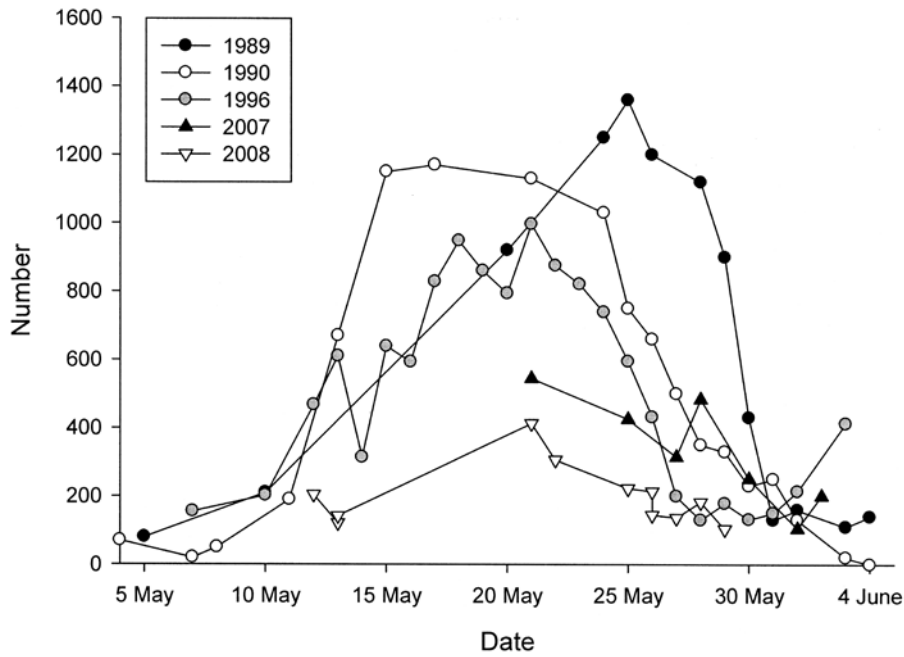


Fig. 6. Sanderling counts at Sandgerði, SW Iceland, during the main spring migration period in 1989, 1990, 1996, 2007 and 2008, indicating a steady decline in numbers over the years.

NW Europe, so the question remains why they put on enough fuel to complete the flight to Greenland in one non-stop flight but still stop in Iceland.

It is unknown how many Sanderlings occur on the east coast of Iceland, but probably not many (G.A. Gudmundsson pers. comm.). Also unknown is how the numbers of Sanderlings staging in Iceland fluctuate from year to year. On 19 and 20 May 2008 about 1,000 Sanderlings were observed near Grunnaþfjörður, W Iceland, on soft mudflats (B. Thorisson pers. comm.), indicating that some localities probably hold substantial numbers. Resightings of colour-ringed Sanderlings in the east of Iceland (JR unpubl. data) suggest that an unknown, but probably small, number occurs there too. Most likely areas for Sanderling are Djúpvogur (SE) and Melrakkaslétta (NE) and they have been recorded there, but only in small numbers (G. Gudmundsson pers. comm.).

The coastline of S Iceland consists mainly of black sands and Sanderlings have been seen there in spring and late summer. The importance of this area is not known but it probably will not hold many Sanderlings (GTH unpubl. data). In Sandgerði, Sanderlings have been counted in several years during the main migration period. Ongoing development of the local fishing harbour, as well the increased use of beaches by vehicles, are probably the cause of the large decline since 1996 (Fig. 6, G.A. Gudmundsson, GTH & JR unpubl. data).

During southward migration, Iceland is visited by adult and juvenile Sanderlings. Autumn migration is more protracted and it is unknown how many Sanderlings stop in Iceland or for how long. In August 2007, Sanderlings were counted regularly in Sandgerði, and the largest numbers were 70–90 adults in the first days of August. The number of adults

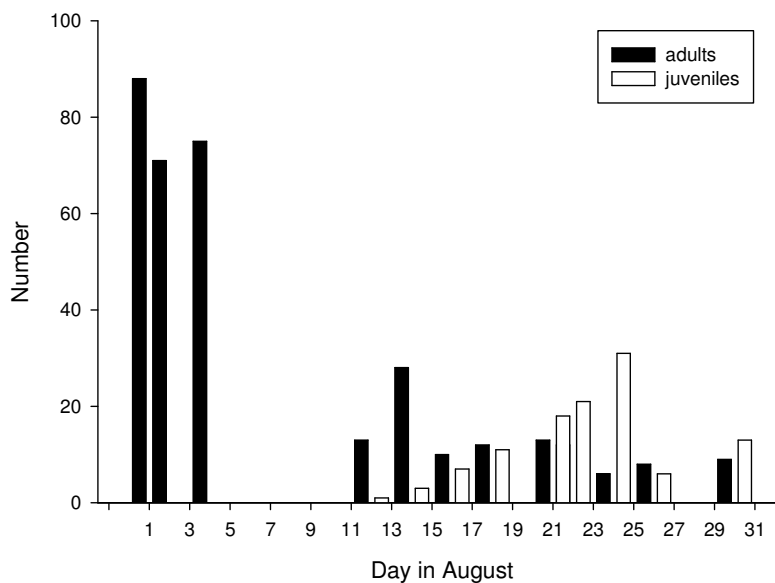


Fig. 7. Number of adult (black bars) and juvenile (white bars) Sanderlings counted in Aug 2007 at Sandgerði, SW Iceland.



Fig. 8. A few colour-ringed Sanderlings in a large flock on one of the beaches of Sandgerði, SW Iceland, 28 May 2007. Studies with colour-ringed Sanderlings are useful to determine stopover duration, site fidelity and total numbers using stopover sites as well as to determine the wintering grounds of birds passing through. (Photo: Jeroen Reneerkens.)

was considerably lower from 10 August onwards (never more than 30) and the first juveniles (up to 30) appeared from then onwards (Fig. 7, GTH unpubl. data). Interestingly, two Sanderlings colour-ringed in winter in Mauritania were observed in two successive autumns in Sandgerði, but were never observed there in spring when more intensive searching for colour-ringed Sanderlings was carried out (JR & GTH unpubl. data, Fig. 8). This could indicate that some Sanderlings overfly Iceland during spring migration but stop there during southward migration.

