Increased variability in bird populations at Zackenberg, high Arctic Greenland 1996-2018, but few unidirectional trends or correlations with local conditions

Hans Meltofte, Jannik Hansen, and Frank Rigét

(Med et dansk resumé: Øget år til år-variation i fuglebestandene ved Zackenberg i højarktisk Grønland 1996-2018, men få bestandsændringer eller korrelationer med lokale forhold)

Abstract The Arctic is changing, but contrary to major ecological changes taking place in several other parts of the Arctic zone, few statistically significant changes were found in bird populations and in the climatic and biological factors potentially influencing bird populations during a 23-year study period at Zackenberg in high Arctic NE Greenland. Out of 14 species of regularly breeding birds at Zackenberg, eight or nine populations fluctuated with no significant trend, four increased, and only one or two decreased. Among the same 14 species, six showed increasing year-to-year variability during the study years. Among 36 climatic as well as biotic factors, only two showed an increasing trend (July mean temperature and fox encounters). The rest remained stable or fluctuating with no trend. Among the same parameters, timing of snowmelt and May mean temperature exhibited increasing variability over the study years. Likewise, we found few statistically significant correlations between bird population numbers and inter-annual variation in the climatic and biological factors studied, with extent of spring snow cover as the most pronounced correlation. Our data support analyses indicating that most tundra bird populations on the East Atlantic Flyway are doing well.

Dansk Orn. Foren. Tidsskr. 114 (2020): 151-167

Introduction

Long-term bird population monitoring takes place annually at only a few places in the Arctic *sensu* the Circumpolar Arctic Vegetation Map (CAVM Team 2003). In fact, Zackenberg in high Arctic NE Greenland (74°30′ N, 20°30′ W) is the only site with a quarter of a century of continuous monitoring of all bird species numbers, their breeding performance and their habitat use (Meltofte & Rasch 2008, Schmidt *et al.* 2019a).

At Zackenberg, bird monitoring is an integral part of a comprehensive geophysical and biological monitoring programme, e.g. the programme collects data on weather variables, snow cover, food availability, mammalian predators and their alternative prey in the form of lemmings *Dicrostonyx groenlandicus* and dead muskoxen *Ovibos moschatus*. The aim of the programme is to shed light on the factors that potentially impact the functioning of a high Arctic ecosystem (Forchhammer *et al.* 2008a).

In this paper, we document the trends and variability in the bird community during the first 23 years of work and investigate whether environmental factors predict bird population numbers with regard to both year-to-year variability and long-term trends. This is a follow up to previous analyses of data from the first years of work (Meltofte 2006a, 2006b, Meltofte *et al.* 2007a, Meltofte *et al.* 2008), which indicated generally stable or fluctuating populations, but also some early trends that were not all upheld during the following years. Furthermore, food availability during the pre-breeding and egg-laying periods appeared to be important for breeding performance of those investigated species which are 'income breeders' (Klaassen *et al.* 2001, Meltofte *et al.* 2007b, 2008), an aspect that together with analyses of the data on breeding phenology, hatching success and habitat use are under preparation in separate papers.

The success of a summer's breeding season and hence it's contribution to the long-term viability of bird populations in the Arctic is influenced by a myriad of more or less interacting drivers where two summers are hardly ever alike. So far, we tundra bird researchers have only been able to show the effects of a few 'obvious' factors, like excessive predation in some years and to some extent the feeding conditions during chick growth (e.g., Meltofte *et al.* 2007c, van Gils *et al.* 2016), but not the intricate mesh of contributing drivers. It will probably take a very long time series to come to grips with this challenge, and our time series of 23 years was still too short. Against this background we consider our analyses to be a first attempt to unravel the mesh of drivers operating primarily on the breeding grounds. We try to put this into perspective at the very end of the paper.

Material and methods

The procedures of the biological monitoring programme are described in detail in annually updated manuals, the most recent by Schmidt *et al.* (2019a). The methodologies of the bird programme have changed only little over time. The most pronounced change was a reduction of the census area when from 2007 onwards the area west of the main river of the Zackenberg valley (Fig. 1) was left out due to logistic and resource constraints. This reduced the census area from 19.3 km² to 15.8 km². In this paper, all data on population sizes refer to the reduced area.

Study site

The census area stretches from the coast of Young Sund fjord and up the 7-16° slopes of Aucellabjerg to an altitude of 600 m (Fig. 1). It is divided into five sections, where borders follow rivers, streams and altitude contours. The habitat is relatively rich, high Arctic tundra (83% vegetation cover) up to an altitude of about 300 m. It then changes to barren and clay dominated areas with scattered *Dryas* spp., *Salix arctica*, and *Poa glauca* dominated communities until it reaches steeper, boulder rock slopes at the upper limit (Meltofte & Rasch 2008). In the lowlands below 100 m a.s.l. there are extensive fens and many more or less temporary ponds and tarns, and a 3.6-hectare lake, Lomsø, close to the coast. A c. 30 m wide river, Zackenbergelven, runs through the valley and forms two deltas at the coast – an ancient delta to the east and the present delta to the west – both with alluvial flats (see Meltofte & Berg 2004).

The area is close to the northern limit of extensive vegetation cover in the lowlands and midway between the cool and foggy outer sea coast, 40 km to the east, and the arid inland close to the Greenland Ice Sheet, about 70 km to the west. The surrounding mountains, of which Zackenberg ('the jagged mountain') is one of the highest, reach up to 1444 m a.s.l. Taken together, the area is rather typical of the fjord and valley intercepted landscape of NE Greenland, with the exception that continuous vegetation reaches higher on the Aucellabjerg mountain slope than in most other areas.

Bird monitoring

We have followed the numbers, breeding phenology, hatching success and distribution of the bird community in the census area at Zackenberg annually since the area was staked out in 1995 (Meltofte 2006a, 2006b, Meltofte & Høye 2007). In most years, the station is staffed by biologists from around 1 June until at least early September. The bird census work consists of an ini-

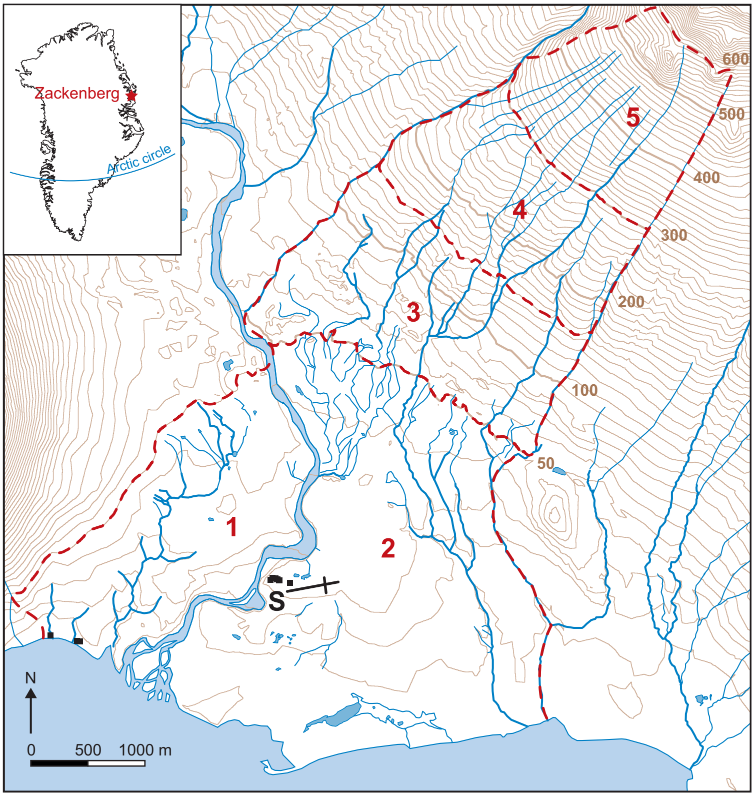

Fig. 1. Map of the study area at Zackenberg with demarcation of sections 1-5 of the census area showing streams, lakes and ponds and 10 m contour lines (m a.s.l.). The research station (S) and runway are at the lower left centre of the lowlands, c. 35 m a.s.l.
Kort over undersøgelsesområdet ved Zackenberg med afgrænsningen af sektionerne 1-5 samt elve, søer, damme og 10 m højdekurver. Forskningsstationen (S) og landingsbanen er vist lidt til venstre for midten af lavlandet i en højde af ca. 35 m.

