

# Effects of Food Availability, Snow and Predation on Breeding Performance of Waders at Zackenberg

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## SUMMARY

The first few weeks after arrival on the tundra in late May and early June appear to be the most critical period in the summer schedule of arctic-breeding waders. Food availability and snow-cover determine population densities and timing of egg-laying, and early egg-laying seems essential, since it increases the chances for re-laying in case of nest failure, optimises timing of hatching of the chicks in relation to the peak period of arthropod food for the young, facilitates early departure of the adults and maximises the time available for the young to grow strong before winter begins in early September.

Conditions for waders in most of high-arctic Greenland seem favourable as compared to several other arctic areas, in that the climate is continental with favourable weather conditions during most summers, and the predation pressure on eggs and chicks is normally moderate. With the projected climate change, the waders of high-arctic Greenland may face more unstable breeding conditions, and in the long term some of the wader species may be hampered by overgrowing of the high-arctic tundra with more lush low-arctic vegetation.

## I. INTRODUCTION

Arctic tundra is hardly an optimal habitat for adult “arctic” waders. They apparently benefit much more from feeding on rich intertidal coasts or inland wetlands in temperate and tropical areas, where they spend 9–11 months of the year, and where they often find extreme densities of fleshy bivalves and crustaceans (Meltofte, 1996; van de Kam *et al.*, 2004). On the tundra, they have to survive mostly on tiny arthropods, which may abound, but also periodically be very limited, particularly early in the season (Meltofte *et al.*, 2007a).

However, the estimated total of 30 million “arctic” waders (CHASM, 2004) can not breed in temperate and tropical wetlands because of high diversity and density of predators and poor feeding conditions for chicks (Meltofte, 1996). Instead, they migrate to the Arctic to take advantage of the short summer abundance of tundra arthropods and the more limited diversity and density of predators than on southern latitudes.

But the breeding conditions for the waders in the Arctic are constrained by several factors, such as timing of snowmelt and food abundance in spring, poor weather during chick growth in summer and the need for adults and juveniles to leave the Arctic as soon as possible, at least before winter begins in September (Meltofte *et al.*, 2007a). Hence, the adults of most species seem to minimise their stay in the Arctic, particularly so in the High Arctic.

## II. THE CRITICAL PRE-NESTING PERIOD AND INITIATION OF EGG-LAYING

Arctic waders depend on rich feeding grounds on their final staging areas in temperate climates to be able to carry out the often thousands of kilometres of non-stop flight to their arctic breeding grounds (van de Kam *et al.*, 2004). However, such optimal areas are most often so far away from the arctic breeding grounds that the weather here has little or no predictive value for progress of spring on the tundra. This means that the waders have to time their arrival in the Arctic according to average acceptable conditions here. In high-arctic Greenland, this is in late May and early June when daily maximum temperatures reach positive values (Meltofte, 1985), and the spring migration is initiated at very much the same date from year to year in the individual birds (e.g., Battley, 2006).

Not only do arctic waders have to build up body stores for their long terminal flights to the Arctic, they also have to secure sufficient body stores for a transformation of organs from “flying mode” to “breeding mode” and for the first critical period on the tundra (Meltofte *et al.*, 2007a).

In preparation for their long flights, waders develop larger flight muscles, while other organs like the digestive system shrink. During their first days on the tundra, waders rebuild their digestive system and “reorganise” other organs in preparation for the breeding season (Piersma *et al.*, 1999). Furthermore, they have to carry sufficient body stores as an insurance against periods of inclement weather like snowfall and hard wind upon arrival. On top of this, female birds have to obtain local nutrients for the production of a clutch, normally of four eggs, which has a total volume of between 50% and 100% of the weight of the female bird herself (Klaassen *et al.*, 2001; Morrison and Hobson, 2004; Box 1). Finally, both mates have to initiate establishment of body stores for the incubation period (Moltofte *et al.*, 2007a).

### Box 1

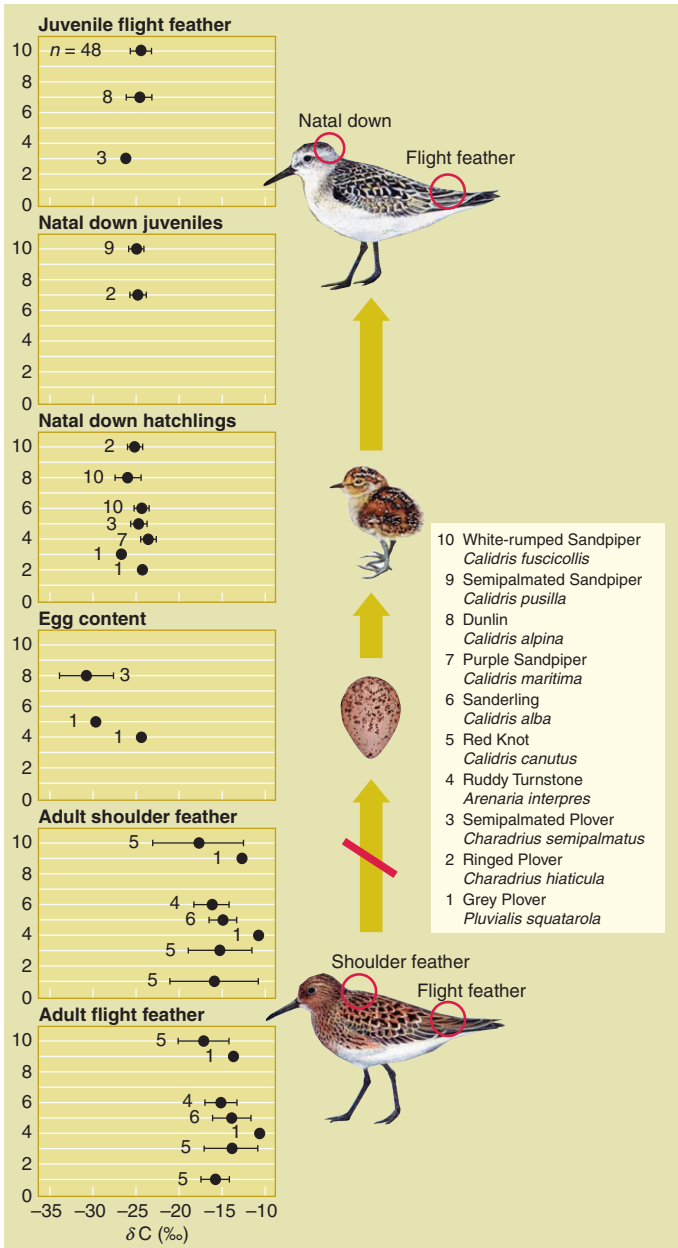
#### Arctic waders are “income breeders”

