Time allocation in Greenland high-arctic waders during summer

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Abstract During the summer of 2000, a preliminary study on time allocation in four arctic wader species (Common Ringed Plover *Charadrius hiaticula*, Sanderling *Calidris alba*, Dunlin *C. alpina*, Ruddy Turnstone *Arenaria interpres*) was conducted at Zackenberg Research Station in high-arctic Northeast Greenland. We scored behaviour of non-disturbed, but not individually recognisable birds in typical habitats. With few exceptions, non-incubating birds (i.e. birds not sitting on eggs) used more than half their daytime for feeding, and during the pre- and post-breeding periods, when waders build up body stores, as much as 75-92% of the daytime was spent feeding. The lowest scores on feeding were obtained at night and in single, non-incubating Ruddy Turnstones and Dunlins on territories (e.g. off-duty breeders), which fed for only 39% and 56% of their time, respectively. Feather care accounted for up to about 21% during breeding proper, but very little during pre- and post-breeding. Conversely, the birds hardly rested during their stay on the territories as opposite to a noticeable part (up to 17%) of the day especially during pre-breeding in most of the species. During young attendance (only studied in Dunlin), 75% of the time was used on resting, being alert, and preening. During post-breeding, much time was used flying, particularly in Dunlins (17%). Aggressive behaviour was not observed among pre-breeding birds and only occasionally during post-breeding, but territorial behaviour is common early in the breeding season. Soil and pitfall trap samples of invertebrates showed that spiders and dipteran imagos and larvae most likely made up the bulk of wader food on the tundra during the summer, and that spiders were unusually numerous during spring 2000. During post-breeding fattening on coastal mudflats, crustaceans may have been most important. 2000 was a year of little snow-cover in early June (54% on 10 June against about 80% in most years), and waders may not have been time-constrained in their feeding. This may be very different in years of much snow, when the pre-breeding period may pose a bottleneck in the annual cycle of arctic waders. During July and August, food for the adults seems to be plentiful.

Introduction

In the summer of 2000, a preliminary study was carried out at Zackenberg Research Station in high-arctic Northeast Greenland (74°28'N, 20°34'W) to quantify how waders of the area allocate their time during different stages of the breeding season. Summer in high-arctic Greenland is a short and intensive affair, and the aim of the study was to see possible indications of time constraints during the birds' stay in the Arctic.

Waders arrive in late May and early June, when daily maximum temperatures begin to reach positive values, and adults start to leave already in early or mid July, when their young have hatched and are only taken care of by one parent, or their breeding attempt has failed (Meltofte 1985). Almost all adults have left by mid August, and the last young birds leave in mid September (Meltofte 1985, Meltofte & Berg 2004).

Since arctic waders are 'income breeders' (Klaassen et al. 2001), females must accumulate a certain amount of protein before egg production can start so that the start of egg-laying is influenced by the availability of invertebrate food during the pre-breeding period on the tundra (Meltofte et al. submitted a). Since early breeding appears to be an important factor determining breeding success, annual variation in climatic conditions will influ-

ence the production of viable young (Meltofte et al. submitted b).

Upon arrival, the birds feed on the relatively limited snow-free vegetated areas, where they may establish territories or wait for other areas to become sufficiently snow-free. During this pre-breeding period, certain favourable areas function as common feeding sites, at least in some years. Data so far from Zackenberg seem to indicate that local populations vary relatively little between most years (Meltofte 2006), but the timing of breeding varies by about two weeks (Meltofte et al. submitted a), and many birds may refrain from breeding in particularly late years (e.g. Meltofte 2000).

From late June or early July, adults gather into post-breeding flocks, mainly feeding in favourable areas at lake and pond margins and other wet areas, but also utilising fjord coasts after these become ice-free during July and early August (Meltofte 1985). Independent juveniles move to the same places, from the last days of July onwards (Meltofte & Berg 2004).

In 2000, spring and summer was characterised by exceptionally little snow cover. In the bird study area, the snow cover was only 54% on 10 June as compared to 76-92% in most other study years (1996-2005); however, in the last few years of this period the snow cover has been even more limited (Meltofte et al. submitted a). The first wader eggs in 2000 were laid around 9-11 June, and median 1st egg dates were just a few days later, which is relatively early (Meltofte et al. submitted a).

Study area and methods

The study area was Zackenbergdalen, i.e. the valley floor around the research station (see Meltofte 2006). The habitat is a mosaic of lush moss and grass/sedge fens interspersed with white arctic bell-heather *Cassiope tetragona* and mountain avens *Dryas* sp. heathland, arctic willow *Salix arctica* snow-beds and exposed dry and poorly vegetated gravel and clay flats and slopes.

Zackenberg has midnight sun from 30 April until 12 August, and only June (2.0°C 1996-2003), July (5.7°C) and August (4.9°C) have mean temperatures above zero (Rasch & Caning 2005).

The bird census area in the valley covers 19 km^2. The species investigated were Common Ringed Plover *Charadrius hiaticula*, Sanderling *Calidris alba*, Dunlin *Calidris alpina* and Ruddy Turnstone *Arenaria interpres*. Red Knot *Calidris canutus* and Red-necked Phalarope *Phalaropus lobatus* also breed in the area, and a total of about 260-300 wader pairs are supposed to occupy territories in the census area (Meltofte 2006). The study area is almost untouched by human activity except for the work being conducted by scientists visiting the research station during summer, i.e. from around 1 June to 1 September (Meltofte 2005).

The amount of food available to the birds during the breeding season of 2000 was estimated in two ways. One was soil samples taken at common feeding sites, and the other was data collected in the BioBasis monitoring programme. Soil samples were taken at three common feeding sites at five different times between early June and mid August. Sampling sites were 1) Gadekæret, fens and shallow ponds close to the research station, where large numbers of waders fed mainly during pre-breeding, 2) Sydkærene, an area of fens and ponds where some birds fed during pre-breeding and which contained several territories during breeding, and 3) the old delta, the inner area of the former Zackenbergelven delta, where mudflats exposed at low tide attracted many waders during post-breeding, i.e. during pre-migratory fattening. The samples were taken with a cylinder core drill with a diameter of 5 cm, down to depth of 7 cm. The samples were sifted and all potential food items collected. Weighing of all food items in each sample was attempted, but due to problems with handling and drying the minute organisms and the following unreliability of results, the weights are not included here.