tial total mapping of bird 'territories' in the entire census area by one person around mid-June (Fig. 2), followed by checking of uncertain records for possible confirmation of territories together with searching for nests and broods and checking on them during the rest of June and all of July (Schmidt *et al.* 2019a). A total census of the study area takes seven days to complete, beginning in the lowlands and progressing uphill on the Aucellabjerg slopes. In total, the annual fieldwork amounted to between c. 180 and c. 240 hours in most years.

The census focuses on territorial pairs/individuals, regardless of whether they actually breed or not, i.e. a 'territory' is here considered the unit in the analyses. This means that a 'site' or 'territory' can represent a pair as well as a single 'site claiming' individual. Hence, we considered the sum of pairs and of singing, alarm calling or otherwise auditory individuals to represent minimum figures, while stationary silent individuals were taken to represent uncertain/possible territories giving the maximum figures. The detection probability inevitably varies between species (quantified by Meltofte 1979), but the census method builds on the knowledge that the territory establishment, mating and egg-laying period is optimal for a high detection rate (Meltofte 2001).

For Sanderling *Calidris alba*, the population estimates might be overestimated if a single female lays two clutches in rapid succession, one incubated by the male, the other by herself (see Reneerkens *et al.* 2014). The same apply to the phalaropes, but these are so few that it is no problem. In this paper we have chosen to maintain the 'one site = one pair' ratio, bearing in mind that sites/territories for the rest of the species may also not necessarily represent breeding pairs (see above). For simplicity, we use the term territories in the text to denote pairs/sites/territories.

In most years we managed to perform the initial census largely during mid-June (Fig. 2), which is the relatively narrow 'window of opportunity' between dispersal of the last birds in the terrain after arrival and the declining intensity of singing and other territorial behaviour after egg-laying (Meltofte 2001). In years with very late snowmelt and/or poor weather conditions, the census was conducted up to about a week later. In 2012, 2014 and 2015 this was so late (23 June - 7 July, 25 June - 7 July,

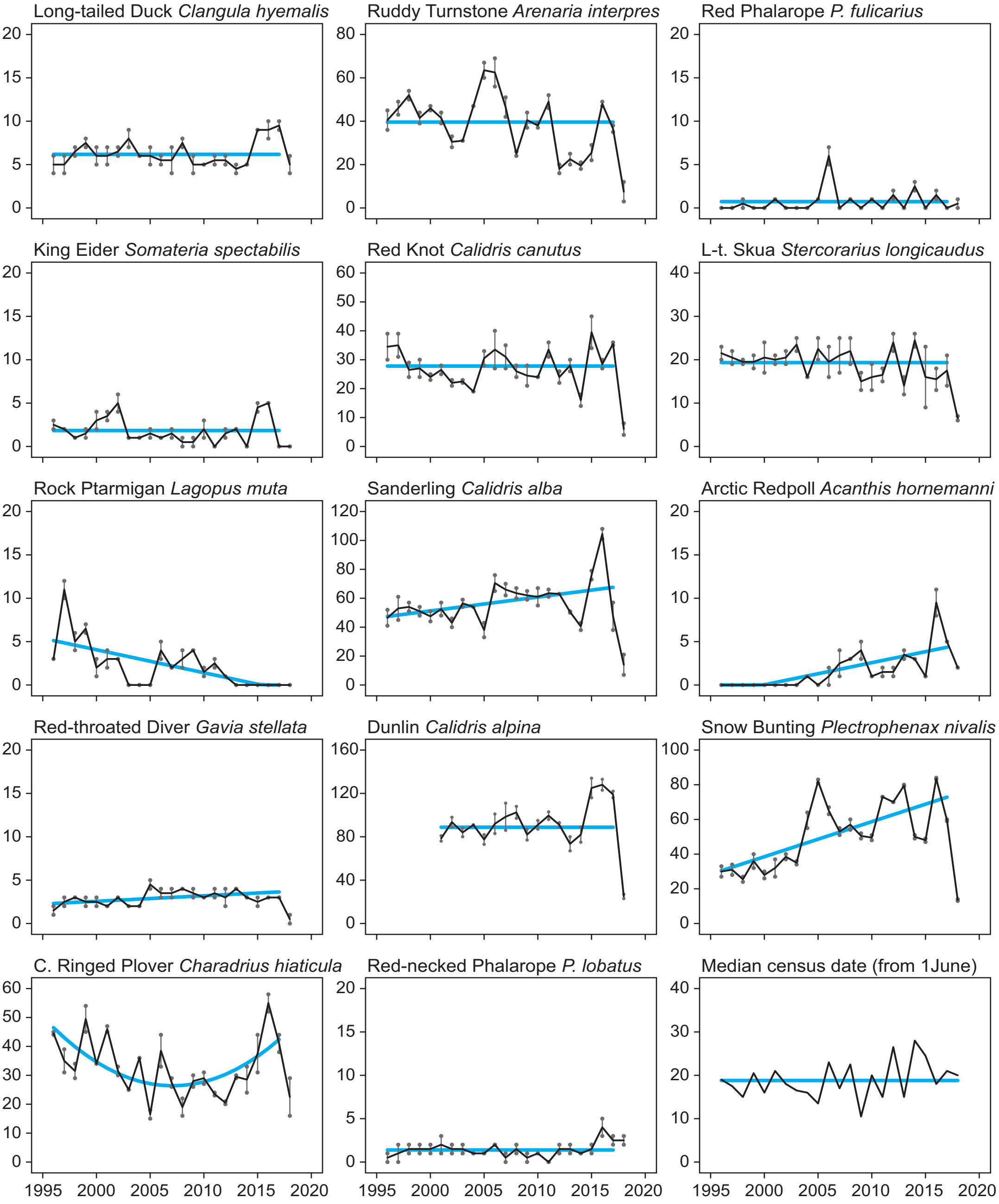

Fig. 2. Trends in numbers of territories for regularly breeding bird species together with median bird census dates in the census area (sections 2-5 in Fig. 1) at Zackenberg 1996-2018 with trend lines 1996-2017 representing the results of the final polynomial regression model after removal of non-significant higher order polynomial terms (see Material and methods). Annual minimum and maximum numbers of territories are given as range bars for the birds.

Udviklingen i antal territorier af regelmæssigt ynglende fuglearter sammen med medianen for optællingerne ved Zackenberg 1996-2018 vist med statistiske trendlinjer 1996-2017. Årlige minimum- og maksimum-bestandstal er vist med lodrette streger for fuglene. Arterne er fra oven i venstre kolonne: Havlit, Kongeederfugl, Fjeldrype, Rødstrubet Lom, Stor Præstekrave; i midten Stenvender, Islandsk Ryle, Sandløber, Almindelig Ryle, Odinshane, og til højre Thorshane, Lille Kjove, Hvidsisken og Snespurv samt mediandatoen for optællingerne.

and 20 June - 1 July, respectively) that census efficiency may have been reduced due to reduced bird activity during incubation and failed breeders having left their sites. In Dunlin *Calidris alpina*, where the early figures from east of the river were most likely underestimated (see Meltofte 2006a), we have excluded the 1996-2000 data.