Geese and other large waterbirds often carry so rich body stores to the Arctic in the form of fat and proteins that they need few resources from the breeding grounds, before the female can produce a clutch of eggs (Drent and Daan, 1980). They are so-called “capital breeders.” This implies that they can lay eggs from a few days after arrival on the often more or less snow-covered breeding grounds.

Analyses of egg and newly hatched chick proteins show that arctic waders are not capable of doing this (Klaassen *et al.*, 2001; Morrison and Hobson, 2004). At Zackenberg, we collected small samples of neck down from 166 freshly hatched chicks from 58 broods besides a few unhatched eggs of common ringed plover, red knot, sanderling, dunlin and ruddy turnstone in 1999 and 2000, which together with similar samples from waders in arctic Canada were analysed for carbon stable-isotope ( $^{13}\text{C}/^{12}\text{C}$ ) ratios (Klaassen *et al.*, 2001). Carbon isotope ratios in live organisms are markedly different between marine and terrestrial habitats, and since adult waders of the species considered spend virtually all their non-breeding time in staging and wintering areas along marine coasts, the isotope ratios of their eggs and thereby natal down of chicks would reflect this, if the resources for the production of eggs derived from coasts. However, when the waders arrive in the Arctic during late May and early June, the coasts are covered in thick ice, and they feed exclusively on tundra resources, primarily arthropods. In accordance with this, the isotope ratios of natal down were similar to those of juvenile feathers later grown on the tundra and distinctly different from isotope ratios of adult feathers grown during the adults’ stay on marine coasts (Box Figure 1): they are “income breeders.”

(continued)

Box 1 (continued)



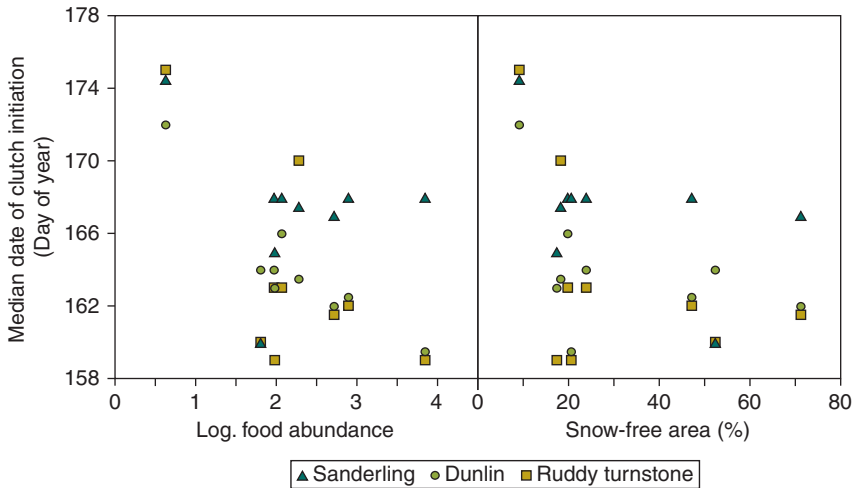
Box Figure 1 Carbon stable isotope ratios ( $\delta C$ ) of eggs, natal down and feathers of different species of arctic-breeding waders at different times during the year. All samples were collected in arctic Canada and Northeast

Greenland in 1999 and 2000. Feathers collected from nest-attending adults were grown in winter (adult primary flight feathers) and during spring migration (adult shoulder feathers; data are averages across individuals  $\pm$ SD). Eggs were collected from deserted nests (egg content), natal down from hatchlings (data are averages across clutches  $\pm$ SD per species). Data for natal down still attached to the tips of head and neck feathers of freshly hatched chicks, and for secondary flight feathers from independent young are averages across individuals  $\pm$ SD (reproduced from [Klaassen, 2003](#) with kind permission from Springer Science and Business Media).

The two sampling years at Zackenberg were very much different, in that 1999 had the latest snowmelt recorded during our study years, while 2000 was very early (see [Figure 1](#)). Accordingly, egg-laying in waders was much delayed in 1999 as compared to 2000 and other early seasons since then. A minimum of 5–8 days are needed after the arrival of the adult waders on the tundra until they can produce eggs ([Roudybush et al., 1979](#)), and this was very much so in 2000, while in 1999, they had to spend 1–2 weeks more on the tundra, before egg-laying could commence (see [Figure 1](#)). This means that the waders had been feeding two to three times as long on the tundra in the late breeding season as in the early. But this did not result in any difference in isotope ratios between the years. This means that even in the season with early egg-laying, the resources for the eggs derived from the tundra.

That the pre-breeding period may be critical to arctic waders is further supported by the finding that the four common wader species at Zackenberg used 75–92% of their daytime hours to feed during pre-nesting in an optimal year ([Meltote and Lahrmann, 2006](#)). For comparison, temperate breeding lapwings *Vanellus vanellus* used only between 18% (males) and 32% of their pre-nesting daytime for feeding ([Zöllner, 2002](#)), and feeding time used during pre-nesting at Zackenberg was higher or in the high end of what was found in waders on wintering and spring pre-migratory fattening sites ([Hötter, 1995, 1999](#); [Kirby, 1997](#); [Ntiamao-Baidu et al., 1998](#); [Leon and Smith, 1999](#); [Masero and Pérez-Hurtado, 2001](#); [Shepherd, 2001](#); [Scheiffarth et al., 2002](#)).