As part of the standard BioBasis monitoring programme, window and pitfall traps are situated in different habitats and operated all summer (Meltofte & Berg 2005). The pitfall traps are yellow plastic cups with a diameter of 10 cm, containing salt water and detergent and dug down into the soil, so that the upper edge is level with the soil surface. All traps are emptied on a weekly basis. Data from three pitfall trap stations with eight traps each are used here, namely one in the wet fen of Gadekæret dominated by mosses and grasses/sedges and two on early snow free and dry heath habitats with an almost complete cover of lichens ('organic crust') and further dominated by mountain avens, arctic willow and Bellard's kobresia *Kobresia myosuroides*. Both habitats were important for feeding waders, and the station in Gadekæret is in the same fen area as was sampled with the cylinder core drill (see under Results).

The soil samples taken at common feeding sites, and the catches from the pitfall traps were used to complement each other, since soil sampling does not include flying and fast moving insects and spi-

ders, while pitfall traps do not give a clear picture of the presence of organisms with limited mobility.

Activity observations on gatherings of feeding waders during the pre-breeding as well as post-breeding periods were done by scan sampling (Altmann 1974) at 10 minute intervals during all observation hours. During each scan, the species and activity of all birds present at the site were scored. Observations on single birds and breeding pairs in their territories were done in periods of 2 minutes, where the birds were followed continuously and their activity scored every 10 seconds. Periods covering less than one minute (e.g., because the birds moved out of sight of the observer) were omitted. In the following the remaining periods are generally referred to as 2-minute observations, although some covered between one and two minutes only. Hereafter the total dataset consisted of 1642 scan samplings (involving one or more species) and 241 2-minute observations on the four species studied. Most observations were done between 7 and 23 hours local time, and only for the Dunlin have we sufficient 'night' time observations to be presented (the coolest period is 22:30-02:30). All observations were done with a spotting scope at such a distance as not to disturb the birds in any way. This was at least 75 m and up to 250 m for birds attending chicks. Scored individuals were not individually recognisable.

The scored activities were Feeding (Feed.), resting without being visibly observant (Rest.), being alert (Alert), preening feathers (Pree.), bathing (Bath.), flying (Fly.), singing (Sing.) and other activities (Other) – besides incubating. Not all species displayed all types of activities, and flight pursuits, seen particularly in Dunlin and Ruddy Turnstone, did not occur during our observations.

The season was divided into the following periods in relation to breeding:

Early pre-breeding, 5-9 June at common feeding sites
In the beginning of June observations were made on the birds feeding at the common feeding site in Gadekæret. Between 7 a.m. and 11 p.m. species and activity were noted for each bird present up to 16 times per day. All Common Ringed Plovers, Sanderlings and Ruddy Turnstones were on dry land and in the fens, while Dunlins were also utilising shallow water and exposed mud in the ponds. It is unknown to what extent the birds utilising communal feeding sites in early June belonged to the breeding populations of the census area.

Late pre-breeding, 10-16 June at common feeding sites
After most birds had initiated breeding, non-territorial birds were still using the common feeding site in Gadekæret. This group may include off-duty breeders away from their territories. Only for the Dunlin were sufficient data obtained to treat this period separately from the early pre-breeding period. For the other species pre-breeding denotes birds in Gadekæret during the entire period 5-16 June.

Singles on territories, 6 June – 3 July
During the period when most birds were nesting, single birds without an observed mate were studied. None of them were sitting on eggs, but this group may include off-duty breeders away from their own territory.

Pairs on territories, 12 June – 3 July
During the period when most birds were nesting, territorial pairs with or without eggs were studied. None of the observed Common Ringed Plovers and Sanderlings were sitting on eggs, while this was observed in both Dunlin and Ruddy Turnstone. However, birds sitting on eggs were excluded from the calculations.

Attending chicks, 13-28 July
When attending pulli, waders leave their territories and wander around in optimal feeding areas. Dunlin family groups, from which the females often leave about one week after hatching, were watched from elevated sites, so that they could be followed over some distance, and the activity of the adult birds was noted.

Post-breeding, 6 July – 18 August at common feeding sites
Observations were made on waders flocking at low tide on the mudflats of the old delta of Zackenbergelven. These were adults as well as some juvenile birds.

Casual observations from other seasons are included, when appropriate.

For statistical tests, each scan sampling during pre-breeding and post-breeding together with the 10 s samplings during each 2 minute watch during breeding were transformed into ratios. Differences between ratios were tested using the standard Kruskal-Wallis rank sum test, where each of the compared samples consisted of ratios from all 2-min. watches/scan sample for the given activity and species.

Table 1. Invertebrate sampling results from wader feeding sites at Zackenberg, June-August 2000 (individuals per m²). On each occasion six samples were taken from each site, representing a total of 118 cm² per site. Gadekæret is a fen area used for feeding particularly during pre-breeding, and together with the fens of Sydkærene also by local breeders later on. The old delta is mudflats used for feeding by waders during post-breeding, i.e. during pre-migratory fattening. The exposed mudflats in early June in the ponds of Gadekæret were not sampled.
Hvirvelløse dyr indsamlet i de fourageringsområder, som vadefuglene benyttede i løbet af sæsonen juni-august 2000 i Zackenberg (dyr pr m²). Ved hvert indsamlingstilfælde blev der taget seks prøver med et samlet areal på 118 cm². Prøverne i Gadekæret blev taget i kærvegetationen, som blev udnyttet som et fælles fourageringsområde for vadefugle tidligt på sæsonen og siden hen, sammen med Sydkærene, som fourageringsområde for lokale ynglefugle. Det gamle delta (Old delta) består af mudderflader, som blev benyttet af mange vadefugle under opfedningen inden efterårstrækket.