The field work was covered by only two persons (HM and JH), who shared the period almost equally and included a year of overlap to ensure comparable recording. Besides the bird census taker, a team of ornithologists worked on Red Knot *Calidris canutus* in 2003 (Piersma *et al.* 2006) and on Sanderling every year from 2007 onwards (Reneerkens *et al.* 2009), which probably improved the accuracy of data on these species (see Discussion).

The final year, 2018, was extreme in the time-series covered here (Schmidt *et al.* 2019b). Large amounts of snow fell in spring (April and May) and the mean June temperature was the lowest recorded so far (mean 0.43 °C compared to a long-term average of 2.25 °C 1996-2018), so snowmelt was greatly delayed (Fig. 3). In early June, snow cover was more extensive and deeper than had ever been measured before in our study period, i.e. 95% cover on 10 June in sections 1-4 (Fig. 1 and 3; see also Fig. 5). The traps monitoring invertebrate food availability could not be opened until after the standard early season period 3-17 June (see below). A month later, in early July, snow cover was still more than 50%. Few pairs established territories, and it was close to a non-breeding season for most bird species (see Results and Discussion). Because of these extreme conditions, we have not included data from 2018 in our statistical tests. Furthermore, since severe events are often very different, their effects are hard to show in what is after all a relatively short statistical time-series analysis like ours. Since such extreme events may be important and even increase in frequency in the future (ACIA 2005), we have described the events of 2018 and other extreme events both in the Results and Discussion sections instead.

Monitoring of environmental variables

In order to map the variability of the environment of the breeding birds at Zackenberg during the 23 study years, we selected a wide variety of climatic as well as biotic variables routinely monitored at the station and potentially influencing the bird populations (see Fig. 3 and 4). Several of the factors selected for analysis, such as spring snow cover and lemming occurrence, have earlier been found to impact on Arctic bird populations and their fluctuations (e.g., Meltofte *et al.* 2007c), while others such as weather and NAO have been found to impact bird populations in other regions either through impacts on settlement, mortality or reproduction – or a combination of these (e.g., Forchhammer *et al.* 1998; Martin & Wiebe 2004, Robinson *et al.* 2007 and references therein).

Climatic parameters are primarily monitored at a climate station centrally in the valley (Kandrup & Iversen 2010, Skov *et al.* 2018). In our pairwise correlation analyses, besides mean temperatures for the pre-nesting period 20 May – 10 June, we focused on overall mean and average daily minimum temperatures together with precipitation for the spring and summer months (Fig. 3). Furthermore, we followed the progress of snowmelt in the study area by means of daily photos taken automatically from 480 m a.s.l. on Zackenberg mountain or by satellite images depending on which one was of best quality (Skov *et al.* 2018). For the bird monitoring, we have selected the extent of snow cover on 10 June below 300 m a.s.l. in the census area as representative of snow conditions in the individual years, but maintained the separation of snow cover in the individual sections in Fig. 3 to illustrate that snow cover is not a uniform metric for the entire study area. The 10th of June has been chosen as a standard measure because it is close to the first egg dates of most tundra birds. For conditions during winter and early spring, when most of the birds are in western Europe and West Africa, we use NAO-data for December-March (DJFM) from Hurrell (2018).

Invertebrate food for the insectivorous birds is monitored at five pitfall trap stations distributed in different habitats in the lowlands (Schmidt *et al.* 2019a). Each trap station has four to eight standardized yellow pitfall traps, each 10 cm in diameter and half filled with salt water and a few drops of odourless detergent (Schmidt *et al.* 2019a). In the current work we focused on two different sets of data. The first data set covers invertebrate food in the pre-laying and egg-laying periods for most of the tundra birds in early and mid-June, i.e. the dipteran flies (Diptera) and spiders (Aranea) that constitute the vast majority of food items for insectivorous birds in Greenland (Salomonsen 1950). Here, the measure was numbers of individuals caught per trap day in three early snow-free trap stations between 3 June and 17 June (Fig. 4). The three sites selected as typical early season feeding areas, particularly for waders, were a wet fen (Arthropod trap station 2), a relatively rich lichen-*Dryas* heath (Arthropod trap station 5) and a more exposed and sparsely vegetated lichen-*Dryas* heath (Arthropod trap station 7). The second data set includes the same invertebrate groups caught per trap day in all five pitfall

Fig. 3. Trends in selected climatic parameters recorded at Zackenberg 1996-2018 with trendlines 1996-2017 representing the results of the final polynomial regression model after removing non-significant higher order polynomial terms (see Material and methods). NAO DJFM is the North Atlantic Oscillation Index for December-March.
Udviklingen i udvalgte klimaparametre registreret ved Zackenberg 1996-2018 med statistiske trendlinjer 1996-2017. Graferne viser snedækket i de enkelte sektioner af undersøgelsesområdet den 10. juni hvert år, tidspunkterne for 50 % snedække samt middel- og minimum-temperaturer og nedbør i maj, juni, juli og august. NAO DJFM er det nordatlantiske oscillationsindeks for december-marts.