In the Faroe Islands, Sanderlings are rarely seen during spring migration, and only in moderate numbers (flocks rarely exceeding 150) during autumn migration. Sandavágur on the island Vágar, is the only site where larger flocks have been recorded (J-K. Jensen, pers. com.).

Northward migration: when and where Sanderlings from Africa and Europe meet

Observations of colour-ringed Sanderlings show that in both spring and autumn migrants stopover on European coasts that are also occupied by Sanderlings that have wintered there. Based on percentages of juveniles, it has been suggested that the Banc d’Arguin (Mauritania) is also used by Sanderlings that winter south of Mauritania during spring migration (Zwarts & Piersma 1990). Waders, including Sanderling, wintering in Ghana cross the Sahara during northward and most likely also on southward migration (Grimes 1974). During spring migration, Sanderlings from Africa will mix with Sanderlings that spent the winter along the coasts of Europe, resulting in peak counts especially in the second half of May

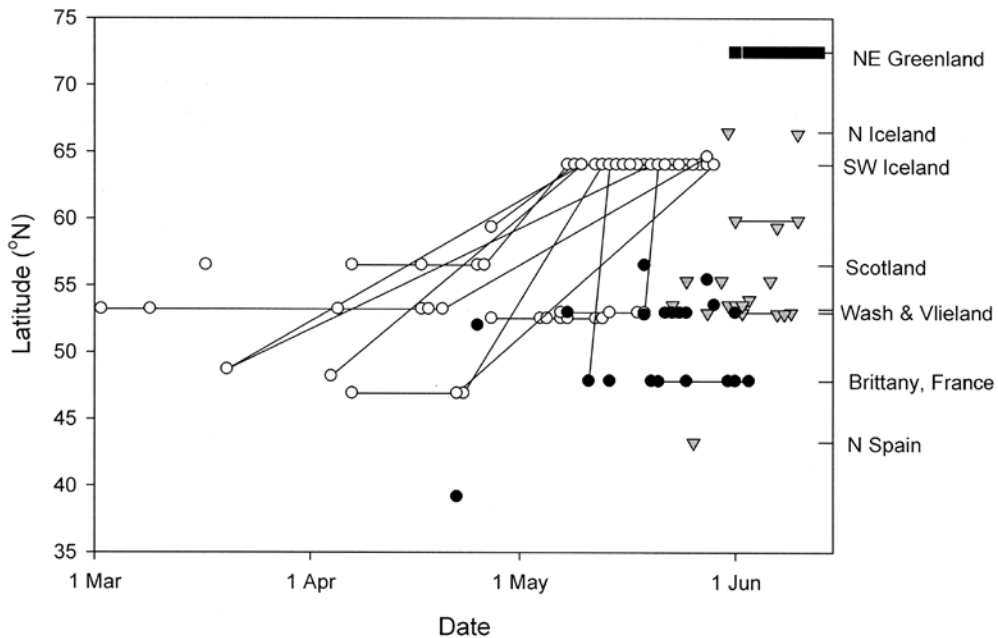


Fig. 9. Spring migration of colour-ringed Sanderlings that have spent the non-breeding season at different latitudes. Each symbol represents an individual resighting at a given date and latitude. Individual birds that were observed repeatedly during the same spring migration period are connected with lines. European winterers are Sanderlings colour-marked in May and early June in SW Iceland that have been resighted between 10 Oct and 10 Mar in Europe, the birds from Ghana and Mauritania were colour-ringed locally. The black bar in the top right corner depicts the period after which the first Sanderlings colour-ringed in Zackenberg, NE Greenland, in summer 2007 were resighted there in 2008.

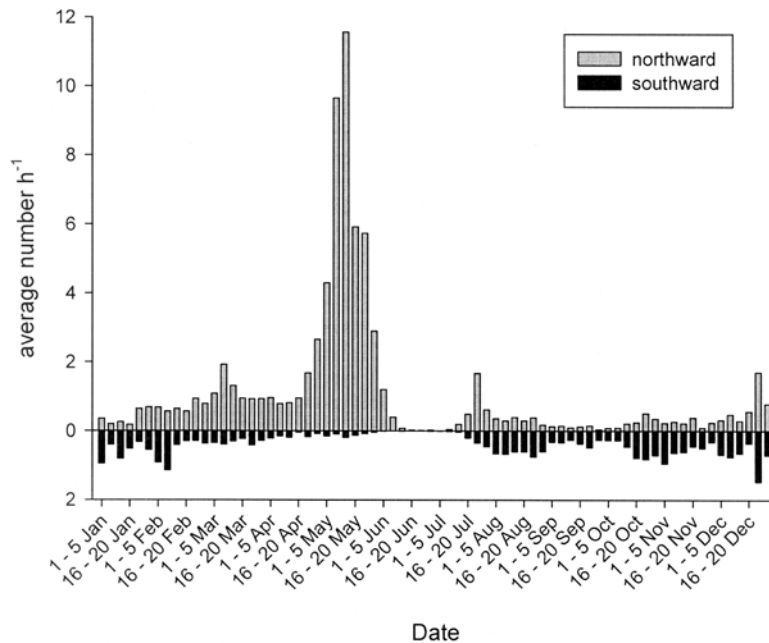


Fig. 10. Average number of Sanderlings observed passing by northwards or southwards by volunteer birdwatchers in five-day periods along the Dutch North Sea coast during 1972–2007 (source: Nederlandse Zeevogelgroep/Club van Zeetrekwaarnemers).