	Gade-kæret	Syd-kærene	Old delta
7 June			
Nematodes	255	339	
Tardigrades	0	0	
Crustaceans	0	0	
Springtails	170	679	
Midge larvae	594	933	
Fly larvae	0	0	
Mites	0	255	
23 June			
Nematodes	849	509	
Tardigrades	0	0	
Crustaceans	0	0	
Springtails	509	933	
Midge larvae	679	255	
Fly larvae	0	85	
Mites	170	255	
11 July			
Nematodes			849
Tardigrades			764
Crustaceans			594
Springtails			0
Midge larvae			0
Fly larvae			0
Mites			0
21 July			
Nematodes	679	849	
Tardigrades	85	85	
Crustaceans	0	0	
Springtails	255	1442	
Midge larvae	933	594	
Fly larvae	0	0	
Mites	0	0	
17 August			
Nematodes			1442
Tardigrades			1018
Crustaceans			1188
Springtails			0
Midge larvae			0
Fly larvae			0
Mites			0

Results

Soil samples of potential food. The sampling of soil invertebrates in 2000 must be considered rather crude, and the results are only used to indicate the kind and density of potentially available food. Seven invertebrate types were found in the soil samples: nematodes, tardigrades, springtails, fly larvae, midge larvae and mites, and in the delta even crustaceans, predominantly amphipods (Table 1). To which extent the smallest organisms, the mites, springtails and tardigrades, are being taken by the birds is unknown, but they do not make up an important food source for waders on the tundra (Cramp & Simmons 1983). Spiders and all other mobile species were grossly underrepresented in the samples from Gadekæret and Sydkærene, as were the crustaceans in the samples from the old delta. Much better data on spiders are found in the pitfall trap data (see below), while no further data are yet available on the crustaceans, which are likely to be one of the main food sources for birds feeding in the old delta.

Prey organisms were sitting in the top layer of the samples, and the sample depth of 7 cm must be considered more than enough. The number of organisms found in samples taken at short distances from each other showed large variation, and a greater number of samples and a somewhat larger sample width must be recommended for future work.

The preferred feeding habitat particularly for Dunlins during pre-breeding, the exposed mudflats in the ponds of Gadekæret, was not sampled. Most likely, waders found high densities of dipteran larvae here, but perhaps also crustaceans deep-frozen during the previous autumn and now becoming available following ice-melt. Røen (1965) reported that King Eiders *Somateria spectabilis* in Peary Land consumed large amounts of thawed fairy shrimps *Branchinecta paludosa* upon arrival on shallow ponds and lakes. Fairy shrimps are not found in the ponds of Gadekæret, but tadpole shrimps *Lepidurus arcticus* are very common.

Pitfall trap data. Pitfall trap station no. 2 of the BioBasis monitoring programme is situated in the middle of the fen area in Gadekæret, where pre-breeding waders – mainly Dunlins and Ruddy Turnstones – feed during early June and a few local Dunlins even during the rest of June and July. The heath habitat (represented by trap stations 5 and 7), which may be humid or even wet during snowmelt, is the prime feeding habitat for Common Ringed Plovers, Sanderlings and Ruddy Turnstones during June and July.

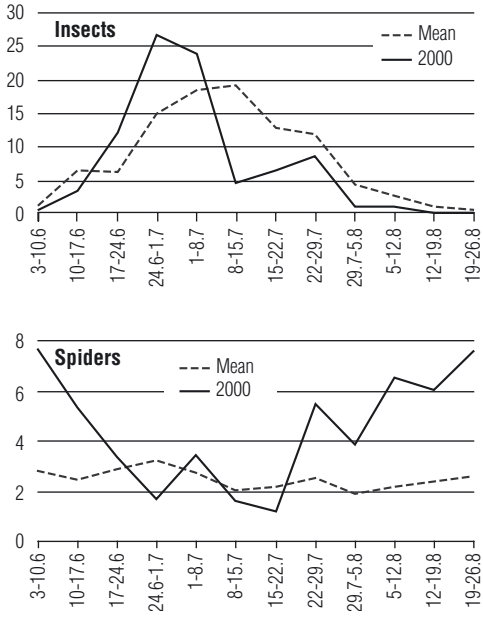

Fig. 1. Average catches of insects and spiders per pitfall trap per day in the wet fens of Gadekæret (arthropod station 2 of BioBasis; see text) during 1996-2002, and during 2000 separately. Note different scales.
Det gennemsnitlige antal insekter og edderkopper fanget pr dag pr gul faldfælde i de våde kær i Gadekæret 1996-2002, samt fangsterne i 2000 vist separat. Bemærk de forskellige skalaer.

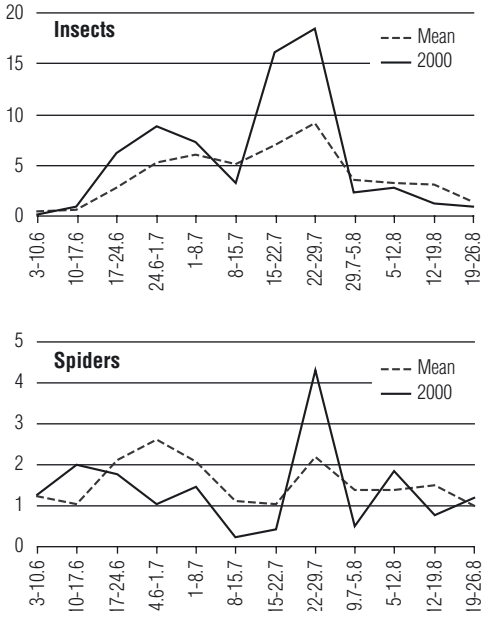

Fig. 2. Average catches of insects and spiders, respectively, per pitfall trap per day on dry heath (arthropod stations 5 and 7 of BioBasis; see text) during 1996-2002, and during 2000 separately. The peak in spiders during 22-29 July 2000 was due to large numbers of juveniles. Note different scales.
Det gennemsnitlige antal insekter og edderkopper fanget pr dag pr gul faldfælde på tør hede 1996-2002, samt fangsterne i 2000 vist separat. Toppen i edderkopper i ugen 22.-29. juli 2000 skyldes et stort antal juvenile edderkopper. Bemærk de forskellige skalaer.