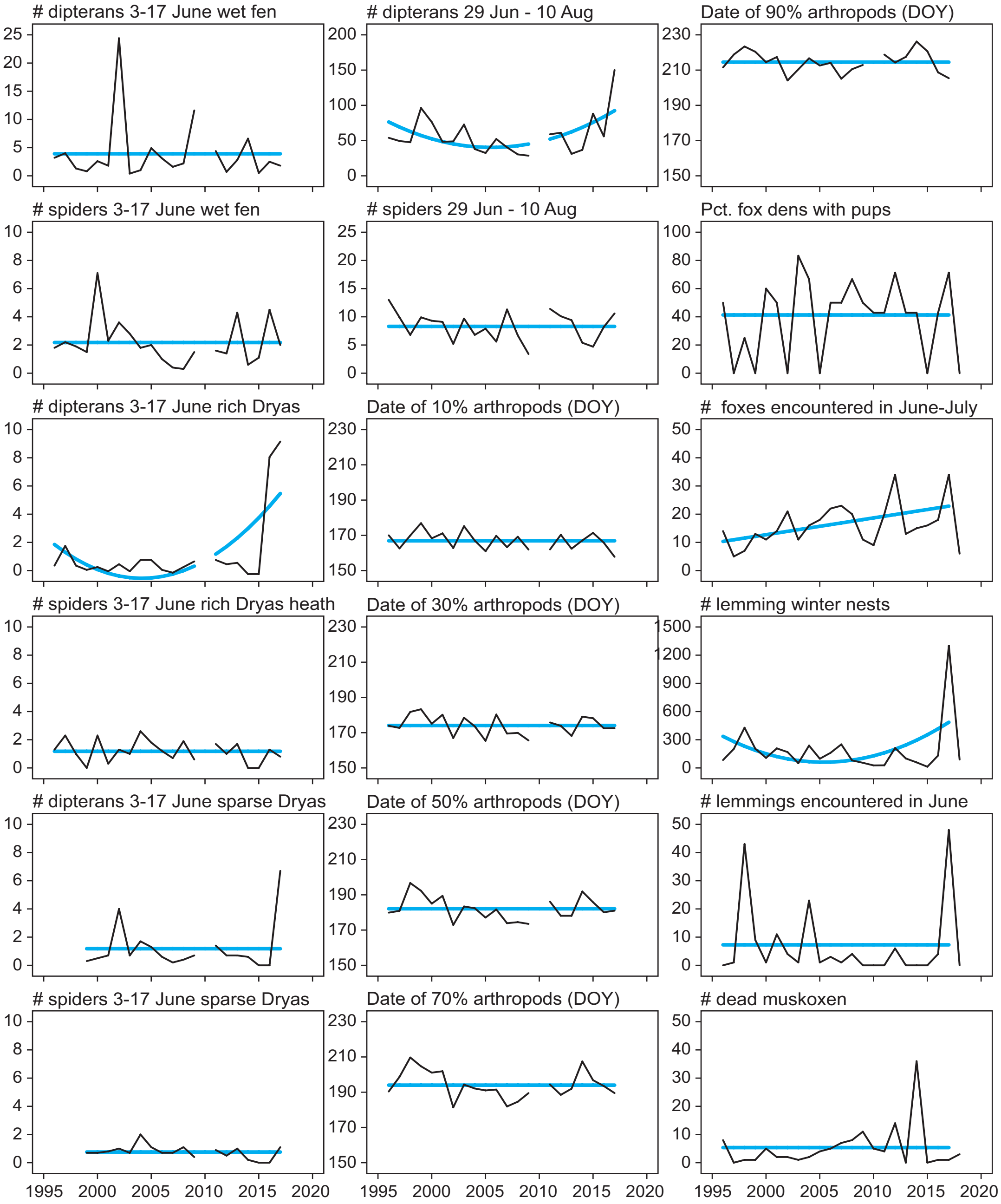

Fig. 4. Trends in selected biotic parameters recorded at Zackenberg 1996-2018 with trendlines 1996-2017 representing the results of the final polynomial regression model after removal of non-significant higher order polynomial terms (see Material and methods). DOY is day of year. The missing arthropod data for 2010 are due to loss of all samples from that year. *Udviklingen i udvalgte biologiske parametre registreret ved Zackenberg 1996-2018 med statistiske trendlinjer 1996-2017. DOY er dag på året, og graferne viser forekomsterne af tovinger* (dipterans), *edderkopper* (spiders), *tidspunkterne for 10, 30, 50, 70 og 90 % leddyr* (arthropods) *i løbet af sommeren, samt indekser for polarræve, lemminger og døde moskusokser som alternativ føde for rævene, der kan tænkes at lette prædationstrykket på fuglenes æg og unger i de foregående år og dermed påvirke antallet af ynglefugle efterfølgende. De manglende leddyrdata for 2010 skyldes tab af prøverne fra det år.*

trap stations during the entire season, June through August, mainly to provide data on the general feeding possibilities especially for young insectivorous birds during the fledging period to analyse for effects on recruitment one and two years later.

Mammalian predators are mainly represented by Arctic fox *Vulpes alopex* and the much less common stoat *Mustela erminea*. Seven fox den complexes are found within the valley, and they are monitored weekly during spring and summer for occupation and pups. However, not all of these dens were known from the very beginning of our study, so here we express dens with pups as a ratio of the numbers of dens known in the individual years (Fig. 4). Additionally, we use the number of foxes encountered by the bird monitoring field worker in June and July as a standardized measure of fox activity in the area.

Foxes at Zackenberg primarily prey on collared lemmings, Arctic char *Salvelinus alpinus* and muskoxen that have died during the winter (Schmidt *et al.* 2008; see also Dalerum & Angerbjörn 2000). Lemmings are monitored by mapping deserted winter nests after snowmelt in a 1.06 km^2 plot centrally in the valley and by recording numbers of live individuals seen by the bird monitoring field worker during June each year (Fig. 4; see Fauteux *et al.* 2018). Numbers of muskoxen that died during the preceding winter are recorded each summer within the study area (sections 1-5; Fig. 1). The availability of Arctic char depends on numbers of char accidentally 'stranded' in shallow parts of the river Zackenbergelven during summer, which was beyond our capacity to monitor.

Statistical analyses

The time series for all tabled bird populations were tested for time trends and for correlations with all tabled biotic as well as climatic factors, i.e. all measured variables that we expected to potentially having a bearing on the bird populations. Averages were used in all statistical calculations of annual bird population numbers consisting of minimum and maximum figures. The temporal trends of the most common breeding birds together with selected climatic and biotic parameters were tested by a second order polynomial regression analysis ($y = \beta_0 + \beta_1 X + \beta_2 X^2 + \varepsilon$). The first order term in the regression model is equivalent to no trend but a variability around an overall mean, the second term is equivalent to a linear relationship, and the second order term is equivalent to a quadratic relationship. Terms were removed one by one from the polynomial regression models by applying a significance level of 10%, starting with the highest order. The 10% significance level was chosen instead of the more commonly used 5% because we wanted to reduce the risk of making a Type II error (incorrectly accept the influence of the variable), which is a common practice when multiple testing is involved. No lower order terms were removed if a higher order term was significant.

As part of our screening for correlates in the dataset, we tested for pairwise year-by-year correlation between the species population numbers to elucidate any synchronous variation resulting from common predictors. Here we even tested for pairwise year-by-year correlations for detrended data in bird species showing significant positive or negative trends. The detrending of data was done by removing the effect of year from both the species and the climatic parameters by extracting the residuals from independent regressions, with year as the predictor. These residuals were then tested by correlation analysis.

For correlations between territory numbers of each species and each climatic and biotic variable, a principal component analysis (PCA) ought to have been used. This is because several of the potential impact factors are interrelated, such as spring temperatures, spring snow cover and invertebrate phenology. However, due to incomplete data series, we refrained from applying PCA. Had we done so, we would have had to either exclude data from the first 3-5 years due to missing values for Dunlin and for invertebrates from the trap station in the very early snow free and therefore important lichen-*Dryas* heath (station 7) used by waders, skuas and passerines upon arrival, or to have omitted trap station 7. We would also have had to skip all data from 2010, since all invertebrate samples from this year were lost. Furthermore, the dataset consisted of both discrete and continuous data, which creates problems with the assumption of multivariate normality if analysed together with e.g. multiple regressions analyses. Instead, we tested for pairwise correlations using the non-parametric Spearman's rank correlation between territory numbers of each species and each climatic and biotic variable. Furthermore, we applied Spearman's rank correlation to the data for each specific year, and for one and two preceding years, to analyse for effects on recruitment one and two years later. This means that great care should be taken when evaluating the results due for example to interacting impact factors.

Lastly, we tested for temporal trends in the variability of bird populations as well as biotic and climatic parameters by estimating a five-year running mean of the coefficient of variation (CV), and linear regression was used to test whether it changed over time.

With such large numbers of tests, 'random' correla-

Fig. 5. Drone photo of the snow cover in the lowlands and slopes of Aucellabjerg seen from SSW on 24 June 2018. The river Zackenbergelven has just begun running, and the main breeding area for Dunlin in Rylekærene is totally covered in deep water-soaked snow. Photo: Lars Holst Hansen. *Drone-billede af snedækket i lavlandet og på skråningerne af Aucellabjerg set fra SSV den 24. juni 2018. Zackenbergelven er lige begyndt at løbe, og det vigtigste yngleområde for Almindelige Ryler i Rylekærene er totalt dækket af dyb vanddrukken sne. Dette ekstreme år var et meget dårligt år for ynglefuglene ved Zackenberg, idet kun få ynglede og mange sultede eller endog døde af sult.*

tions are of course a risk. Therefore, we have focused on the strongest correlations and disregard those that were clearly meaningless (cf. Yoccoz 1991).

Results

The vast majority of the breeding bird species in high Arctic Greenland were present in the Zackenberg study area or its immediate surroundings (cf. Boertmann 1994). As elsewhere in high Arctic Greenland, the bird community was numerically dominated by waders Scolopacidae and Charadriidae and Snow Buntings *Plectrophenax nivalis*. In total, the average bird density was 19.7 territories per km^2 in the census area during the study period, with individual insectivore species reaching about 3.2-8.5 territories per km^2 in individual sections of the census area.