All this takes place within the first 1–3 weeks on the tundra, so it was no surprise, when our analyses of the first 10 years of data from Zackenberg revealed that initiation of egg-laying in sanderling *Calidris alba*, dunlin and ruddy turnstone was correlated with food availability and snow-cover during the first weeks after the birds' arrival; the more food and the less snow-cover, the earlier egg-laying ([Figure 1](#); [Meltote et al., 2007b](#)). Food availability turned out to explain more of the inter-annual variation in egg-laying than snow-cover in early spring, but snow-cover apparently had a stronger effect in years where the proportion of snow-free land was below 25%.



**Figure 1** The relationship between median first egg dates (days of the year, June 7–27) of three species of waders and annual food abundance (natural log. transformed number of Diptera and spiders caught between June 3 and 17) and snow-free proportion of land on June 10, respectively, at Zackenberg 1996–2005 (modified from Meltofte *et al.*, 2007b).

### III. THE LAYING PERIOD

In sanderling, dunlin and ruddy turnstone, the very first clutches were laid around June 1 and the latest (re-placement clutches) during the first days of July. Median dates varied from around June 8 as the earliest until around June 22 in the latest breeding seasons. Hence, arctic waders seem to breed as early as conditions permit, and a significant impact of spring snow-cover had already been demonstrated by Meltofte (1976, 1985) and Green *et al.* (1977). Snow-cover per se has an impact unrelated to food availability, since many wader territories in the High Arctic are totally snow-covered far into the laying period, preventing the birds from dispersing on the tundra. The waders have to wait not only for patches of land to become snow free but also for the patches to become so extensive that it is not all too easy for the foxes and other predators to scrutinise them for nests (Byrkjedal, 1980). Furthermore, an impact of temperature had been demonstrated by Nol *et al.* (1997), which was interpreted as a temperature effect on food availability.

The very first turnstones and dunlins to initiate their clutches were up to 5 days earlier than the earliest sanderlings (Figure 1). Apparently, a minor part of the sanderling population at Zackenberg performs double-clutching (Meltofte, 2003; Piersma *et al.*, 2006), where the female lay one clutch for a

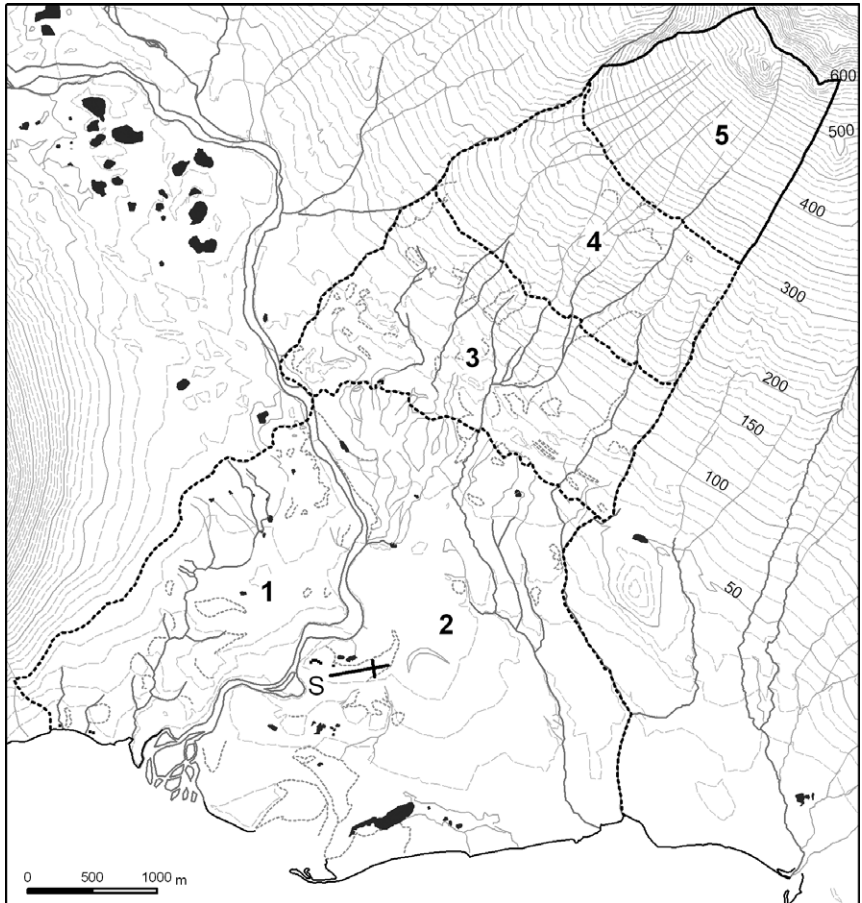
male and then another about a week later for herself. To what extent the later laying dates in this species are the product of such a double-clutching strategy is unknown. Furthermore, the initial laying dates during the last 4 years have been extraordinarily early in that laying dates around June 1 have been recorded only a few times before in high-arctic Greenland (Meltofte, 1985).

Finally, our data confirmed that the total laying period was reduced by up to 2 weeks in late breeding seasons, in that the time around July 1 appears to be the last chance for laying—or re-laying—if the young shall have a chance to fledge and grow strong before winter begins (Meltofte *et al.*, 2007a, Meltofte *et al.*, 2007b). Late egg-laying also resulted in significantly reduced mean clutch sizes in dunlin and ruddy turnstone, but not significantly so in sanderling. This adds to the disadvantage of late breeding, which further includes a more limited time “window” for laying and re-laying in case of failure, increased risk of mismatch between hatching of the chicks and peak occurrence of arthropod food on the tundra, delayed departure of the adults, and reduced time for development of the young before winter begins in September (Meltofte *et al.*, 2007a).