Spiders were common during the whole summer season in both habitats (Figs 1 and 2). In contrast, numbers of insects increased steeply during June to reach a maximum in July, when wader pulli hatch and grow up. In August, numbers were again low, which fits well with the fact that most waders have left the inland areas by then (see Meltofte 1985 and below). On the dry heath, arthropod densities were lower than in the fen (Fig. 2).

Similar results, with spiders being available all summer – or even most abundant early in the season – in contrast to an insect peak some time around July, have been obtained from both high-arctic Siberia (e.g. Schekkerman & van Romen 1995, Tulp et al. 1998) and Alaska (e.g. MacLean & Pitelka 1971). In spite of the somewhat differing pitfall trap types, Schekkerman & van Romen (l.c.) and Tulp et al. (l.c.) caught insects and spiders in numbers in the same order of magnitude in northern Taimyr as at Zackenberg.

In 2000, insect numbers grew relatively fast and to high levels in both habitats, due to the limited snow-cover and the resulting early start of production (Figs 1 and 2). However, a period of severe weather during mid July resulted in low numbers of both insects and spiders (see under Dunlin). Spiders in Gadekæret occurred in higher numbers than recorded in the other years, both early and late in the season (Fig. 1). The spider peak during 22-29 July 2000 on the dry heath (Fig. 2) was the result of a large number of newly hatched spiders in a single trap.

Common Ringed Plover *Charadrius hiaticula*. An estimated total of about 40 pairs established territories in the bird study area annually during 1996-2005 (Meltofte 2006). Since the breeding habitat of Common Ringed Plovers is exposed gravelly flats and slopes with little or no snow during winter, most birds disperse and establish territories at arrival, and pre-breeding flocks are only seen occasionally. However, Common Ringed Plovers most often feed on dry and mesic tundra during

Table 2. Time allocation (percent) of Common Ringed Plover during the breeding season. Explanation as in Table 4.
Den procentvise fordeling af tidsforbruget hos Stor Præstekrave i løbet af sommeren. Forklaring som i Tabel 4.

Common Ringed Plover	Feed.	Rest.	Alert	Pree.	Bath.	Fly.	Other	N
Pre-breeding	75.2	1.9	22.9	0.0	0.0	0.0	0.0	105
Pair on territory	77.9	2.0	0.0	16.4	3.2	0.5	0.0	556
Post-breeding	86.8	5.7	1.9	1.9	0.0	3.8	0.0	104

pre-breeding and breeding. In 2000, a maximum of six was feeding in Gadekæret in early June. During post-breeding, adult and juvenile Common Ringed Plovers were seen singly or in groups on heathland and moist places inland as well as on the coast.

Our observations show that feeding makes up the main activity during all phases of the breeding cycle (Table 2). Since Common Ringed Plovers are 'eyesight'-feeders, they can be alert at the same time. Still, during pre-breeding, alert position was recorded in almost one quarter of the scan samplings, while not at all when on territory. During the incubation period, preening was common, but here incubation naturally made up about half the time budget of the pair members although this activity was not recorded, since we did not keep any birds sitting on eggs under observation. Neither do we have any observations on chick-tending adults, but according to our experience Common Ringed Plovers use much time being alert, and they give alarm calls and join alarm calling neighbours over considerable distances – up to 1300 m has been recorded (Meltofte 1979). Also, male Common Ringed Plovers commonly perform song flight during territory establishment and incubation (e.g. Meltofte 2001a), but this was not observed during our observations.

During post-breeding, up to 31 adults were feeding in the deltas during July and early August, while peak numbers of juveniles were 103 in August. These birds, which were involved with premigratory fattening, used even more time feeding than did birds during pre-breeding and breeding (Table 2), although the difference was not statistically significant. Consequently, all other activities decreased to very low scores during post-breeding.

Sanderling *Calidris alba*. In the bird study area, an estimated total of about 70 pairs occupied territories annually during 1996-2005 (Meltofte 2006). Most feeding of Sanderlings takes place on heath with mountain avens, arctic willow and kobrecia, where most of the birds also nest. This habitat is found on exposed places, where there is no snow cover in winter or where the snow disappears early, so that the Sanderlings can disperse immediately upon arrival. Only small concentrations have been recorded during pre-breeding, and mainly local breeders were seen in Gadekæret in 2000.

In the deltas on the coast of Zackenbergdalen, up to 80 adults were recorded in July 2000 and 69 juveniles in August.

During all phases of the breeding season, feeding is by far the dominating activity (Table 3). We did not record incubating birds. Neither did we record adults attending young, but during this period much time is used on alert behaviour like in the other species. Besides a little resting, the only other activity of any importance was preening during the birds' stay on breeding sites. The single birds observed may have been off-duty nesters or unmated birds, and the pairs on territories may have been engaged in egg-laying. Single males often perform song flight over their territories, but otherwise Sanderlings do not sing much (Meltofte 2001a).

The Sanderlings appeared to spend more time feeding during pre-breeding and post-breeding than during the breeding period proper, and the differences between stages were almost statistically significant ($\chi_3^2 = 7.19$, $P = 0.066$). On the coast, aggression occurred occasionally among Sanderlings feeding close together at particularly good spots.

Table 3. Time allocation (percent) of Sanderlings during the breeding season. Explanation as in Table 4.
Den procentvise fordeling af tidsforbruget hos Sandløber i løbet af sommeren. Forklaring som i Tabel 4.