Most bird populations remained relatively 'stable', i.e. numbers of territories fluctuated from year to year without any significant trend (Fig. 2). The most pronounced exceptions were increasing populations of Sanderlings (1st order polynomial regression, $P = 0.048$), Snow Buntings (1st order polynomial regression, $P < 0.01$) and Arctic Redpolls *Acanthis hornemanni* (1st order polynomial regression, $P < 0.01$), and decreasing numbers of Rock Ptarmigans *Lagopus muta* (1st order polynomial regression, $P < 0.01$). Besides these directional changes, Common Ringed Plover *Charadrius hiaticula* exhibited an initial 10-year decrease followed by recovery in the more recent years of the study period (2nd order polynomial regression, $P < 0.01$; Fig. 2). A similar early decrease was seen in Red Knot territories, but the population had already rebounded to the initial level in the middle of the study period. Red-throated Diver *Gavia stellata* also increased by a few pairs in the beginning of the study period, and Arctic Redpoll immigrated during the period (Fig. 2; see also Discussion).

Comparison of population sizes of the various species across years revealed only a few significant correlations, with the highest being for Sanderling/Dunlin ($\tau = 0.638$, $P = 0.006$) and Arctic Redpoll/Snow Bunting ($\tau = 0.671$, $P < 0.001$).

Among the 18 parameters in the climatic environment which were examined, only July mean temperatures showed a unidirectional increase (1st order polynomial regression, $P < 0.01$) during the study years by no less than 2.32 °C (Fig. 3). May mean temperature also showed an initial increase followed by a decrease (2nd order polynomial regression, $P = 0.04$; Fig. 3). Finally, snow cover on 10 June showed an initial decrease followed by an increase in section 4 of our census area (2nd order polynomial regression, $P = 0.02$). There was a tendency for a similar pattern in all census zones below 300 m a.s.l., where most birds breed (Fig. 3).

A number of years were particularly inclement for tundra birds at Zackenberg, and 2018 came very close to be a non-breeding year (see Material and methods). After arriving, many birds remained and foraged in small flocks during June; some even starved to death while others were of low weight (Schmidt *et al.* 2019b). Not only was the number of occupied territories greatly reduced (Fig. 2) but the few pairs that did breed did so extremely late and predation rate was high (Schmidt *et* *al.* 2019b). The Dunlin habitat in the fens was particularly reduced, with only about 2-3% of the area snow-free in early July (Fig. 5). By that time, most waders had left the valley.

Only two other years had extraordinarily extensive snow cover in early June (91% on 10 June 1999 and 92% in 2015; Fig. 3), but the extent of snow then was still well below that experienced in 2018 and disappeared faster. Nevertheless, between a third and half of the Ruddy Turnstones *Arenaria interpres* – a species that seems particularly sensitive to extensive snow cover (Meltofte 1985, Pellissier *et al.* 2013) – did not breed in 1999 and instead roamed the area as pairs or single individuals until they left the area in late June or early July (Meltofte 2000). In 2001, several waders starved to death or were predated by skuas during a snowstorm in mid-June, and many joined flocks in communal feeding areas (Meltofte 2003). Common Ringed Plovers breeding above 300 m a.s.l. on the Aucellabjerg slopes (see Meltofte 2006a) are occasionally exposed to new snow that may cover the upper slopes for a few days during summer. In 1997, for example, snowfall on 11 June may have reduced the number of Ringed Plover territories on the slopes in that year (Meltofte 1998).

Among the 18 biotic parameters apart from birds that were monitored and selected for analysis here, only fox encounters showed a unidirectional positive trend over the study years (1st order polynomial regression, $P = 0.01$; Fig. 4). Furthermore, based on the numbers of winter nests, the lemming population in the study plot had relatively low peak years, particularly during 2000-2016, followed by an all-time high in 2017 (2nd order polynomial regression, $P = 0.046$; Fig. 4).

Despite the many statistical tests of year-to-year variation between territory numbers and spring and summer temperatures, precipitation, spring snowmelt, invertebrate food availability, mammalian predators, and alternative prey in the form of lemmings and dead muskoxen (including time lags of one or two years), there were only a few significant correlations.

A highly significant correlation was found between year-to-year variation in the small population of Red-throated Divers and spring conditions in the form of snow cover on 10 June in sections 1-4: less snow (i.e. less ice cover on lakes and ponds) was correlated with more nesting diver pairs ($\tau = -0.546$, $P = 0.009$ in year 0; $\tau = -0.515$, $P = 0.014$ in year 0-1).

Similarly, numbers of Snow Bunting territories correlated negatively with snow cover in sections 1-4, i.e. below 300 m a.s.l. on 10 June ($\tau = -0.457$, $P = 0.032$), and so did numbers of Snow Buntings positively with June mean temperatures and negatively with June precipitation ($\tau = 0.501$, $P = 0.018$ and $\tau = -0.478$, $P = 0.028$, respectively). For Arctic Redpoll there was a positive correlation with July mean temperature the previous summer ($\tau = 0.643$, $P = 0.001$).

In contrast to the low number of significant correlations with climatic and biotic parameters (see Discussion), the year-to-year variability increased significantly in several bird populations and potentially important factors. Thus, significantly increasing year-to-year variability was found in particular in May mean temperatures ($R^2 = 0.653$, $P < 0.001$), in snow cover below 300 m a.s.l. on 10 June ($R^2 = 0.815$, $P < 0.001$) and in date of 50% snow cover below 300 m a.s.l. ($R^2 = 0.508$, $P = 0.001$). This tendency would have been even more pronounced if data for 2018 had been included, but snow cover was so extreme in that year that we chose to deal with it separately.

Similarly, there was markedly increased variability in territory numbers of Ruddy Turnstone ($R^2 = 0{,}794$, $P < 0.001$), Red Knot ($R^2 = 0{,}448$, $P = 0.002$), Sanderling ($R^2 = 0{,}275$, $P = 0.025$), Dunlin ($R^2 = 0{,}593$, $P = 0.001$), and Long-tailed Skua *Stercorarius longicaudus* ($R^2 = 0{,}912$, $P < 0.001$) during the study years (see Discussion).

Besides the 14 species presented in Fig. 2, a few pairs of Pink-footed Geese *Anser brachyrhunchus* and Common Eiders *Somateria mollissima* nested in the census area (Meltofte 2006a, 2006b). One or two pairs of Glaucous Gulls *Larus hyperboreus* alternated between nesting in the Zackenbergelven riverbed and lakes just outside the census area during the entire study period. The same applies to Northern Wheatear *Oenanthe oenanthe*, up to three pairs of which have bred just outside the census area in most years and inside it in a few years. One or two pairs of Snowy Owls *Bubo scandiacus* also nested in the valley in 1997 and 2001, respectively (Meltofte *et al.* 2007b). Alarm calling European Golden Plovers *Pluvialis apricaria* were encountered a few times in the census area, but no further indication of breeding was observed. Barnacle Geese *Branta leucopsis* (Meltofte 2006b) and Northern Ravens *Corvus corax* bred in the neighbourhood and brought their offspring to the study area after hatching and fledging, respectively. In 2014, a pair of Arctic Skuas occupied a territory in the census area (Hansen *et al.* 2016), and Lapland Longspur *Calcarius lapponicus* appears to have expanded to nest sporadically in the region.