(Meltofte *et al.* 2003). However, resightings of colour-ringed birds in Ghana, Mauritania and W Europe in Nov–Feb, show that the birds wintering in W Europe, depart on spring migration earlier than the African wintering birds (Fig. 9, also see Kelly 2008). Furthermore, Sanderlings from Ghana migrate through Europe earlier than Mauritanian Sanderlings (Fig. 9). This is consistent with the timing of fuelling of birds from those areas. Sanderlings start gaining body mass in Ghana during March (YN-B, JR & TP unpubl. data), whereas in Mauritania this occurs in April, with departures taking place in May (Piersma *et al.* 1990, Zwarts *et al.* 1990b).

These different migration waves are not detected in European spring wader surveys probably because waves of Sanderlings from different wintering grounds overlap and, apart from any that are colour-ringed, cannot be distinguished visually as coming from different populations. However, we should bear in mind that the spring surveys may also lack the power to identify separate migration waves because they are not conducted with sufficient frequency. Even in the German Wadden Sea, where surveys are conducted twice a month, no distinct migration waves have been found, apart from an increase in numbers during May (Blew *et al.* 2005, JMMB 2008). Meltofte *et al.* (1993) describe spring migration as occurring in two waves through the Wadden Sea, with a first wave in March and April of Sanderlings that probably wintered elsewhere in Europe and another in May and early June of birds likely to be from African wintering grounds. However, they do not provide the evidence for the existence of two waves or their origin. This does not mean that different waves of migration do not exist. Year-round

counts of Sanderlings passing the Dutch mainland coast between 1972–2007 show that the spring migration consists of two peaks, one small one in March and the main passage during May with a pronounced peak between 6 and 16 May (Nederlandse Zeevogelgroep/Club van Zeetrekwaarnemers unpubl. data, Fig. 10).

What is the evidence for a Siberian origin of Sanderlings wintering in NW Europe?

In Green and Greenwood (1978), A.E. Williams is cited as stating that Sanderlings that arrive in July and August on the Wash, Britain, stay there for the winter after body and wing feather moult. Other Sanderlings, however, do not moult, but instead fuel up and migrate to Africa, only to return in May and June in order to gain fuel in preparation for further northward migration to the breeding grounds. Based on a very limited number of ring recoveries, he concluded that the wintering Sanderlings originated from Siberia, whilst the Sanderlings that only occurred on the Wash in autumn and spring bred in Greenland. Also, Meltofte *et al.* (1993) basing their conclusions on the timing of migration, considered that

Fig. 11. Sanderling “G3YYRW” was colour-ringed at Sandgerði, SW Iceland, on 18 May 2007 and stayed there until 2 June 2007. It was next seen the following spring when it was present on the beaches of Sandgerði from 14 to 24 May 2008. In autumn 2008, it showed up at Pointe de Moustierlin, Brittany, France on 21 Jul 2008 when this photo was taken. It moved to a nearby beach, Plage des Sables Blanc, at Concerneau where it was first observed on 18 Oct 2008 and stayed until at least 6 Dec 2008. (Photo: Jacques Le Baill.)



most Sanderlings that pass through the Wadden Sea in spring are on their way to Siberia and suggest that

“the Wadden Sea is of outstanding importance, especially to the E Atlantic Flyway population of Siberian Sanderlings” and

“the proportion of the Sanderlings in the Wadden Sea which breed in high arctic Greenland is unknown, but these birds probably mainly use the Wadden Sea as a staging area in early autumn”.

Since these words were written, the suggestion of a Siberian origin for Sanderlings in W Europe has been repeated in the literature without a critical re-examination of the evidence or consideration of new data from colour-ringing (Langston 2002).

Many Sanderlings ringed in Greenland and during spring migration in Iceland, and hence probably bound for Greenland or NE Canada, have been recovered between mid October and mid March in W Europe, including the United Kingdom (Gudmundsson & Lindström 1992, Reneerkens & Koomson 2008, Reneerkens *et al.* 2008). The majority of recoveries of Sanderlings ringed in Iceland during spring have come from France (Brittany especially, Figs 5 and 11), which is inconsistent with the idea that British wintering Sanderlings are exclusively Siberian.

Departure of Sanderlings from Europe in late May and early June could be interpreted as an indication of Siberian origin because waders generally arrive two to three weeks later in their Siberian breeding area than in Greenland and NE Canada (Meltofte *et al.* 2007 and references therein). However, observations in Schleswig-Holstein of 32 departing flocks (2,645 individuals) indicated that a north-westerly direction was taken and most Sanderlings departing from the Wadden Sea in late May/early June are likely heading to Nearctic breeding grounds (KG unpubl. data). In contrast, Red Knots and Bar-tailed Godwits *Limosa lapponica*, known to breed on the Taimyr Peninsula of Siberia, all showed a north-east departure direction in the same period (KG unpubl. data). Sanderlings departing from England and Scotland in late May and early June also left in a north-westerly direction (Ferns 1980).

Observations of Sanderlings on the Baltic coasts during the migration periods are often regarded as birds using a migratory flyway between W Europe and Siberia. Although this is likely, care should be taken with such an interpretation. The majority of such observations are made during southward migration. Based on colour-ring observations of Sanderlings known (ringed in NE Greenland) or strongly suspected (ringed during spring migration in Iceland) to breed in the Nearctic, it has emerged that as they fly southwards in Jul–Sep the migration takes place over a much broader front compared to northward migration, which occurs along a narrower route that takes them along the coasts of Spain, Portugal, France and Britain (JR unpubl. data). During southward migration, Greenland-breeding Sanderlings regularly occur in Scandinavia and around the Baltic Sea (Gudmundsson & Lindström 1992, Fig. 5). Such an autumn migration over a broad front that even extends into the Baltic has been shown to occur in other Nearctic waders (Wilson 1981) and may lead to the wrong conclusion that such easterly observations indicate a Siberian breeding origin.

Clearly, there is only limited evidence for a Siberian origin of Sanderlings wintering or passing through NW Europe (Figs 1 and 5). A few ring recoveries indicate that Siberian birds occur mixed with those of the Nearctic population in the wintering grounds (for example in southern Africa, see below), but to what extent is unclear, mainly because there

is a lack of Sanderlings ringed or recovered in the Siberian breeding grounds (Langston 2002).