Sanderling	Feed.	Rest.	Alert	Pree.	Bath.	Fly.	Sing.	Other	N
Pre-breeding	91.7	6.2	2.1	0.0	0.0	0.0	0.0	0.0	48
Single on territory	75.8	2.4	1.8	12.7	6.7	0.6	0.0	0.0	330
Pair on territory	81.4	0.3	3.2	10.5	0.0	1.7	0.3	2.6	344
Post-breeding	86.3	7.3	0.0	0.5	0.5	5.4	0.0	0.0	205

Dunlin *Calidris alpina*. An estimated total of about 100 pairs established territories in the bird study area annually during 1996-2005 (Meltofte 2006). Dunlins breed in the most lush fen areas of the Zackenbergdalen valley floor. Since such areas are mostly snow-covered in winter, many Dunlins feed on the limited snow-free fen patches upon arrival, dispersing with the snowmelt during June.

A peak of 77 Dunlins was recorded feeding in the common feeding area in Gadekæret on 4 June 2000. Hereafter, numbers decreased to five on 9 June, after which the site was mainly visited by the few local pairs. These pre-breeding numbers are the highest recorded during 1996-2005, when numbers have fluctuated between nil and about 20 in early June, among other factors depending on the occurrence of exposed mudflats in the ponds (in some years the ponds are covered with snow and ice or filled with water in early June). In 2000, mudflats and shallow water were present in early June, and 73% of the recorded feeding was in the ponds, the remaining 27% occurring on fen vegetation (N = 681); cf. remarks on deep frozen tadpole shrimps under soil samples above.

Most Dunlins apparently feed in Gadekæret in the evening. At night, most birds here were resting – 86% (N = 767) of all the Dunlins present in the daytime were feeding, as opposed to 27% (N = 90) of those present at night (23:30-03:30) during the early pre-breeding period. A similar difference was not apparent at a 24 hour study on 1 June 1979 at Myggbukta, about 100 km south of Zackenberg, where 92% of the total time was used feeding (Elander & Blomqvist 1986). The Dunlins studied at Myggbukta were transient migrants, however, and may have needed 'fuel' for further migration (see further in Discussion).

Dunlins often feed along the edge of the melting snow or even on top of tufts surrounded by snow. Similarly, Summers & Underhill (1996) found that waders fed disproportionally more along edges of melting snow in high-arctic Siberia.

As it appears from Table 4, there were large differences in the time allocation between the different stages of the breeding cycle in Dunlins. First of all, the birds fed more intensively during the pre-breeding and post-breeding periods than during breeding (see further below), and the only other important activity was resting. Little time was used resting during post-breeding, however, when Dunlins spent 17% of their time on the wing. Direct confrontations between birds were not recorded during observation periods.

Dunlins used about 56% of their time feeding when single on territory, and 69% of their non-incubation time when mated on territory, which for singles was significantly less than during pre-breeding ($\chi_1^2 = 7.49$, P = 0.006). The rest of the time was used on a variety of other activities including singing, resting and preening.

During chick attendance, Dunlins used more than a third of their time watching for potential predators, i.e. being alert (Table 4). However, resting and preening etc. include observing as well, since they all take place on top of tufts from where the adults have a good view of the surroundings. Time used for feeding was very limited and significantly lower than for pairs on territories ($\chi_1^2 = 24.08$, P << 0.001), but this result could possibly have been influenced by our presence, since the adults are extremely alert when tending young. Brooding was not recorded, probably because the weather was fine and the young were relatively old.

Table 4. Time allocation (percent) of Dunlins during the breeding season distributed on feeding (Feed.), resting without being visibly observant (Rest.), observing/alertness (Alert), preening feathers (Pree.), bathing (Bath), flying (Fly), territorial singing (Sing), and other activities (Other). Only daytime observations are included.
Den procentvise fordeling af tidsforbruget hos Almindelig Ryle i løbet af sommeren fordelt på fouragering (Feed.), hvile uden at være synligt observant (Rest.), observerende/vagtsom (Alert), fjerpleje (Pree.), badning (Bath.), flyvning (Fly.), sang (Sing.), og andet (Other). Early og Late pre-breeding er hhv. den tidlige og sene del af tiden før æglægningen, Single on territory er enkeltindivider i yngleområder, Pair on territory er par i yngleområder, Attending young er ungeførende fugle, og Post-breeding er fugle, der har forladt yngleområderne, dvs. er under opfedningen til efterårstrækket.

Dunlin	Feed.	Rest.	Alert	Pree.	Bath.	Fly.	Sing.	Other	N
Early pre-breeding	79.2	17.3	3.5	0.0	0.0	0.0	0.0	0.0	831
Late pre-breeding	88.5	0.0	11.5	0.0	0.0	0.0	0.0	0.0	26
Single on territory	56.3	17.0	4.5	6.8	4.0	2.3	9.1	0.0	176
Pair on territory	68.7	0.0	8.0	4.7	0.0	1.5	14.5	2.6	339
Attending young	21.4	17.6	36.9	20.5	0.0	1.4	1.9	0.2	835
Post-breeding	77.3	3.9	0.0	1.5	0.0	17.3	0.0	0.0	260

Table 5. Time allocation (percent) of Ruddy Turnstones during the breeding season. Explanation as in Table 4.
Den procentvise fordeling af tidsforbruget hos Stenvender i løbet af sommeren. Forklaring som i Tabel 4.

Ruddy Turnstone	Feed.	Rest.	Alert	Pree.	Bath.	Fly.	Sing.	Other	N
Pre-breeding	80.9	14.9	4.3	0.0	0.0	0.0	0.0	0.0	47
Single on territory	38.5	5.9	39.1	3.0	0.0	1.2	12.4	0.0	169
Pair on territory	81.1	0.0	6.8	7.1	1.9	1.9	1.2	0.0	316
Post-breeding	85.7	0.0	0.0	0.0	0.0	14.3	0.0	0.0	35

On 17-18 July a snowstorm killed many young, so that large numbers of adults left the inland breeding areas and gathered on the mudflats in the deltas of Zackenbergelven during the following days (Meltofte 2001b). 99 were present already on 18 July, increasing to 160 on 20 July. This is the highest number of adult Dunlins recorded in the deltas during 1996-2005, where maximum numbers have varied between a few and 111. Most of our observations were made on these newly failed breeders, who apparently were able to switch from low intensity feeding during chick attendance to high intensity pre-migratory fattening in a few hours.