Discussion

Increased year-to-year variability in the populations of

Ruddy Turnstone, Red Knot, Sanderling, Dunlin, and Long-tailed Skua were the most pronounced trends in population size and variability found where increasingly variable spring conditions may be involved. The increased variability would have been even more pronounced if 2018 had been included in the analyses; but as this was the last year in the data series, to include 2018 would have exaggerated the variability to an unrealistic level. For Long-tailed Skua, the reduced lemming peaks during 2000-2016 may have added to population instability (see Schmidt *et al.* 2012a), but no statistically significant correlation was found with the lemming indices.

As demonstrated, there were more increasing than decreasing populations, while more than half the populations remained 'stable' or fluctuating without any statistically significant trend. Among the increasing populations, we are confident that Sanderling, Arctic Redpoll, and Snow Bunting represent real increases, whereas for Sanderling, the greater focus on this species from 2007 onwards resulted in more nests and broods found, which may therefore have added to the increase.

The most pronounced increases were found in Snow Bunting, where a doubling in numbers of territories was recorded, and in Arctic Redpoll, which immigrated to the study area in 2004 (Fig. 2). Both species correlated negatively with extent of spring snow cover, whereas the increases took place despite the largely unchanged numbers and phenology of invertebrates trapped and increasing numbers of fox encounters (Fig. 3 and 4). Furthermore, the statistically significant correlation between year-to-year variability of Sanderling and Dunlin numbers remained even after detrending the data.

The similarity between the two passerine species is the likely explanation for the highly significant correlation between their year-to-year territory numbers. Arctic Redpoll has been breeding in the region all the time, but not within our census area up until 2004. Similarly, Northern Wheatear may have increased from a single pair, breeding irregularly in the valley for decades, to a maximum of three pairs in 2009 (Hansen *et al.* 2010). Lapland Longspur was also found breeding for the first time in 2010 as the hitherto northernmost record in East Greenland, but this record was surpassed by a breeding record 1000 km farther north in 2017 (Lee 2018). These changes may be the first signs of climate change effects such as the increasing July mean temperatures and changing plant community composition and increased gross primary production in the fens, in particular (Schmidt *et al.* 2012b, Tagesson *et al.* 2012).

The increase of Red-throated Divers by a few pairs and the fluctuation of the population in relation to timing of ice clearance on the breeding ponds and lakes may be indicative of the dependency of this species on early ice out on breeding ponds and lakes (see also Meltofte 2006b).

Only Rock Ptarmigan showed a significant decreasing trend, which probably reflects the decreasing phase in the well-known, pronounced population fluctuations of this species (Hansen *et al.* 2008, Fuglei *et al.* 2020). But we also suspect that the Ruddy Turnstone population may have decreased – or at least has shown decreased breeding effort – as indicated by falling numbers of

A small population of up to five pairs of King Eider was present in the census area during the study years. Photo: Erik Thomsen.
Op til fem par Kongeederfugle har ynglet i optællingsområdet i undersøgelsesperioden.

nests and broods found (see also Meltofte 2006a) despite the increased field activity by the Sanderling study team since 2007. In some years several pairs were actually recorded early in the season but did not result in records of breeding activity later on (Hansen *et al.* 2014). As with the Sanderling discussed above, the search for Turnstone or other bird nests and broods was not standardized by effort. Nevertheless, numbers were found to have decreased linearly ($R^2 = 0.396$, $P = 0.002$) and it was increasingly difficult to establish a sample of at least 10 nests and broods compared to the up to 23 nests and broods found twice in the early years of the study period (1998 and 2000). Hence, if the Turnstone population has actually decreased at Zackenberg, this trend is paralleled by decreasing populations since the 1970s in Ørsted Dal and at Danmarks Havn farther south and north in NE Greenland, respectively (Boertmann *et al.* 1991, Meltofte & Dinesen 2010) but contrasts with moderately increasing/fluctuating flyway trends (van Roomen *et al.* 2018). The latter could be caused by substantial parts of this population breeding in NW Greenland and the NE Canadian high Arctic (Meltofte 1985, 2001), where conditions may be very different from NE Greenland.

Only Red-throated Diver and Snow Bunting showed strong correlations with June snow/ice and weather conditions (see Results). The few relevant correlations obtained with the many climatic parameters but no correlations with the biotic parameters can be interpreted as a result of too much stochastic variation in bird numbers (both real and due to census inaccuracy) and too complex an interplay between e.g. timing of snowmelt, spring temperatures, spring food availability, and weather and food during the fledging period of young during the preceding years. As an example, the statistically significant correlations between Red Knot and Ruddy Turnstone territories and July conditions found two years earlier in previous analyses (Meltofte 2006a, Meltofte *et al.* 2007b) were not confirmed in the current study (see also Ryabitsev & Alekseeva 1998). We have no doubt that all the presented factors impact on bird populations but with varying strength from year to year, and with few of them apparently strong and dominating enough to achieve statistical significance. We think that both local conditions at territory establishment, regional breeding success in the previous 1-2 years, and factors operating at flyway population level impact bird populations in an area like ours. Therefore, we consider this analysis only as a first attempt to unravel the entire mesh of drivers that determines the wellbeing of tundra bird populations in high Arctic Greenland.

The densities of tundra birds at Zackenberg are in the upper range of what has been reported from other sites in high Arctic Greenland, where densities of about the same level and down to about one tenth of densities at Zackenberg have been documented (cf. Meltofte 1985, Boertmann *et al.* 1991, Mortensen 2000, Meltofte & Dinesen 2010). The high densities at Zackenberg suggest that conditions there are more favourable than in many other sites in the region (Meltofte 1985, Meltofte *et al.* 2008). If this is the case, changes in bird populations may be occurring more slowly at Zackenberg than in more marginal habitats (Meltofte 1985, see also Ward *et al.* 2018). Whether this is so may depend among other things on whether the bird populations are saturated or not in an area like Zackenberg. Since we have only little evidence of such saturation (Forchhammer *et al.* 2008b), we can only speculate that the relatively few significant population changes may not be representative of population trends in a wider area like central NE Greenland and even less so for the entire flyway of the populations involved. Instead, the changes found in a few species may reflect local conditions (see below). Furthermore, most of the bird populations at Zackenberg belong to site-faithful and long-lived 'conservative' species with relatively slow population turnover (Cramp 1977-1994, Meltofte *et al.* 2007c, Saalfeld & Lanctot 2015). This may explain the low number of correlations with the year-to-year variability in breeding conditions both in the concomitant year and in the previous two years.

Tundra bird populations are much denser in large parts of low Arctic Siberia and North America and therefore bird censuses can be performed using nest records in relatively manageable areas. In contrast, we were only able to try to map territories in our much larger study area (Meltofte 2001, 2006a, Piersma *et al.* 2006). This means that our data may be less accurate, and that year-to-year variation may include an element of stochasticity. In our opinion, however, this does not change the general impression of relatively 'stable' populations in most species and very little impact of inter-annual environmental variability on concomitant bird populations. In addition, the 23-year time series from Zackenberg was largely covered by only two field workers (see Material and methods).

As mentioned, the census results from a relatively favourable area like Zackenberg do not necessarily have much bearing on overall flyway trends. Furthermore, good flyway population data exist only for a limited number of species found in our census area. Even for some of the well monitored flyway numbers, the subspecies found in NE Greenland are 'swamped' by other

The population of Snow Bunting in the census area has doubled during the study years and varied statistically significantly with spring snow cover and June precipitation (both negatively) and June temperatures (positively). Photo: Tom Versluijs.
Bestanden af Snespurve i optællingsområdet er fordoblet i løbet af undersøgelsesperioden, og den varierede signifikant negativt med forårssnedækket og juni-nedbøren, og positivt med juni-temperaturerne.

populations wintering in the same areas, for example as is the case for Common Ringed Plover and Dunlin wintering in West Africa (Delany *et al.* 2009). Flyway trends in Nearctic Red Knots wintering on the East Atlantic flyway are predominantly stable like at Zackenberg, while Nearctic Sanderlings wintering in the same area show increasing trends (van Roomen *et al.* 2018) like at Zackenberg. Overall, tundra bird populations breeding in high Arctic Greenland and north-easternmost high Arctic Canada and wintering on the East Atlantic Flyway are faring better than tundra birds in other major flyways in that no populations are declining (Smith *et al.* 2020).