#### IV. POPULATION DENSITIES AND HABITAT SELECTION

In high-arctic Greenland, wader breeding densities are low,  $\leq 2$  pairs  $\text{km}^{-2}$ , in the far north due to the desert-like conditions with often less than 5% vegetation cover and thereby limited food resources (Meltofte, 1976, 1985). Densities are also relatively low, 1–3 pairs  $\text{km}^{-2}$  but locally up to 10 pairs  $\text{km}^{-2}$  in the “lush” southernmost parts of Northeast Greenland, where the often long-lasting snow-cover prevents the birds from utilising large expanses of otherwise well-vegetated ground sufficiently early in the season for breeding (Mortensen, 2000). Densities peak with typically 5–10 pairs  $\text{km}^{-2}$ , but locally up to 16 pairs  $\text{km}^{-2}$  in central Northeast Greenland, where there is extensive vegetation cover in many places and moderate snow-cover in early spring. Hence, densities are best correlated with the ratio of snow-free, vegetated ground in early June (Meltofte, 1985; Mortensen, 2000). This emphasises the importance of pre-breeding feeding conditions already pointed out above. Pre-breeding feeding conditions determine not only the timing of egg-laying but also population densities. Hence, local population sizes seem to be determined by the amount of land, which allow egg-laying in early/mid June. In such areas, egg-laying may then be delayed until after mid June in year with late snow-cover (Meltofte, 1985; Meltofte *et al.*, 2007b).

Six species of waders breed in the 19.3 km<sup>2</sup> bird census area at Zackenberg with an average of about 260–300 pairs in total (Tables 1), and the density of about 14–15 pairs or territories km<sup>-2</sup> is among the highest recorded in high-arctic Greenland (Table 2; Mortensen, 2000; Meltofte, 2006a). The individual species have different habitat preferences. This is illustrated by the distribution within different sections of the census area (Figure 2, Table 2). Common ringed plovers are found on poorly vegetated gravel expanses in the lowland and particularly in the areas above 300 m a.s.l., but always close to vegetated areas. The high slopes clear early from snow in spring, but they are



**Figure 2** Map of the study area at Zackenberg (74°30'N, 20°30'W) giving demarcation of the individual sections 1–5 together with rivers/streams, lakes/ponds (black) and landscape features (dotted) together with the position of the research station (S) and runway in the lower left centre. Altitudes are given in metres.



often covered in new snow during the summer season, which regularly cover the ground for short spells down to 300–400 m a.s.l. Red knots *Calidris canutus* and sanderlings are mainly found on mesic dwarf shrub heath with low topographic profile—the sanderling apparently on less stony ground than the knot—in the lowlands and particularly on the slopes of Aucella-bjerg. Dunlins breed exclusively in and around wet fens, which primarily are found in the lowlands. Finally, ruddy turnstones breed on gravelly and stony sites, often with hills and ridges. This is why most are found in Oksebakkerne (Musk Ox Hills) between 50 m a.s.l. and 150 m a.s.l., where relatively few sanderlings are found (Meltofte, 2006a). In spite of these differing habitat preferences among the species, the resulting total densities are surprisingly similar below 300 m a.s.l. (Table 2).

According to analyses by Forchhammer *et al.* (2008a, this volume), the inter-annual population variations in common ringed plover, sanderling and dunlin display indications of density dependence, while this is not the case in red knot and ruddy turnstone. Already Meltofte (1985) estimated that the breeding populations of the three former species in high-arctic Greenland were more or less saturated, while the latter two were not. Furthermore, Forchhammer *et al.* (2008a, this volume) analysed that population densities of the ruddy turnstone were negatively affected in years of extensive snow-cover. This again corresponds to previous results for this species in particular (Meltofte, 1985).

## V. POPULATION TRENDS

Unlike several other arctic animals, waders at Zackenberg show rather limited year-to-year variation in population sizes (Table 1; Meltofte 2006a). Only common ringed plover and red knot present year-to-year fluctuations of up to a factor 2, while the other species are even more stable. The species involved are relatively long-lived and site tenacious, reappearing in the same territories year after year (Cramp and Simmons, 1983). Even in sanderlings, who show nomadic tendencies in other arctic regions (Tomkovich and Soloviev, 2001), we have recovered adults as well as chicks ringed in our study area in previous years (see also Tomkovich and Soloviev, 1994). Hence, sanderlings were recorded in relatively stable numbers during most study years (Table 1), and the increase seen in dunlins during the first row of study years is probably due to improved census efficiency (Meltofte, 2006a). By contrast, common ringed plovers and possibly even red knots decreased significantly during the study years, while ruddy turnstone showed reduced numbers particularly during 2002–2004. Furthermore, the numbers recorded of red knot and ruddy turnstone showed significant correlation with

**Table 1** Annual minimum and maximum estimates of pairs/territories of waders in the 19.3 km<sup>2</sup> bird census area at Zackenberg, 1996–2005

Species	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
Common ringed plover	54–56	40–48	38–45	51–65	41–43	51–54	37–41	29	35–40	17–20
European golden plover	0	0	0	0	0	1	0	0	0	0
Red knot	33–43	35–44	27–32	25–33	24–27	27–30	24–27	24–25	16–20	30–36
Sanderling	50–63	55–70	62–70	60–67	58–66	58–72	49–55	67–74	61–73	38–49
Dunlin	69–81	75–91	75–94	80–94	98–103	104–111	120–132	105–114	110–122	92–102
Ruddy turnstone	41–51	49–58	56–63	43–49	48–50	45–51	31–37	33–34	45	65–74
Red-necked phalarope	0–1	0–2	1–2	1–2	1–2	1–2	1–2	1–2	1	1
Red phalarope	0	0	0–1	0	0	1	0	0	0	1

Source: Data from [Meltofte \(2006a\)](#).