Migration routes and non-breeding distribution of Sanderlings from Siberia

Although we have a fairly good idea of the non-breeding distribution of Sanderlings breeding in Greenland and NE Canada (e.g. Gudmundsson & Lindström 1992, Lyngs 2003, Reneerkens & Koomson 2008) we have a much less clear picture of the migration routes, numbers, non-breeding distribution and migration phenology of Siberian Sanderlings, that are suspected to mix with the Nearctic Sanderlings on the non-breeding grounds as well as during migration periods (Smit & Piersma 1989, Wymenga *et al.* 1990). The breeding distribution in Eurasia is centred on the Taimyr Peninsula and islands to the north (Lappo 1998, Lappo *et al.* in prep.), but locations with large numbers of breeding Sanderlings have rarely been visited by ornithological expeditions. Of the 37 ring recoveries available at the Moscow Bird Ringing Centre, 19 suggest that Sanderlings from the eastern part of the Siberian breeding distribution (east of 120°E, the vicinity of the delta of the Lena River and the New Siberian Islands) use the Australasian Flyway (but see Fig. 1 and Minton 2005), for which Chaivo Bay in N Sakhalin island may be a crucial migration stop-over site (Andrey Blokhin in prep.). There is one recovery that links Europe with Siberia (Fig. 1) and two recoveries on the Taimyr Peninsula from South Africa (Summers *et al.* 1987). In addition, there are eight spring and autumn recoveries linking the Black and Caspian seas with S Africa (Summers *et al.* 1987). Those recoveries suggest that Siberian Sanderlings that use the E Atlantic and the Mediterranean, W Asia/E African Flyway breed in the more western part of the Siberian breeding distribution (Tomkovich *et al.* 2000, PST unpubl.). Of the six recoveries from Europe, three indirectly (i.e. not in the same migration period) link Russia with Britain. One ringed Sanderling found as falcon prey remains at the lower Lena River, Siberia on 25 June 1974 was ringed on 9 May 1971 at Snettisham on the Wash, United Kingdom. Two other adult Sanderlings ringed in Britain during northward migration on 13 April 1968 and 16 May 1972 were recovered on the Kola Peninsula on 19 June 1970 and 16 July 1974, respectively (Fig. 1). Although the evidence is limited, the three recoveries mentioned above suggest that Sanderlings from Siberia mix with those of Nearctic origin during northward migration.

The migration connectivity of N-central Siberia (the Taimyr Peninsula) with southern Africa is much more certain. As well as the twelve ringing recoveries (both within and between migration seasons) mentioned above, many more ring recoveries of Sanderlings link Sanderlings in Namibia and South Africa with other locations north of southern Africa (Summers *et al.* 1987, Underhill *et al.* 1999). Those data suggest there may be a clockwise loop migration with Sanderlings migrating northward in April and May to the Gulf of Guinea and cross the Sahara (cf. Grimes 1974) to the Mediterranean and North Sea coasts and onwards to Siberia (Summers *et al.* 1987, van der Winden *et al.* 2001). Sanderling numbers do not peak in Ghana during the period of northward migration (YN-B, JR & TP unpubl. data), suggesting that Sanderlings from southern Africa do not stopover in Ghana. Southward migration takes place via the Azov-Black and Caspian seas and perhaps south down to the east coast of Africa (Summers *et al.* 1987). Sanderlings are abundant on the west coast of the Caspian Sea in autumn, but rare during spring migration (Shubin 1998). However, many Sanderlings also return south

via the North Sea coasts, so there is also a westerly route south (Summers *et al.* 1987, Underhill 1997, Underhill *et al.* 1999). Observations of three Sanderlings colour-ringed in August 2007 and 2008 in Ghana and seen from November 2008 to January 2009 in Namibia are consistent with the existence of this westerly route south (JR unpubl. data). However, an increased reporting rate of Sanderlings on the Namibian coast during the period of northward migration in Mar–Apr adds some support to the hypothesis of loop migration (Underhill *et al.* 1999).

We have only limited knowledge of the numbers and timing of the migration of Sanderlings stopping over during spring in the Mediterranean basin, though small numbers occur on several beaches (de Nobel 1995, Kivit *et al.* 1994, Meininger & Atta 1994, Schekkerman & van Roomen 1993, Spiekman *et al.* 1993). Possibly, a large proportion of the Sanderlings which spend the non-breeding season in Africa occurs scattered around the Mediterranean in spring, because it would seem unlikely that they would not need to refuel after crossing the Sahara, and also with a large area of land without feeding possibilities ahead of them. Adult Sanderlings in southern Africa gain body mass in preparation for northbound migration between mid-March and late April at a rate of 0.8 g/day, to an average peak mass of 88 g in early May (Summers & Waltner 1979). The subsequent migratory journey takes approximately seven weeks (Summers *et al.* 1987). First-year Sanderlings do not increase in mass and most remain south for the austral winter (Summers *et al.* 1995).

Birds of habit: site fidelity in Sanderlings

All studies of marked Sanderlings indicate that they tend to be faithful to their non-breeding sites (e.g. Evans *et al.* 1980, Reneerkens & Koomson 2008, Summers *et al.* 1987, Fig. 11) both within and between years. Langston (2002) mentions a Sanderling in the Wash that was recaptured there 13 times over 12 years. Similarly, on the German North Sea island of Helgoland, an adult Sanderling was colour-ringed in January 1993 and was recorded in 15 consecutive winters until winter 2007/2008 (V. Dierschke & F. Jachmann unpubl. data). The average observed return rate (i.e. not corrected for resighting probability) from one year to the other was 74.5% at Iwik, Banc d'Arguin, Mauritania (JR unpubl. data). This high degree of site fidelity in Sanderlings, their enormous variation in wintering latitude, the fact that they generally live in open habitats and are easy to approach by human observers makes them exceptionally suitable for mark–resighting survival analyses (Koomson 2007, Fig. 11).