Ruddy Turnstone *Arenaria interpres*. In most years, about 40-60 pairs established territories in the bird study area annually during 1996-2005 (Meltofte 2006). Ruddy Turnstones are quite flexible in their choice of feeding habitat, while their prime breeding habitat is stony and gravely hills and slopes with mountain avens and arctic willow. Especially during pre-breeding much feeding occurs in the fens that become snow-free early. On 4 June 2000 a maximum of 12 was recorded in the common feeding area in Gadekæret.

During post-breeding, most Ruddy Turnstones seek the same feeding sites as other waders – moist ponds and lake margins and silty coasts. In 2000, a maximum of 25 was recorded in the deltas after the snowstorm in mid July (see under Dunlin).

Like in the other waders, Ruddy Turnstones fed intensively during pre-breeding, while most of the remaining time was spent resting (Table 5). When single on territories, much less time was spent feeding than during pre-breeding ($\chi_1^2 = 9.06$, P = 0.003). This was not the case for pairs on territory, however, which fed significantly more than singles on territories ($\chi_1^2 = 6.80$, P = 0.009). Much time was spent alert and "alarm calling", especially by singles which were highly vigilant, many of them probably being off-duty breeders, perhaps on feeding excursions away from their territory. When the Ruddy Turnstone is considered some influence on behaviour by the presence of the observer should not be ruled out.

During post-breeding, feeding was again the dominating activity. Feeding is mainly by 'eyesight' search in the vegetation or among stones and kelp on the coast, and aggression was observed occasionally when Ruddy Turnstones were feeding close together at particularly good spots.

Comparison of species. During *pre-breeding*, feeding was by far the most important activity in all the species, each using more than 75% of their daytime feeding (Table 6). Common Ringed Plovers spent significantly less time resting than did Dunlins ($\chi_1^2 = 28.23$, P << 0.001) and Ruddy Turnstones ($\chi_1^2 = 3.85$, P = 0.050), and clearly spent their 'free time' being alert rather than truly resting.

Strikingly, the resting behaviour seen during pre-breeding in the three other species (Sanderling, Dunlin, Ruddy Turnstone) was virtually absent once the birds were *mated and moved into their territories* (Table 7). Instead, the 'non-feeding' time was used preening or being alert. Dunlin was the only species to spend a considerable amount of time (15%) singing when on territory

Table 6. Comparison between species of time allocation (percent) for feeding (Feed.), resting (Rest.) and observing/alertness (Alert) during pre-breeding. Only daytime observations are included.
Artsvis sammenligning af tidsforbruget (procent) til fødesøgning (Feed.), hvile (Rest.) og observerende/vagtsom (Alert) i tiden før æglægningen.

Pre-breeding period	Feed.	Rest.	Alert
Common Ringed Plover *Stor Præstekrave*	75.2	1.9	22.9
Sanderling *Sandløber*	91.7	6.2	2.1
Dunlin *Almindelig Ryle*	79.5	16.8	3.7
Ruddy Turnstone *Stenvender*	80.9	14.9	4.3

Table 7. Comparison between species of time allocation (percent) for feeding (Feed.), resting (Rest.), observing/alertness (Alert), preening (Pree.), territorial singing (Sing.), and other activities (Other), when pairs are on territory. Only daytime observations are included.
Artsvis sammenligning af tidsforbruget (procent) til fødesøgning (Feed.), hvile (Rest.), observerende/vagtsom (Obs.), fjerpleje (Pree.), sang (Sing.) og andet (Other) hos par på yngleplads.

Pairs on territory	Feed.	Rest.	Alert	Pree.	Sing.	Other
Common Ringed Plover *Stor Præstekrave*	77.9	2.0	0.0	16.4	0.0	3.7
Sanderling *Sandløber*	81.4	0.3	3.2	10.5	0.3	4.3
Dunlin *Almindelig Ryle*	68.7	0.0	8.0	4.7	14.5	4.1
Ruddy Turnstone *Stenvender*	81.1	0.0	6.8	7.1	1.2	3.8

(Table 7). In Dunlins, most preening took place while attending chicks (Table 4) whereas in the other species, including Common Ringed Plover, most preening was observed when the birds stayed on territories (either singly or mated) (Tables 2-5); note, however, that we have no data on chick-attending adults of these species.

During *post-breeding*, the difference between species in time allocation was no longer so pronounced (Table 8). All four species again spent more than 75% of their time feeding, and little time was allocated to resting and being alert, the latter probably made possible through flocking which permitted each individual to be less vigilant. Dunlins and Ruddy Turnstones also spent a significant amount of time flying around in the area; Dunlins were most prone to show unrest in this way, being on the wing for 17% of the time.

Discussion

Two main characteristics stand out from these preliminary observations: During pre-breeding as well as post-breeding most individuals of the four species were feeding, at least during daytime. During pre-breeding, the birds have to secure sufficient body stores after a 1000 km flight from Iceland or even a direct 2500 km flight from northwest Europe to be able to withstand periods of inclement weather upon arrival (see review by Meltofte 1985). Furthermore, during this period the females have to accumulate sufficient nutrients for the production of four large eggs (Klaassen et al. 2001). And during post-breeding, the birds must undergo a fast pre-migratory fattening before initiating the southbound journey.

Similarly, Ashkenazie & Safriel (1979) found that pre-laying female Semipalmated Sandpipers *Calidris pusilla* in Alaska spent about 70% of their time feeding, and that both male and female post-breeders spent 80% of their time feeding during the pre-migratory fattening.