**Table 2** Area size (km<sup>2</sup>) and average population densities (means based on annual averages of minimum and maximum estimates of pairs/territories) of waders in five sections of the 19.3 km<sup>2</sup> bird study area at Zackenberg, 1996–2005

Section	Area	<i>C. hia.</i>	<i>C. can.</i>	<i>C. alb.</i>	<i>C. alp.</i>	<i>A. int.</i>	All
5 (300–600 m)	2.24	4.78	0.31	2.28	0.58	0.04	7.99
4 (150–300 m)	2.51	4.04	2.51	5.00	0.88	0.94	13.37
3 (50–150 m)	3.33	1.23	2.66	1.13	4.31	5.29	14.62
2 (0–50 m)	7.77	1.18	1.38	3.67	7.08	2.98	16.29
1 (0–50 m)	3.47	2.19	0.73	3.16	7.41	1.47	14.96
Total	19.32	2.15	1.53	3.16	5.10	2.51	14.45

Note: See map Figure 2 for position of sections.

Source: Data from [Meltofte \(2006a\)](#).

July temperatures 2 years earlier, which suggest an influence of chick survival on population fluctuations 2 years later, when these chicks mature ([Meltofte, 2006a](#); see [Section VI.A](#) below).

These conclusions are not without reservations, however, since arctic waders are notoriously difficult to census ([Meltofte, 2001a, 2006a](#)), and we need more data to confirm these results. If the decline in common ringed plover is valid and is of more than local bearing, then it corresponds to decreasing numbers found on the wintering grounds of this population in West Africa ([Meltofte, 2006a](#)). The same apply to ruddy turnstone, which has been declining on the Northwest European wintering ground during the last decade ([Stroud et al., 2004](#)). The most obvious problems having appeared during the study years are three problematic breeding seasons (1999–2001), with extremely extensive and long-lasting snow-cover in 1999, and genuine snowstorms in July and June 2000 and 2001, respectively. In 1999, between one half and two thirds of the ruddy turnstone population apparently did not lay eggs, and the snowstorms in 2000 and 2001 killed many eggs and young ([Meltofte, 2000, 2001b, 2003](#)). Taken together, these problematic years could have had an effect, particularly on ruddy turnstone numbers, during the following years.

Few other population change data exist for waders in high-arctic Greenland. In a bird census area at Danmarkshavn Weather Station about 265 km north of Zackenberg, most populations remained much the same between three counts (1969–1975) and four counts (1986–1989) ([Boertmann et al., 1991](#)). However, ruddy turnstones halved between the two periods (from 14–17 pairs to 5–9 pairs), and the species did not breed at all in this area in 1907–1908. This is noteworthy, since indications of similar marked population changes have also been found in this species in other parts of high-arctic Greenland ([Meltofte, 1985](#)). Turnstones are sensitive to early

spring snow-cover, and they are not found in very snow-rich areas. Similar requirements may exist for the red knot, but here we have even less data (Meltofte, 1985).

Other changes in wader populations in high-arctic Greenland involve European golden plover *Pluvialis apricaria* and wimbrel *Numenius phaeopus*, who apparently began to breed in southern Northeast Greenland a few decades ago, possibly as a result of climate amelioration (Meltofte, 1985; Meltofte *et al.*, in press).

## VI. BREEDING SUCCESS

Breeding success is hard to measure in arctic waders. Nest success is the most easy parameter to record, but an unknown part of the failures is caused by visits by research workers at the nests, providing olfactory cues for predators like arctic foxes (Tulp *et al.*, 2000). Fledging success is next to impossible to quantify in widely scattered populations, since wader chicks are precocial, leaving the nest within a day after hatching and then wandering widely over the tundra. However, particularly long-tailed skuas *Stercorarius longicaudus* may exert an important predation pressure on wader chicks (Maher, 1970; de Korte and Wattel, 1988).

At Zackenberg, nest success shows no correlation with fox activity as measured by numbers of fox encounters by bird census workers on the tundra during June–July or the number of fox dens with pups in the area (see Schmidt *et al.*, 2008, this volume), and generally waders had more stable reproductive success than the almost “eruptive” breeding success in divers, waterfowl and long-tailed skuas at Zackenberg (Meltofte, 2006b; Meltofte and Høye, 2007). Neither did we find the close negative correlation between alternative prey for the foxes, the lemmings and predation, as has been demonstrated in so many other areas (Meltofte *et al.*, in press). Only in 2004 did we see the classical situation of many lemmings, many foxes and little nest depredation (Thorup and Meltofte, 2005). Nest depredation for all waders pooled has been around 50–60% in most years, which is moderate as compared to many other arctic areas (Meltofte *et al.*, 2007a).

Neither have we seen many clear signs of chick mortality due to inclement weather during chick growth in July, as has been found in other high-arctic areas (Meltofte *et al.*, 2007a). Only in 1997 did we see so unfavourable conditions that we found examples of reduced growth in wader chicks (Meltofte, 1998). The obvious explanation is the more continental climate of Northeast Greenland than, for example, northernmost Siberia, where cold spells with strong wind, sleet and rain are much more common (Tulp and Schekkerman, 2007). Still, a positive correlation was found between

temperatures in July, when most chicks grow up, and population size in red knot and ruddy turnstone 2 years later, when these chicks mature (see above). Also in the Siberian Arctic, a significant positive correlation was found between July temperatures and juvenile production (Schekkerman *et al.*, 1998; Soloviev *et al.*, 2006).

Most years we see plenty of juvenile waders on the tundra and on the coasts in August (Hansen and Møltofte, 2006). Only red knots seem to disappear without us being able to observe where they go—or the local population produces very few juveniles (see below).

### A. The Red Knot as an Example of Varying Breeding Success

Besides breeding success data from the breeding grounds, the percentage of juveniles in the populations on the wintering grounds serves as an indicator of breeding success (Robinson *et al.*, 2005). Unfortunately, among Greenland waders such data are available only for red knots wintering in Northwest Europe (Boyd and Piersma, 2001). To be able to back-calculate juvenile percentages on the wintering grounds into successful pairs on the tundra, we have used average numbers of fledged juveniles in broods still accompanied by adults. At Zackenberg, we have encountered 70 such wader broods during 1995–2005 with samples of at least 10 broods for sanderling (mean 1.6,  $N = 18$ ), dunlin (mean 1.8,  $N = 10$ ) and ruddy turnstone (mean 2.1,  $N = 32$ ). In red knot, we have six broods averaging 2.5 juveniles, and for all 70 wader broods combined (also including common ringed plovers), the average is 1.93 young produced per successful pair. Here we ignore that some sanderlings may double-clutch, and hence double their annual production.