Myers *et al.* (1988) experimentally showed that adult Sanderlings were more prone to return to the location from which they were translocated (c. 200 km) than juveniles. However, this age difference was only present when the translocation occurred just after southward migration (in Oct or Nov). The different return rate between translocated adults and juveniles was not present in Sanderlings translocated in January (Myers *et al.* 1988). This suggests that prior knowledge of a location plays a role in Sanderling site fidelity, although in January both adults and juveniles rarely returned to the site from which they were translocated. Many juveniles caught in Mauritania, returned as adults to their first non-breeding site (JR unpubl. data). To our knowledge, Sanderlings are not subject to movements during long periods of severe weather, although a small peak in birds passing the Dutch mainland coast occurs in December (Nederlandse Zeevogelgroep/Club van Zeetrekwaarnemers unpubl. data, Fig. 10). In the Wadden Sea, the Sanderling is the only wader that does not

show differences in numbers between cold and mild winters (JMJB 2007).

Sanderlings are also faithful to stopover sites during migration (Diederichs 1999, Gudmundsson & Lindström 1992, Myers *et al.* 1990, Scott *et al.* 2004, Fig. 11) although possibly to a lesser extent than to their wintering grounds. Of 155 Sanderlings colour-ringed in SW Iceland in May 2007, 71 (46%) were resighted at the same location a year later (JR & GTH unpubl. data). The probability of being resighted was correlated with body mass. Sanderlings with below average body mass (corrected for size) for the time of year, were less likely to return. If they did return, they arrived significantly later at the stopover site than Sanderlings with above average body masses the year before (JR & GTH unpubl. data).

Annual return rates of Sanderlings to breeding sites are lower than to non-breeding sites and migration stopover sites. This may be the result of low environmental predictability in the high Arctic, where Sanderling move relative opportunistically in search of suitable (e.g. snow-free) environments to breed, and partly because some pairs are formed during the last stage of migration (Tomkovich & Soloviev 2001). Underhill *et al.* (1993) calculated an annual return rate of 11.1% for the local breeding population as a whole. Tomkovich & Soloviev (1994) found a difference in breeding site fidelity between males (20.3% returned in the following year) and females (6.8% returned). A similar sexual difference, but with larger return rates was found in Zackenberg, NE Greenland with 57% and 21% of adult males and females, respectively, returning the following year (JR *et al.* unpubl. data). Nests of both males and females that did return in the following year were always located <500 m, and in most cases <100 m, from the nest site of the previous year (JR *et al.* unpubl. data). This is consistent with the findings of Parmelee (1970) in the Canadian Arctic. On the Taimyr Peninsula, inter-year movements between successive nests were within 1 km (Tomkovich & Soloviev 1994).

Phenology and bird numbers during migration periods

During peak migration in Aug and May, several stopover sites hold many more Sanderlings than during winter. For example, in Britain the total number of Sanderlings may be twice as high as in winter, and four locations (Ribble Estuary, Alt Estuary, Carmarthen Bay and the Wash) support >1% of the flyway population at such times. In the Netherlands and Germany, it has been shown that in May and early June, Sanderlings occur much more in mudflat areas than on sandy beaches where they are most numerous in winter (Diederichs 1999, Süß 2006, van Turnhout & van Roomen, 2008). The large number of people on the beaches during May and August may be the cause of this, but a change in food availability should also not be ruled out. It is important to realise that these numbers are usually based on single counts during each month. Van Turnhout & van Roomen (2008) indicated that in the Netherlands the majority of Sanderlings prepare for onward northbound migration during the latter half of May. The monthly counts do not always take place during the peak of migration. In 2003, when the survey was performed relatively late (on 17 and 18 May) about 23,000 (20% of the estimated flyway population) was counted in the Netherlands. To get a better measure of the timing of migration and likely year to year variation in timing (e.g. Gudmundsson & Lindström 1992) more regular counts at known important stopover sites during the migration periods would be needed. These could be combined with colour ringing and resighting

to estimate the total number of birds using a given stop-over site (e.g. Schaub *et al.* 2001, Fig. 6). Using this approach, many more sites are likely to be identified as of international importance. Given the site fidelity at stopover sites, such methods could have important consequences for the conservation of Sanderlings.

Using the variation in non-breeding latitude to understand migration patterns and population structure

Sanderlings are special in inhabiting non-breeding areas as far north as Scotland and as far south as South Africa, while breeding on the high Arctic tundra. The question arises why some individuals take long migratory flights whereas others have shorter migration distances. What are the costs and benefits of different life history strategies? The Sanderling is a suitable species to study such a fundamental question (e.g. Koomson 2007). This would involve survival studies using mark-recapture analysis in which annual survival probabilities could tell us whether different decisions for a non-breeding site have different consequences in terms of survival. By studying seasonal survival (which involves more intensive marking and resighting), one can determine when the highest mortality takes place, and whether it differs between wintering sites at different latitudes (Koomson 2007). To interpret differences in survival between different latitudes, it would also be important to measure the energy expenditure associated with wintering at a particular latitude and site (particularly climate, e.g. Castro *et al.* 1992) and energy intake (food availability and quality, see Diet and foraging behaviour section), as well as the risk of predation and disease (Piersma 2007).

Different selection pressures at different locations may result in specific behavioural and/or physiological adaptations by the birds to cope with the different demands. For example, different age structures and sex ratios within populations at different sites may help us to interpret how different selection pressures within non-breeding areas impact on populations.