To the best of our knowledge, no other all-species long-term census data on tundra bird trends have been published from other parts of the Arctic, but data do exist particularly for waders. Thus, in a broken time series of 60 years from Utqiagvik/Barrow in Alaska, a decrease in 'northern' wader species and an increase in 'southern' species took place between 1951 and 2012 (Taylor *et al.* 2018). Comparing few years of observation since the 1960s from Cambridge Bay, Nunavut, Canada, Lok & Vink (2012) found similar shifts but otherwise stable numbers for most species (see also Pattie 1990). And at the Mackenzie Delta also in Canada, wader populations remained stable according to a broken time series since the late 1960s (Rauch & Johnston 2012). However, based on breeding areas monitoring, passage counts and winter site censuses, varying shares of species have been declining in the world's major flyways during recent decades; this decline is partly considered to be the result of climate change affecting the tundra, and partly habitat changes on staging and wintering sites together with shooting and netting (Gratto-Trevor *et al.* 2011, Studds *et al.* 2017, van Roomen *et al.* 2018, Meltofte *et al.* 2019, Smith *et al.* 2020).

There are relatively few records in the literature of extensive non-breeding years in high Arctic Greenland (Meltofte 1985) or in the Arctic for that matter with 1992 being best documented (Ganter & Boyd 2000, Boyd & Piersma 2001). However, there are no previous detailed 'on-the-ground' records of such events from high Arctic Greenland, and even in 1992, neither particularly late timing of snowmelt nor exceptionally low numbers of breeding tundra birds were found at Karup Elv 245 km south of Zackenberg (Meltofte *et al.* 2007b). Besides the pronounced effects at Zackenberg, 2018 may have had much more geographically extensive impacts, since similarly late snowmelt and reduced breeding of waders etc. was reported from sites as far apart as Jameson Land in the south of high Arctic Greenland more than 400 km south of Zackenberg (K. de Korte *in litt.*) and Hochstetter Forland 80 km farther north (O. Gilg *in litt.*). In a reflection of these impacts, extremely few Barnacle Goose goslings arrived at the wintering grounds of the NE Greenland population on the Isle of Islay in Scotland the autumn and winter of 2018-2019, and 2018 marked the worst-ever breeding success on record for this population, with the juvenile percentage at just 1.1% and mean brood size of 1.09 (M. Ogilvie *in litt.*). Yet, ratios of juvenile waders were not exceptionally low in passage and wintering areas of these populations in North-western Europe the following autumn and winter, indicating that breeding success may have been better in other areas within the breeding range of these flyway populations (Meltofte *et al.* submitted).

In 2019, all bird populations were back to within the ranges of previous years, except for Sanderling that decreased to 30-32 territories compared to annual averages of between 41 and 104 before the 2018 event. With 98-107 territories, also Dunlin was down from the high figures of 2015-2017, i.e. to the more regular numbers of the previous years (see above).

In conclusion, according to our results most of the bird populations at Zackenberg appear to be stable or even increasing. This may be related to the relatively few unidirectional changes of local conditions discussed above. We still see little effect on population level of the ongoing warming of summer temperatures or the increased variability in spring conditions. Even Long-tailed Skuas have not decreased significantly despite reduced lemming peaks during the 16 years preceding the all-time lemming high in 2017 (Barraquand *et al.* 2014). A few bird populations have increased, maybe as a result of milder summer conditions. This is in contrast to well documented changes taking place in other parts of the Arctic, where several tundra bird populations are declining (Smith *et al.* 2020) due to a range of climate and other anthropogenic-related pressures, such as tree and shrub encroachment on the tundra (Ballantyne & Nol 2011), possibly reduced invertebrate food availability on the tundra during chick growth (van Gils *et al.* 2016), and habitat loss on key staging and wintering areas (MacKinnon *et al.* 2012, Piersma *et al.* 2016, Szabo *et al.* 2016). However, in species dependent on high annual adult survival, like most of those breeding at Zackenberg (see Weiser *et al.* 2018), the effects of extreme events like in 1972, 1974, 1979, 1992, 2001 and 2018 in high Arctic Greenland / NE Canadian Arctic with enlarged adult mortality (see Boyd & Madsen 1997, Boyd & Piersma 2001, Lyngs 2003, Meltofte *et al.* 2007c) may become a more decisive factor in the future with a higher frequency of such events as a result of climate change (ACIA 2005, Seneviratne *et al.* 2012, Landrum & Holland 2020), as also indicated in this study. This is contrary to the findings by Weiser *et al.* (2018) that conditions in the Arctic has little effect on adult wader survival, however based on only five breeding seasons. In fact, the severe events mentioned above are considered to have been the reason for the significant reduction seen in the flyway population of the *islandica* subspecies of Red Knot during the 1970s and 1980s (Delany *et al.* 2009).

Furthermore, the expected habitat shrinkage for Arctic breeding birds as a result of northwards expansion of 'southern' plant and animal species and habitats due to climate amelioration (e.g., Meltofte 2013, Wauchope *et al.* 2017); i.e., unsuitable habitats for high Arctic specialist waders already start 400 km south of Zackenberg (Mortensen 2000) and dwarf shrubs are expected to expand in the study area under current climate change scenarios (Stewart *et al.* 2018).

Our results underscore that the Arctic is not one uniform area of unidirectional change in relation to climate variability and change, but a diverse and intricate mosaic of positive and negative trends both in bird populations and in the factors that potentially influence their wellbeing where two summers are hardly ever alike. On this background we consider our analyses as a first attempt to map out the entire mesh of drivers.

Acknowledgements

Data were provided by the Greenland Ecosystem Monitoring Programme. We are most grateful to the Aage V. Jensen Charity Foundation for financial support in analysing the data and writing the paper. We further thank Zackenberg Ecological Research Operations for logistic support during the entire study period and Jeroen Reneerkens for contributing plenty data. Juana Jacobsen, Aarhus University, drew the graphs, Nick Quist Nathaniels checked our English, and five anonymous reviewers together with Martin Bulla provided comprehensive suggestions for improving earlier drafts.

Resumé

Øget år til år-variation i fuglebestandene ved Zackenberg i højarktisk Grønland 1996-2018, men få bestandsændringer eller korrelationer med lokale forhold

Arktis er under forandring, men i modsætning til de store økologiske ændringer, der finder sted i flere andre dele af den arktiske zone, fandt vi kun få statistisk signifikante ændringer i fuglebestandene og i de klimatiske og biologiske faktorer, der potentielt kunne påvirke fuglebestandene i en 23-årig undersøgelsesperiode ved Zackenberg i højarktisk Nordøstgrønland (se Fig. 1).

Ud af 14 arter af regelmæssigt ynglende fugle ved Zackenberg svingede otte eller ni bestande uden nogen signifikant tendens, fire steg i antal, mens kun en eller to aftog (Fig. 2). Blandt de samme 14 arter viste seks stigende variation fra år til år i løbet af undersøgelsesårene.