Little is known about juvenile mortality from fledging to the time of sampling on the wintering grounds. To establish a theoretical calculation of the fraction of successful pairs during different years, we have used estimates of 33% and 50%, respectively (Table 3), and an estimated further mortality of 50% from sampling to their second summer (2 years of age) and thereby supposed arrival on the breeding grounds. Based on Boyd and Piersma (2001), who found that the ratio of juvenile red knots in catches of Nearctic birds wintering in the Wash in southeast England varied from 12.1% in a period of population decline (1969–1977), over 13.8% in a relatively stable period (1985–1995) to 28.8% in a period with population growth (1977–1985), we have used three ratios of juveniles in the wintering population, that is, 10%, 20% and 30%. The adult mortality from summer to midwinter was estimated to be 10%.

These calculations (Table 3) indicate that in periods of low juvenile ratios on the wintering grounds, about 80% of the potentially breeding population

**Table 3** Exploration of the parameter space that determines the fraction of red knot pairs arriving back on the tundra breeding areas in early spring that successfully fledge two young based on the known range of juveniles ratios recorded in cannon net catches on the British wintering grounds of Nearctic-breeding red knots (see text for explanation)

Assumptions		Outcome
Post-fledging mortality	Midwinter-juvenile percentage	Percentage of pairs that fledged young
0.33	10	16
0.33	20	39
0.33	30	74
0.5	10	21
0.5	20	51
0.5	30	98

*Notes:* The fraction of young birds that die between fledging on the tundra and sampling on the European wintering areas 1–9 months later is largely unknown and has here been assessed, for example to be either 0.33 or 0.5. Similarly, we assume that half the average annual adult mortality of 0.2 occurs between breeding and midwinter. We further assume that in their second year, birds remain on the wintering grounds, and that half of the young birds reaching the wintering grounds survive to the next winter.

do not produce any fledged young, be it due to breeding failure or non-breeding in part of the individuals. In stating this, we do not think of the few aberrant years with extremely inclement conditions, for example, in the form of exceptionally late snowmelt or snowstorms in the middle of the breeding season (see, e.g., [Meltofte, 1985, 2001b, 2003](#); [Ganter and Boyd, 2000](#)), but of the lengthier periods of poor survival and reproduction described by [Boyd and Piersma \(2001\)](#). Of the examples of 20% and 30% juveniles in the wintering population, the calculations for “20%” seem most realistic. In such years about 40–50% of the population would produce fledged juveniles, which point to a situation where most of the pairs lay eggs and suffer the “normal” predation and other failure. On the contrary, the calculations for 30% juveniles seem to give unrealistically high predictions of breeding success—at least with a 50% juvenile mortality. Such high juvenile percentages may be due to overrepresentation of juveniles in the winter catches or too high estimates of juvenile mortality.

These examples may support the possibility that red knots have been reproducing poorly at Zackenberg during recent years, thus providing an explanation for the reduced population in some of the last years. Total midwinter population sizes as recorded in Northwest Europe do not indicate a decline on population level, however ([Stroud \*et al.\*, 2004](#)).

## VII. BREEDING CONDITIONS IN HIGH-ARCTIC GREENLAND IN A CIRCUMPOLAR PERSPECTIVE AND IN THE FUTURE

As mentioned above, the breeding conditions for waders in high-arctic Greenland are generally more favourable than, for example, in the Siberian High Arctic. The climate is continental, with the exception of a narrow fringe of cool outer coasts. This means that the weather is generally favourable with few spells of inclement weather during the breeding season. Also, few years have so much snow and so late snowmelt that it prevents a large proportion of the waders from breeding. Predation on nests and young is moderate in most years, as opposite to the often severe predation pressure experienced by, for example, Siberian waders (Meltofte *et al.*, 2007a). This means that we do not see the same widely fluctuating numbers of juveniles as is so typical for Siberian populations (Meltofte *et al.*, in press).

Furthermore, most of the wader species of high-arctic Greenland have a “conservative” breeding strategy with high site and mate faithfulness. In contrast, the Siberian wader assembly holds a high ratio of “opportunistic” species, which breed one year in one area and the next year in another (Tomkovich and Soloviev, 1994).

Also adult mortality seems to be low in high-arctic Greenland, but there are exceptions to this. During a snowstorm in mid June 2001, a pair of arctic skuas *Stercorarius parasiticus* systematically hunted adult waders, of which many may have been exhausted and several may have died from hunger (Meltofte, 2003). Wader populations are generally supposed to be more sensitive to adult survival than to recruitment (e.g. Hitchcock and Gratto-Trevor, 1997), but recruitment may also be relatively important under certain conditions (Ryabitshev, 1993; Troy, 1996; Boyd and Piersma, 2001; Atkinson *et al.*, 2003).

The prospects for high-arctic Greenland waders under future climate scenarios are uncertain. As dealt with by Stendel *et al.* (2008, this volume), snow precipitation will probably increase, but spring temperatures will also increase, possibly balancing each other out, so that snowmelt on wader breeding habitats may not change much on average (Hinkler *et al.*, 2005). Snow accumulation areas will see even more snow accumulation, making them even more unsuitable as wader breeding habitat. And in a year with much more snow in combination with a cold spring, large areas may clear too late for breeding. On top of this comes the possibility even for a more maritime summer climate with more frequent fog, rain and sleet increasing chick mortality. All of this means that the frequency of late and poor breeding seasons may increase significantly.