There are clear indications that the fraction of first-year, high-arctic waders varies at different non-breeding locations along the flyway after variation in reproductive success has been taken into account (cf. Blomqvist *et al.* 2002, Underhill 1987) and there is age-dependent site selection within estuaries (van de Have *et al.* 1984). For example, the annual variation in the percentage of first-year birds was 33–65% during the winters 2002/03 to 2008/09 at Iwik village (Banc d'Arguin, Mauritania, $n = 26$ –200 in different years). This contrasts with Esiam beach (Ghana) where the first-year percentage was just 1–3% in Nov–Feb 2006/07 and 2007/08 (1/39 and 1/78, respectively). Interestingly, in Nov–Jan 2008/09 the first-year percentage was 16.7% (33/191), considerably larger. Similar changes in the percentage of juveniles were recorded at Barr al Hikman, Oman, where no juveniles were caught in a sample of 18 Sanderlings in 2007/08, but there were 11 juveniles out of 87 (12.6%) caught in 2008/09 (J. de Fouw & R. Klaassen unpubl. data). Some of these sample sizes are not large so the percentage of juveniles among birds caught might not be an accurate reflection of the percentage in local populations. Moreover it is known that different age classes of some *Calidris* waders can have differing local distributions and this may lead to bias in proportions caught (cf., van de Have *et al.* 1984, van den Hout *et al.* 2008, unpubl. data). Firm conclusions as to how age-ratios change along the flyway will have to await the accumulation of more data.

Given the small variation in the bill length of Sanderlings (6–8%, Engelmoer & Roselaar 1998), but significant size difference between males and females (and hence different requirements for food and ability to resist cold) as well as the likelihood that males need to arrive earlier on the breeding grounds in order to claim territories, a sex-related non-breeding distribution could exist (cf. Myers 1981, Nebel 2005, Nebel & Ydenberg 2005). In Nov–Dec 2005, the sex ratio of birds caught in Mauritania and molecularly sexed (Reneerkens *et al.* 2005) was significantly skewed towards males (69% males, $n = 198$, binomial test, $p < 0.001$). Moreover the skewing applied to both age classes (62 and 75% male first-year and adult birds respectively, $n = 102$ and 96).

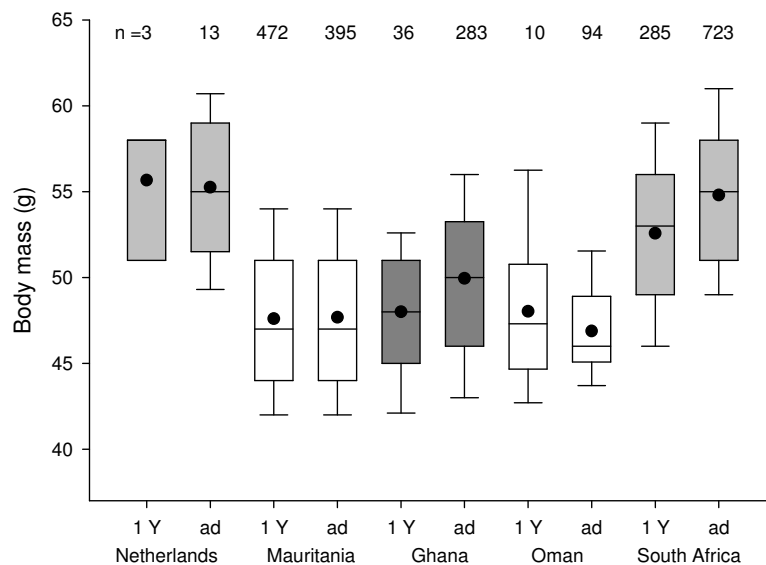


Fig. 12. Body mass of first-year and adult Sanderlings in the Netherlands, Mauritania, Ghana, Oman and South Africa between 1 Nov and 1 Mar. The boxes enclose the middle 50% of the values and the vertical lines with whiskers show the range of the mean masses of individual catches. The dividing lines within the boxes indicate the median, and the black dots indicate the mean of all the catches. For juvenile Sanderlings from the Netherlands only the average and median are shown because of the small sample size. The South African data have been published before (Summers & Waltner 1979, Summers *et al.* 1987).

However, although the sex ratio was skewed slightly in the same direction at the same location and period in 2007, the skewing was much less and was not significant (57% ($n = 54$) and 55% ($n = 49$) first-year and adult males respectively, binomial test, $p = 0.303$, age-classes lumped, JR *et al.* unpubl. data). At Langebaan Lagoon, South Africa, the sex-ratio was strongly biased to males (56 males in a sample of 78 (72%), Summers *et al.* 1987) which suggests that male Sanderlings do not winter close to the nesting grounds in order to be in a better position to claim a breeding territory as appears to be the case in Western Sandpiper *Calidris mauri* (Nebel 2005). We need to compare sex ratios at different locations and in different years in order to understand the reasons for these biases in sex-ratio.

It has been shown before that birds of many species store extra body lipids in colder environments (e.g. in a temperate climate such as the Netherlands or South Africa), in response to unpredictable feeding conditions and energy demands (Davidson 1980, Kelly & Weathers 2002, Lima 1986). Consistent with such observations is the fact that the body masses of Sanderlings in Nov–Feb differed between populations from different latitudes (ANOVA, $F_{2285, 4} = 183.3$ $p < 0.001$) but not between age classes $F_{2285, 1} = 0.618$ $p = 0.342$; Fig. 12). However, the interaction between site and age was significant ($F_{2285, 4} = 6.157$, $p < 0.001$). This appears to relate to the fact that adults sampled in South Africa and Ghana were relatively heavier than juveniles. The explanation for this is probably that some adults caught in late February were already fuelling up for migration. Unlike the adults, first-year birds do not accumulate fuel for migration in Mar and Apr and remain south for the austral winter (Summers *et al.* 1987). Fuelling occurs much later in the season in the Netherlands. Sanderlings in Mauritania were always caught in Nov or Dec and hence no difference in mass between first-year and older birds is expected. Site differences in body mass may also reflect differences in the risk of predation with birds shedding mass in order to maintain the ability to out-manoeuvre predators such as falcons (van den Hout *et al.* 2008). In these comparisons, body composition needs to be taken into account. In Ghana we expect birds to have larger gizzards and intestines to process their mollusc diet (cf. Dekinga *et al.* 2001, Piersma *et al.* 1993).