Hötker (1995) found that feeding took up 'only' between 30% and 76% of the time during pre-breeding in Grey Plover *Pluvialis squatarola*, Pacific Golden Plover *Pluvialis fulva*, Little Stint *Calidris minuta*, Curlew Sandpiper *Calidris ferruginea* and Ruddy Turnstone in Taimyr, northern Siberia. However, the birds feeding less than half the pre-breeding time were all males – female Grey Plovers as well as the other species all used 56% or more of their time feeding, and shortly after arrival even Grey Plovers of both sexes combined used most of their time feeding.

In contrast to these findings, T. Piersma, R.I.G. Morrison and N.C. Davidson (in litt.) found that Red Knots and Ruddy Turnstones showed reduced feeding during the first week after their arrival to the breeding grounds in north Ellesmere Island, instead spending much of the day resting after the long flight from Iceland. Piersma et al. (l.c.) speculate that this resting was possible because the birds still had fat reserves to use after arrival.

Table 8. Comparison between species of time allocation (percent) for feeding (Feed.), resting (Rest.), observing/alertness (Alert), flying (Fly.), and other activities (Other) during post-breeding. Only daytime observations are included.
Artsvis sammenligning af tidsforbruget (procent) til fødesøgning (Feed.), hvile (Rest.), observerende/vagtsom (Alert), flyvning (Fly.) og andet (Other) hos fugle under opfedning inden efterårstrækket.

Post-breeding period	Feed.	Rest.	Alert	Fly.	Other
Common Ringed Plover *Stor Præstekrave*	86.8	5.7	1.9	3.8	1.9
Sanderling *Sandløber*	86.3	7.3	0.0	5.4	1.0
Dunlin *Almindelig Ryle*	77.3	3.9	0.0	17.3	1.5
Ruddy Turnstone *Stenvender*	85.7	0.0	0.0	14.3	0.0

Conditions are very different between the pre-breeding and the post-breeding periods in the Arctic. During pre-breeding, the birds are only able to feed on small patches of vegetated and snow-free land, and spells of severe weather may put the birds under considerable pressure, as was observed at Zackenberg in 2001 (Meltofte 2003). Furthermore, in high-arctic Greenland food appears to be very limited early in the season, except for spiders and dipteran (nematoceran) larvae (Table 1, Figs 1 and 2), and waders have been observed to feed on vegetable matter during this period (see review by Meltofte 1985). During post-breeding, food appears to be abundant both on the snow-free tundra in July and on the tidal flats after mid July (Table 1, Figs 1 and 2; cf. Holmes 1966, Nettleship 1973, 1974, Schekkerman & van Romen 1995 and Tulp et al. 1998 for other arctic areas). Yet, wader chicks may suffer from reduced growth during spells of inclement weather during this period (Schekkerman & van Romen l.c., Meltofte 1998, Tulp et al. l.c.).

Still, the waders at Zackenberg used some of their time resting even during pre-breeding. This was particularly the case during night-time observations of Dunlins. This 'surplus' of time could be the result of the favourable conditions experienced by the waders at Zackenberg in June 2000, when 1) snow-free areas were much more extensive than in most years, 2) spiders were unusually numerous in the fens (Fig. 1), 3) food-rich mud was exposed in several ponds, and 4) the weather was fine. In cold springs with extensive snow cover, pre-breeding and incubating waders in high-arctic Siberia have been shown to have reduced body mass (Soloviev & Tomkovich 1997).

The reason for the high amount of resting during night is unclear. The sun is on the sky 24 hours a day, but it is colder during night than during day – in early June temperatures are mostly below zero at night. This will influence the activity of invertebrates, but that should not hamper foraging in waders, since cold-still insects and spiders may well be easier to catch, and Dunlins are tactile feeders anyway. However, cold-still insects may be more difficult to detect. Exo & Stepanova (2000) found no difference between day- and night-time activity in Grey Plover during the second half of the incubation period – around the clock, off-duty individuals spent on average 52-57% of their time feeding and 35-40% resting, quite different from our observations. Amlaner & Ball (1983) stated that three arctic wader species slept on average between 2.7 and 3.5 hours per day during summer.

Intra- or inter-specific aggression was never observed on common pre-breeding feeding sites, but territorial conflicts are always common on the tundra during June and early July. Apparently, these 'encounters' are related to competition for breeding territories and mates only, and they cease after hatching, when family groups may wander widely (Meltofte 1985). Still territoriality may be important in securing sufficient food during egg-formation and incubation, but territories may also provide a 'rendezvous' for mates or ensure nest-spacing (an anti-predator precaution; see review by Meltofte 1985).

Holmes & Pitelka (1968) found that the diet of four sandpiper species overlapped broadly near Point Barrow in Alaska, but that this to some extent was counteracted by habitat separation and differences in bill proportions etc.; the same appears to be the case at Zackenberg.

Neither during post-breeding seem the adults to have been under nutritional stress, except perhaps during the snowstorm in mid July. The only aggression observed was a few instances among 'eyesight' feeding Sanderlings and Ruddy Turnstones at particularly favourable spots on the coast, whereas Dunlins at the same sites were not aggressive.

Time budgets during incubation, and particularly during young attendance, differed from pre-breeding budgets. Feeding activity was reduced, especially in single Dunlins and Ruddy Turnstones, while Common Ringed Plovers and Sanderlings still fed quite actively. This difference is understandable for the Common Ringed Plovers which are 'eyesight' feeders occupying relatively poor habitats. In the Sanderling, the single birds observed may have been off-duty incubators, and the pairs on territories may still have been engaged in egg-laying. Yet, high-arctic waders have maximum body mass in the middle of the incubation period, probably as an insurance against spells of inclement weather, which are more common early in the season than later on (Tulp et al. 2002). During chick rearing in July, when food is abundant, the adults have low body mass, probably because they do not need the same level of insurance and at the same time need maximum manoeuvrability during anti-predator behaviour.