At the same time, an increase in plant growth is expected in the Arctic (Callaghan *et al.*, 2005). This is likely to involve at least some of the plant

communities in high-arctic Greenland (Elberling *et al.*, 2008a, this volume), and more lush vegetation will reduce the quality of heath habitats for most of the waders, in that most high-arctic waders are dependent on very low vegetation (Meltofte, 1985; Mortensen, 2000). On the other hand, more precipitation may result in presently barren gravel expanses, particularly in high-arctic desert areas, being vegetated (Callaghan *et al.*, 2005), thereby increasing the extent of breeding habitat for most waders in the presently poorly vegetated end of the habitat scale. Also the endemic *arctica* subspecies of the dunlin may benefit from more extensive and lush fens.

## VIII. CONCLUSIONS

During 1996–2005, an average of between 260 and 300 pairs of six species of waders bred in the Zackenberg bird census area of 19 km<sup>2</sup>, and their inter-annual variability in population density together with timing of reproduction and breeding success were monitored. Early spring food availability turned out to be the most important determinant of timing of egg-laying, followed by snow-cover in years with less than average snow-free land in early June. Mean clutch size decreased during June–July and the total length of the laying period was shortened in years of late snowmelt, meaning that the chances for re-laying in case of failure were limited in such years. All this point to reduced breeding success in late breeding seasons. Events of inclement weather and predation, including availability of alternative prey for the predators, had little effect on breeding success in most years.

Densities of breeding waders in high-arctic Greenland are low both in the desert-like north and in the snow-rich south, while higher densities are found in central Northeast Greenland. Here, the balance between spring snow-cover and vegetation cover available for the waders during the critical pre-laying period is more favourable. Hence, densities at Zackenberg are among the highest recorded in Northeast Greenland, and the populations show relatively limited year-to-year variation. Yet, common ringed plover seems to have decreased significantly.

The results are compared with conditions in other parts of the Arctic, focusing on the effects of the more continental climate in high-arctic Greenland than in most other parts of the Arctic. The future of Greenland's high-arctic waders is uncertain. According to climate scenarios, the frequency of poor breeding seasons may increase, and spread of lush low-arctic vegetation into the high-arctic may reduce the area of breeding habitat for most of the specialised high-arctic species. On the other hand, vegetation may expand onto presently barren expanses and the secondary productivity of the tundra may increase, benefiting some of the waders including the possibility for more southern species to move into the area.



## ACKNOWLEDGMENTS

The monitoring data for this chapter were provided by the BioBasis programme, run by the National Environmental Research Institute, University of Aarhus, and financed by the Danish Environmental Protection Agency, Danish Ministry of the Environment. We further thank the Danish Polar Center for access and accommodation at the Zackenberg Research Station during all the years. Dr. Pavel Tomkovich kindly criticised an earlier draft of the manuscript and provided valuable suggestions for improvements.

## REFERENCES

- Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J., Clark, J.A. and Ireland, P.L. (2003) *Biol. Conserv.* **114**, 127–141.
- Battley, P.F. (2006) *Biol. Lett.* doi:10.1098/rsbl.2006.0535.
- Boertmann, D., Meltofte, H. and Forchhammer, M. (1991) *Dansk Orn. Foren. Tidsskr.* **85**, 151–160.
- Boyd, H. and Piersma, T. (2001) *Ardea* **89**, 301–317.
- Byrkjedal, I. (1980) *Ornis Scand.* **11**, 249–252.
- Callaghan, T., Björn, L.O., Chapin, III, F.S., Chernov, Y., Christensen, T.R., Huntley, B., Ims, R., Johansson, M., Riedlinger, D.J., Jonasson, S., Matveyeva, N., Oechel, W., *et al.* (2005) *Arctic Climate Impact Assessment*, chapter 8, pp. 243–352. Cambridge University Press, Cambridge.
- CHASM (The Committee for HolArctic Shorebird Monitoring) (2004) *Wader Study Group Bull.* **103**, 2–5.
- Cramp, S. and Simmons, K.E.L. (1983) *The Birds of the Western Palearctic. Vol. 3. Waders to Gulls*, Oxford University Press, Oxford.
- Drent, R.H. and Daan, S. (1980) *Ardea* **68**, 225–252.
- Ganter, B. and Boyd, H. (2000) *Arctic* **53**, 289–305.
- Green, G.H., Greenwood, J.J.D. and Lloyd, C.S. (1977) *J. Zool. Lond.* **183**, 311–328.
- Hansen, J. and Meltofte, H. (2006) In: *Zackenberg Ecological Research Operations, 11th Annual Report, 2005* (Ed. by M. Rasch and K. Caning), pp. 57–68. Danish Polar Center, Ministry of Science, Technology and Innovation, Copenhagen.
- Hinkler, J., Hansen, B.U., Tamstorf, M.P. and Meltofte, H. (2005) In: *From digital cameras to large scale sea-ice dynamics*, pp. 159–173, The Faculty of Science, Unpublished Ph.D. thesis by J. Hinkler, University of Copenhagen, Denmark.
- Hitchcock, C.L. and Gratto-Trevor, C. (1997) *Ecology* **78**, 522–534.
- Hötker, H. (1995) *J. Ornithol.* **136**, 105–126.
- Hötker, H. (1999) *J. Ornithol.* **140**, 57–71.
- Kirby, J.S. (1997) *Bird Study* **44**, 97–110.
- Klaassen, M. (2003) In: *Avian Migration* (Ed. by P. Berthold, E. Gwinner and E. Sonnenschein), pp. 237–249. Springer-Verlag, Berlin Heidelberg.
- Klaassen, M., Lindström, Å., Meltofte, H. and Piersma, T. (2001) *Nature* **413**, 794.
- de Korte, J. and Wattel, J. (1988) *Ardea* **76**, 27–41.
- Leon, M.T.D. and Smith, L.M. (1999) *Condor* **101**, 645–654.
- Masero, J.A. and Pérez-Hurtado, A. (2001) *Condor* **103**, 21–30.
- Maher, W.J. (1970) *Arctic* **23**, 112–129.