REPRODUCTION

Breeding densities

Breeding densities in pairs, nests and/or broods of 0.3 (Hötker 1995) and 0.8–1.0 km^{-2} (Tulp *et al.* 1998) were recorded for Cape Sterlegov, 0.86–2.14 km^{-2} for the Knipovich Bay area (Tomkovich *et al.* 1994) and 0.5–0.64 km^{-2} (Schekkerman & van Roomen 1995) and 0.26 km^{-2} (Spiekman & Groen 1993) for the tundra near Lake Pronchishcheva. From NE Greenland, densities are known from Karupelv on Traill Ø (1.0 km^{-2} in 1998; B. Sittler, pers. comm.), from Danmarkshavn (average density 1.8 km^{-2} (range: 0.7–2.9 km^{-2}); Meltofte 1975, 1979, M. Forchhammer unpubl. data) and from Zackenberg (average density in 2003, 2007 and 2008 3.7 km^{-2} (range: 3.37–3.92 km^{-2} ; Meltofte 2004, Hansen *et al.* 2008, JR & JH unpubl. data). Only eight or nine breeding pairs were reported breeding on Svalbard during 1960–1980 (Norderhaug 1989), but Strøm (2006) estimated the population at 20–100 pairs.

Breeding system: do Sanderlings double-clutch?

Sandpipers (Scolopacidae) have a variety of breeding systems (Pitelka *et al.* 1974, Piersma 1996). Sanderlings in the Canadian Arctic are thought to double-clutch, a breeding system in



Fig. 13. A pair of Sanderlings incubating their newborn chicks at Zackenberg, NE Greenland, 8 Jul 2007. The female (left) was ringed as an eight-day old chick on 23 Jul 1997 and was also observed in Zackenberg with chicks in Jul 2003, 2007 and 2008. In Zackenberg, Sanderlings have been shown to have a mixed breeding strategy with sole adults or pairs raising a clutch. (Photo: Jeroen Reneerkens.)



Fig. 14. A male Sanderling with four 4-days old chicks, Zackenberg, Greenland, 19 Jul 2007. Parentage analysis using microsatellite markers may confirm whether Sanderlings have a double-clutching breeding system. (Photo: Jeroen Reneerkens.)

which mates of a pair of birds divide incubation between two clutches that are laid in rapid succession (Parmelee & Payne 1973). This conclusion was based on 24 hr observations at one nest and repeated visits at nine other nests. At each nest, the incubating bird was invariably found to be the same individual on every visit. In addition, examination of the ovaries of two dissected Sanderlings during the incubation period indicated the laying of eight eggs (two complete clutches) in rapid succession. However, a later study in NE Greenland found only cooperating pairs of incubating Sanderlings (Pienkowski & Green 1976). The only other published study of the breeding system of Sanderlings is that of Tomkovich & Soloviev (2001) in N Taimyr, Siberia. They observed both cooperating pairs and solitary incubating birds and suggested that some Sanderlings in Siberia may double-clutch but others do not. The fact that 12 clutches of uniparental females hatched later than those of uniparental males supported the notion that the uniparental birds were indeed double-clutching, because females are expected to incubate their second laid clutch which would result in later hatching dates than the males that incubate the first laid clutch (Tomkovich & Soloviev 2001). Based on preliminary observations, it was concluded that such

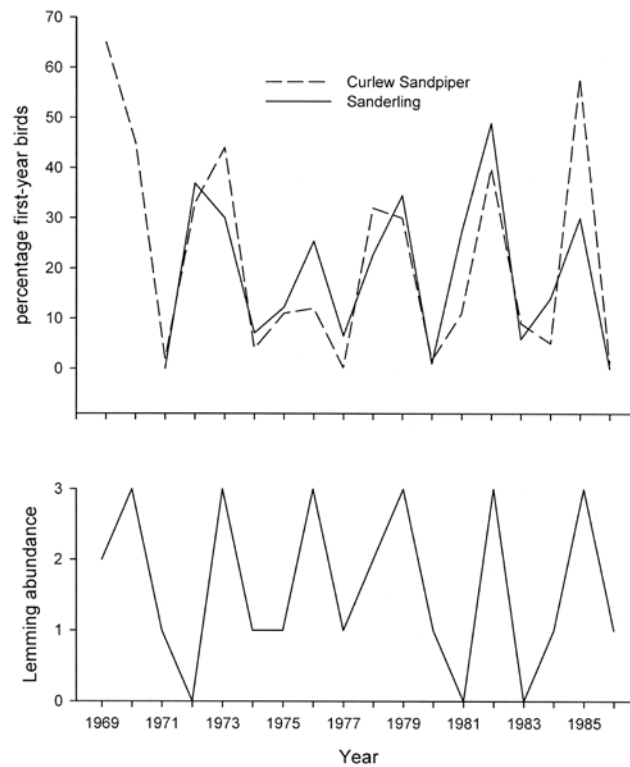


Fig. 15. The percentage of first-year Sanderlings and Curlew Sandpipers in South Africa in the austral summers 1969–1986 in relation to lemming abundance during the preceding breeding season on the Taimyr Peninsula, Siberia. Year refers to the previous breeding season (source: Summers & Underhill 1987).

a mixed strategy may also occur in the breeding population at Zackenberg, NE Greenland (Meltofte 2001, 2004, Piersma *et al.* 2006, Fig. 13). By use of thermologgers and passive integrated transponders (PITs) it has now been shown that a proportion of the Sanderling pairs incubate biparentally, while other nests are uniparentally incubated, by either males or females (Reneerkens *et al.* 2008a, unpubl. data). The latter is consistent with double-clutching. Future parentage analyses using microsatellite markers could potentially show whether uniparental incubation is the result of a double-clutching breeding system (Fig. 14).