Unfortunately, we only have observations on young-attending adults in the Dunlin. Here feeding was reduced to only a minor part of the day, while alert behaviour, preening and resting occupied most of the time. From our general experience, a high involvement in alert behaviour and low feeding rates occur in the other species as

During the pre-breeding period in early June, when most of the tundra is covered in snow, waders at Zackenberg used 75-92% of the daytime hours for feeding. Photo: Erik Thomsen.
I begyndelsen af juni, umiddelbart efter vadefuglenes ankomst til Zackenberg, brugte de 75-92% af dagtimerne på fouragering. På det tidspunkt er store dele af tundraen dækket af sne.

well, which fits well into the fact that attendance of young takes place in July, when food is abundant and body mass of the birds at a minimum (see above and Meltofte 1985).

Preening and bathing is almost entirely confined to the breeding season proper. Here it takes up as much as 20% in non-incubating Common Ringed Plovers and 21% in chick-tending Dunlins, while non-incubating Ruddy Turnstones used only 9% of their time on feather care. According to Ferns (1978), more than 70% of the Northeast Greenland waders (except the Dunlin) initiate post-nuptial body moult from about mid July.

The fast switch from low intensity feeding during breeding to high intensity feeding during pre-migratory fattening is remarkable and well illustrated by the reaction to the snowstorm in mid July (see under Dunlin). Even in 'normal' years the birds change behaviour 'overnight', from a dispersed life concerned with territoriality and chick attendance to the intensive feeding within flocks on the staging areas.

In conclusion, in 2000 the waders at Zackenberg may not have been at the limit of their feeding capacity neither during pre-breeding nor during post-breeding fattening. The situation may be different during pre-breeding and egg-laying in years with more extensive snow-cover, late snow-melt and/or severe weather in June, as occurred in both 1999 and 2001 (Meltofte 2000, 2003). We find it likely that high-arctic waders experience an energetic bottleneck during the pre-breeding period, which partly explains the positive correlation between the available snow-free and vegetated area in early June (i.e. the feeding area) and the population density in various parts of high-arctic Greenland, as well as the strong negative correlation between timing of egg-laying and snow-free land/food availability in early June (earlier egg-laying in years with much snow-free land and abundant food; see review by Meltofte 1985, Meltofte et al. submitted a).

The impact of such a bottleneck will depend on the birds' ability to produce eggs, and of their ability to build up body stores, and will influence the timing of egg-laying and thereby the production and survival of offspring. Later egg-laying means smaller clutches and fewer surviving juveniles in the following spring (Meltofte 1985, Nol et al. 1997, Meltofte et al. submitted a). The bottleneck may only have significant effects in unfavourable

years, but it would still keep local populations within certain limits. A mechanism of population limitation as described would be consistent with the suggestion that arctic waders evolutionarily have been exposed to limited resources during the breeding season and to a surplus of resources during non-breeding (Alerstam & Högstedt 1982, Meltofte 1996 versus e.g. Pienkowski & Evans 1985, Zwarts et al. 1990).

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Resumé

Tidsbudgetter hos vadefugle i højarktisk Grønland
I sommeren 2000 gennemførte vi et pilotstudium af tidsallokering hos vadefugle ved Zackenberg Forskningsstation i Nordøstgrønland, som ligger i den højarktiske klimazone. De undersøgte arter var Stor Præstekrave *Charadrius hiaticula*, Sandløber *Calidris alba*, Almindelig Ryle *C. alpina* og Stenvender *Arenaria interpres*, og de undersøgte aktiviteter var fouragering, hvil (uden at være synligt på vagt), observeren/væren vagtsom, fjerpleje, badning, flyvning, og andet. Med få undtagelser brugte fuglene mere end halvdelen af dagtimerne på fouragering (fraregnet rugende fugles tid på reden).

Under opbygningen af fedt- og proteinreserver umiddelbart efter ankomsten (som forsikring mod perioder med dårligt vejr og, for hunner, til produktion af æg) og igen inden borttrækket brugte fuglene hele 75-92% af tiden på fouragering. Det laveste tidsforbrug til fouragering sås hos enlige Stenvendere og Almindelige Ryler (ikke-rugende fugle), som fouragerede hhv. 39% og 56% af tiden i dagtimerne. Fjerpleje tog op til 21% af tiden i selve yngletiden, men meget lidt af tiden før æglægningen og igen inden borttrækket. Til gengæld hvilede ynglefuglene sig knap nok i selve yngletiden, i modsætning til op til 17% af tiden umiddelbart efter ankomsten (endnu mere om natten) og inden borttrækket. Under ungeføringen brugte de Almindelige Ryler derimod 75% af tiden til hvile, vagtsomhed eller fjerpleje, hvilket for alle tre aktiviteters vedkommende kunne kombineres med at være på udkig efter prædatorer, så ungerne kunne advares i god tid. Under opfedningen inden borttrækket fløj fuglene meget omkring. Specielt de Almindelige Ryler viste megen trækuro (17% af tiden på vingerne). Aggressiv adfærd sås ikke blandt fuglene før æglægningsperioden og kun sporadisk under opfedningen inden borttrækket, men territorialadfærd såsom sang blev der brugt der en del tid på under etableringen af territorierne og i rugetiden.

Jordprøver i fuglenes fourageringsområder samt fældefangster af leddyr i nogle af de samme områder sandsynliggør, at edderkopper samt tovingede insekter (primært dansemyg) og deres larver udgør hovedparten af vadefuglenes føde under opholdet på tundraen. Under opfedningen før borttrækket flytter fuglene ud på vadeflader langs kysterne, hvor hovedføden formentlig er krebsdyr.

I foråret 2000 var der usædvanlig lidt snedække efter fuglenes ankomst sidst i maj og begyndelsen af juni (54% den 10. juni mod oftest omkring 80%), og vadefuglene havde tilsyneladende ikke problemer med at få tilfredsstillet deres fødebehov. Især var edderkopper meget talrige dette forår. Forholdene kan være ganske anderledes i år med omfattende snedække og sen snesmeltning, hvor tiden efter ankomsten måske kan udgøre en flaskehals i disse vadefugles årscyklus. I juli og august forekommer føden derimod at være rigelig.

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