- Meltofte, H. (1976) *Meddr Grønland* **205**, 1, 1–57.
- Meltofte, H. (1985) *Meddr Grønland, Biosci.* **16**, 1–43.
- Meltofte, H. (1996) *Ardea* **84**, 31–44.
- Meltofte, H. (1998) In: *Zackenberg Ecological Research Operations, 3rd Annual Report, 1997* (Ed. by H. Meltofte and M. Rasch), pp. 27–31. Danish Polar Center, Ministry of Research and Information Technology, Copenhagen.
- Meltofte, H. (2000) In: *Zackenberg Ecological Research Operations, 5th Annual Report, 1999* (Ed. by K. Caning and M. Rasch), pp. 32–39. Danish Polar Center, Ministry of Research and Information Technology, Copenhagen.
- Meltofte, H. (2001a) *Arctic* **54**, 367–376.
- Meltofte, H. (2001b) In: *Zackenberg Ecological Research Operations, 6th Annual Report, 2000* (Ed. by K. Caning and M. Rasch), pp. 30–39. Danish Polar Center, Ministry of Research and Information Technology, Copenhagen.
- Meltofte, H. (2003) In: *Zackenberg Ecological Research Operations, 7th Annual Report, 2001* (Ed. by K. Caning and M. Rasch), pp. 30–44. Danish Polar Center, Ministry of Science, Technology and Innovation, Copenhagen.
- Meltofte, H. (2006a) *Dansk Orn. Foren. Tidsskr.* **100**, 16–28.
- Meltofte, H. (2006b) *Wildfowl* **56**, 129–151.
- Meltofte, H. and Høye, T.T. (2007) *Dansk Orn. Foren. Tidsskr.* **101**, 109–119.
- Meltofte, H. and Lahrmann, D.P. (2006) *Dansk Orn. Foren. Tidsskr.* **100**, 75–87.
- Meltofte, H., Sittler, B., and Hansen, J. (in press) *Arctic Birds*.
- Meltofte, H., Piersma, T., Boyd, H., McCaffery, B., Golovnyuk, V.V., Graham, K., Morrison, R.I.G., Nol, E., Schamel, D., Schekkerman, H., Soloviev, M.Y., Tomkovich, P.S., et al. (2007a) *Meddr Grønland, Biosci.* **59**, 1–48.
- Meltofte, H., Høye, T.T., Schmidt, N.M. and Forchhammer, M.C. (2007b) *Polar Biol.* **30**, 601–606.
- Morrison, R.I.G. and Hobson, K.A. (2004) *Auk* **121**, 33–344.
- Mortensen, C.E. (2000) *Dansk Orn. Foren. Tidsskr.* **94**, 29–41 (in Danish, with English summary).
- Nol, E., Blanken, M.S. and Flynn, L. (1997) *Condor* **99**, 389–396.
- Ntiamao-Baidu, Y., Piersma, T., Wiersma, P., Poot, M., Battley, P. and Gordon, C. (1998) *Ibis* **140**, 89–103.
- Piersma, T., Gudmundsson, G.A. and Lilliendahl, K. (1999) *Physiol. Biochem. Zool.* **72**, 405–415.
- Piersma, T., Meltofte, H., Jukema, J., Reneerkens, J., de Goeij, P. and Ekster, W. (2006) *Wader Study Group Bull.* **109**, 83–87.
- Robinson, R.A., Clark, N.A., Lanctot, R., Nebel, S., Harrington, B., Clark, J.A., Gill, J.A., Meltofte, H., Rogers, D.I., Rogers, K.G., Ens, B.J., Reynolds, C.M., et al. (2005) *Wader Study Group Bull.* **106**, 17–29.
- Roudybush, T.E., Grau, C.R., Peterson, M.R., Ainley, D.G., Hirsch, K.V., Gilman, A.P. and Patten, S.M. (1979) *Condor* **81**, 293–298.
- Ryabitshev, V.K. (1993) *Territorial Relations and Dynamics of Bird Communities in Subarctic*. Nauka Publ., Ekaterinburg (In Russian).
- Scheiffarth, G., Wahls, S., Ketzenberg, C. and Exo, K.-M. (2002) *Oikos* **96**, 346–354.
- Schekkerman, H., van Roomen, M.J.W. and Underhill, L.G. (1998) *Ardea* **86**, 153–168.
- Shepherd, P. (2001) *Wader Study Group Bull.* **97**, 17.
- Soloviev, M.Y., Minton, C.D.T. and Tomkovich, P.S. (2006) In: *Waterbirds Around the World* (Ed. by G.C. Boere, C.A. Galbraith and D.A. Stroud), pp. 131–137. The Stationery Office, Edinburgh, UK.

- Stroud, D.A., Davidson, N.C., West, R., Scott, D.A., Haanstra, L., Thorup, O., Ganter, B. and Delany, S. (2004) *Status of migratory wader populations in Africa and Western Eurasia in the 1990s*, International Wader Studies no.15.
- Tomkovich, P.S. and Soloviev, M.Y. (1994) *Ostrich* **65**, 174–180.
- Tomkovich, P.S. and Soloviev, M.Y. (2001) *Ornithologia* **29**, 125–136.
- Thorup, O. and Meltofte, H. (2005) In: *Zackenbergs Ecological Research Operations, 10th Annual Report, 2004* (Ed. by K. Caning and M. Rasch), pp. 43–51. Danish Polar Center, Ministry of Research and Information Technology, Copenhagen.
- Troy, D.M. (1996) In: *Shorebird Ecology and Conservation in the Western Hemisphere* (Ed. by P. Hicklin, A.J. Erskine and J. Jehl), *International Wader Studies*, **8**, pp. 15–27.
- Tulp, I. and Schekkerman, H. (2007) In: *Environmental forcing on the timing of breeding in long-distance migrant shorebirds* I. Tulp, PhD thesis, University of Groningen.
- Tulp, I., Schekkerman, H. and Klaassen, R. (2000) *Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2000*. Altera report 219, Wageningen, The Netherlands.
- van de Kam, J., Ens, B.J., Piersma, T. and Zwarts, L. (2004) *Shorebirds. An Illustrated Behavioural Ecology*, KNNV Publishers, Utrecht.
- Zöllner, T. (2002) *Charadrius* **38**, 9–23.