It will also be valuable to understand intraspecific variation in breeding effort. Uniparentally incubating Sanderlings spend a smaller proportion of time incubating and, in contrast to biparentally incubating birds, adjust their incubation patterns to ambient temperature (Reneerkens *et al.* 2008a, unpubl.). During cold weather, less time is spent foraging. This suggests that uniparental incubation is only possible in areas and years with higher temperatures and/or high food abundance (Reneerkens *et al.* 2008a, unpubl.) and may depend on the condition in which Sanderlings arrive in the breeding areas. Such carry-over effects could be caused by differences in non-breeding areas (e.g. distance to breeding grounds, pathogen pressure) and conditions during migration (e.g. head or tail wind during flight, and/or fuelling conditions at stopover sites).

Counts of juvenile Sanderlings in the non-breeding grounds could give us information about annual productivity. Such counts should be carried out before juveniles moult into their first winter plumage (before mid October) and thereby become difficult to distinguish from adults. Because juveniles and adults may have a (partially) segregated distribution both within and between sites, care should be taken to take account of potential age-ratio biases (e.g. Rogers *et*

al. 2005). It should be possible to avoid these by performing counts and making catches in a standardised way and at numerous locations. The proportion of juveniles in autumn catches near Puck Bay, Poland, varied considerably from year to year but did not correlate with lemming cycles in Siberia or with age-ratios of Curlew Sandpipers *Calidris ferruginea* that have a similar Siberian breeding distribution to that of eastern Sanderling populations (Meissner & Włodarczak 1999). This indicates that these Sanderlings may not have been of Siberian origin. In contrast, age-ratios of Sanderlings in S Africa were positively and significantly correlated with lemming abundance on the Taimyr Peninsula of Siberia and with age-ratios of Curlew Sandpipers in S Africa, indicating that S African Sanderlings are primarily of Siberian origin (Summers *et al.* 1987, Fig. 15).

IMPORTANT INFORMATION GAPS

In this review, we have tried to summarise most available knowledge about Sanderlings occurring in Europe and on the west coast of Africa and to indicate gaps in our present understanding. Clearly, there is still a lot we have to learn.

Quite apart from intensive individual studies on different aspects of Sanderling ecology, much could be gained by researchers joining forces, pooling ringing and catching data and carrying out co-ordinated fieldwork throughout the flyway.

Already we have accumulated a substantial, but still largely unanalysed, colour-ringing database that we can use to substantially increase our understanding of migration routes and population connectivity. The same applies in respect of data on biometrics, sex, age and body mass of birds at different locations and at different times of the year.

For the future, it would be most valuable if arrangements

could be developed for Sanderlings to be reliably and systematically sexed throughout the flyway using molecular methods. Stable isotope analyses also deserve more attention and could help unravel population structure and migration patterns. For example, they could yield better information about the normal southern limit of birds using the E Atlantic Flyway (Scott in prep.).

In migration studies, as well as applying such modern techniques as geolocators and radio transmitters, we could also learn much by increasing monitoring efforts spatially (e.g. more surveys on African sandy beaches) and temporarily (more frequent and regular counts at key locations). It is probably unrealistic to expect complete coverage of all available habitats at regular time intervals along the whole flyway. Nevertheless, with ongoing counting schemes, such as those coordinated by Wetlands International (Dodman & Diagana 2003, Dodman & Sa 2005) we should be able to make substantial progress. To begin with, we suggest focusing on areas with indications of contrasting population trends, such as the coast of S Africa (probably negative) and France (positive). At the same time, we recommend a more thorough analysis of available data for France in relation to what seems to have been a recovery following better protection in the early 1970s.

We encourage increased (colour-) ringing and efforts to find colour-ringed birds in the White Sea area during migration periods, for example on the Kola Peninsula, NW Russia. To date, two British Sanderlings have been recaptured there. Such efforts would help to establish whether (and where) Siberian Sanderlings mix with the Greenland birds in their winter quarters. More wader counts in Iceland during spring migration would also be most valuable. The development of genetic markers for Sanderlings from different breeding populations is a key priority as this will yield valuable information concerning the possible mixing of Sanderlings from different breeding populations in the non-breeding grounds.

Another challenge for the future is to measure annual variation in productivity reliably for each breeding population using age-ratios and also distinguishing such variation from age-related site selection.

It will be especially valuable to reach an understanding of the breeding system of Sanderlings using genetic techniques (parentage analysis) and to confirm double-clutching and the degree to which this behaviour varies in time and space.

Another key information gap is an understanding of moult patterns, especially primary moult. Since the one-paragraph summary on Sanderling moult in Ginn & Melville (1983), relatively little has been published on the subject. Serra (2000) and Underhill (2003) both suggest that knowledge of the timing of moult, which can be taken down to the level of the individual primary, can provide insights into the strategies used to cope with constraints, such as time and weather, in the annual cycle. Underhill's (2003) analysis of the timing of primary moult, feather-by-feather, for six wader species, including Sanderling in S Africa, demonstrated wide variability of strategies within and between species. The Sanderling, with its wide latitudinal range during the non-breeding season, is an ideal species for evaluating the potential of this approach.

Sanderlings: a new International Wader Study Group project

Many of the suggestions for future research made above involve catching, ringing, colour-ring observations, increased counting effort and more specialised observations. This work

is already ongoing in the context of research collaboration between the University of Groningen, the Royal Netherlands Institute of Sea Research and the University of Ghana, under the umbrella of the Global Flyway Network (Piersma 2007). However, the value of these efforts could be greatly increased by setting up a large network of amateur and professional wader enthusiasts to co-operate on Sanderling studies throughout the flyway. During the discussion session of the Workshop on Sanderlings during winter, migration and reproduction held in October 2008 at Jastrzębia Góra, Poland, it was decided to instigate a new International Wader Study Group project on Sanderlings. The aims of this project are to create a large international network of collaborators who will be encouraged to step up colour-ringing and resighting Sanderlings, especially in currently underrepresented countries. Another goal is to conduct large-scale, targeted counts of Sanderlings, to increase counting coverage in areas where needed, to get a better idea of stop-over duration, phenology and turnover during migration and to measure annual productivity by a combination of juvenile counts and age-ratios from catches. We encourage everyone interested in Sanderlings and in contributing to this project to register at our website at <http://www.waderstudygroup.org/res/project/sanderling.html>.

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