Blandt 36 klimatiske såvel som biologiske faktorer viste kun to en stigende tendens (juli-middeltemperatur og ræveobservationer; Fig. 3 og 4). Resten forblev stabile eller svingende uden nogen signifikant tendens. Blandt de samme parametre udviste det tidsmæssige forløb af snesmeltningen og maj-middeltemperaturerne stigende variation i løbet af undersøgelsesårene; forskellene fra år til år blev med andre ord større og større

i overensstemmelse med, at klimaforandringerne forventes at medføre mere ustabile forhold inklusive flere ekstremer. Den ekstremt sene snesmeltning i 2018 kan være et eksempel herpå (Fig. 5). Det år var der meget få fugle, der ynglede, og en del sultede eller døde ligefrem af sult.

Vi fandt kun få statistisk signifikante sammenhænge mellem svingningerne i fuglebestandenes størrelse og variationer mellem de årlige klimatiske og biologiske faktorer, med omfanget af forårs-snedække som den mest udtalte korrelation (jo mere sne- og isfrit, jo flere Rødstrubede Lommer og Snespurve). Det kræver givetvis længere tidsserier for at udrede det omfattende net af faktorer, der påvirker antallet af ynglefugle i de enkelte år og på længere sigt. Vores data understøtter, at de fleste tundrafuglebestande på den østatlantiske trækvej indtil videre klarer sig godt, hvilket dog ikke er det samme som, at de også vil gøre det, efterhånden som klimaændringerne gør sig langt stærkere gældende.

References

ACIA 2005: Arctic climate impact assessment. – Cambridge University Press.

Ballantyne, K. & E. Nol 2011: Nesting habitat selection and hatching success of Whimbrels near Churchill, Manitoba, Canada. – Waterbirds 34: 151-159.

Barraquand, F., T.T. Høye, J.-A. Henden, N.G. Yoccoz, O. Gilg *et al*. 2014: Demographic responses of a site-faithful and territorial predator to its fluctuating prey: long-tailed skuas and arctic lemmings. – J. Animal Ecol. 83: 375-387.

Boertmann, D. 1994: An annotated checklist to the birds of Greenland. – Meddr. Grønland / Monographs on Greenland, Bioscience 38: 1-63.

Boertmann, D., H. Meltofte & M. Forchhammer 1991: Population densities of birds in central Northeast Greenland. – Dansk Orn. Foren. Tidsskr. 85: 151-160.

Boyd, H. & J. Madsen 1997: Impacts of Global Change on Arctic-Breeding Bird Populations and Migration. Pp. 201-217 in: W.C. Oechel, T. Callaghan, T. Gilmanov, J.I. Holten, B. Maxwell *et al.* (eds): Global Change and Arctic Terrestrial Ecosystems. – Springer Verlag, New York.

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

CAVM Team 2003: Circumpolar Arctic vegetation map. Scale 1:7,500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. – U.S. Fish and Wildlife Service, Anchorage.

Cramp, S. 1977-1994: Handbook of the birds of Europe, the Middle East, and North Africa. – Oxford University Press.

Dalerum, F. & A. Angerbjörn 2000: Arctic Fox (*Alopex lagopus*) Diet in Karupelv Valley, East Greenland, during a summer with Low Lemming Density. – Arctic 53: 1-8.

Delany, S., D. Scott, T. Dodman & D. Stroud (eds) 2009: An atlas of wader populations in Africa and Western Eurasia. – Wetlands International and International Wader Study Group.

Doyle, S., A. Gray & B.J. McMahon 2020: Anthropogenic impacts on the demographics of Arctic-breeding birds. – Polar Biol. doi.org/10.1007/s00300-020-02756-6

Fauteux, D., G. Gauthier, M.J. Mazerolle, N. Coallier, J. Bêty & D. Berteaux 2018: Evaluation of invasive and non-invasive methods to monitor rodent abundance in the Arctic. – Ecosphere 9:e02124.

Forchhammer, M.C., E. Post & N.C. Stenseth 1998: Breeding phenology and climate... – Nature 391: 29-30.

Forchhammer, M.C., T.R. Christensen, B.U. Hansen, M.P. Tamstorf, N.M. Schmidt *et al.* 2008a: Zackenberg in a circumpolar context. Pp. 499-544 in: H., Meltofte, T.R. Christensen, B. Elberling, M.C. Forchhammer & M. Rasch (eds): High-Arctic ecosystem dynamics in a changing climate. – Advances in Ecological Research 40, Academic Press.

Forchhammer, M.C., N.M. Schmidt, T.T. Høye, T.B. Berg, D.K. Hendrichsen & E. Post 2008b: Population dynamical responses to climate change. Pp. 391-420 in: H. Meltofte, T.R. Christensen, B. Elberling, M.C. Forchhammer & M. Rasch (eds): High-Arctic ecosystem dynamics in a changing climate. – Advances in Eco-

After Dunlin, the Sanderling was the most common breeding wader in the census area, with the Sanderling population and its year-to-year variability increasing during the study years. Photo: Erik Thomsen.
Næstefter Almindelig Ryle er Sandløberen den almindeligst ynglende vadefugl i optællingsområdet, og både bestanden og år til år-variationen er tiltaget.

logical Research 40, Academic Press.

Fuglei, E., J.-A. Henden, C.T. Callahan, O. Gilg, J. Hansen *et al.* 2020: Circumpolar status of Arctic ptarmigan: Population dynamics and trends. – Ambio 49: 749-761.

Ganter, B. & H. Boyd 2000: A tropical volcano, high predation pressure, and the breeding biology of Arctic waterbirds: a circumpolar review of breeding failure in the summer of 1992. – Arctic 53: 289-305.

Gratto-Trevor, C., R.I.G. Morrison, B. Collins, J. Rausch, M. Drever & V. Johnston 2011: Trends in Canadian Shorebirds. – Canadian Biodiversity: Ecosystem Status and Trends 2010, Technical Thematic Report No. 13. Canadian Councils of Resource Ministers. Ottawa.

Hansen, J., H. Meltofte & T.T. Høye 2008: Population fluctuations in Rock Ptarmigan in high-arctic Greenland. – Dansk Orn. Foren. Tidsskr. 102: 319-324.

Hansen, J., L.H. Hansen, K. Boesgaard, K. Albert, S. Svendsen *et al.* 2010: Zackenberg Basic: The BioBasis programme. Pp. 46-81 in: L.M. Jensen & M. Rasch (eds.): Zackenberg Ecological Research Operations, 15th Annual Report, 2009. – National Environmental Research Institute, Aarhus University.

Hansen, L.H., J. Hansen, P.S. Nielsen, J. Humaidan, K.S. Christoffersen & N.M. Schmidt 2014: Zackenberg Basic: The BioBasis programme. Pp. 39-65 in: L.M. Jensen, T.R. Christensen & N.M. Schmidt (eds.): Zackenberg Ecological Research Operations 19th Annual Report, 2013. – Aarhus University.

Hansen, L.H., J. Hansen, P.S. Nielsen, K.S. Christoffersen, J.B. Mosbacher & N.M. Schmidt 2016: Zackenberg Basic: The BioBasis programme. Pp. 38-64 in: L.M. Jensen, E. Topp-Jørgensen, T.R. Christensen & N.M. Schmidt (eds.): Zackenberg Ecological Research Operations 20th Annual Report, 2014. – Aarhus University.

Hurrell, J. (eds) 2018: The climate data guide: Hurrell North Atlantic Oscillation (NAO) Index (station-based). Retrieved from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based (last modified 04 Aug 2018).

Kandrup, N. & K.M. Iversen 2010: ClimateBasis Manual. – Asiaq.

Klaassen, M., Å. Lindström, H. Meltofte & T. Piersma 2001: Arctic waders are not capital breeders. – Nature 413: 794.

Landrum, L. & M.M. Holland 2020: Extremes become routine in an emerging new Arctic. – Nat. Clim. Chang. doi.org/10.1038/s41558-020-0892-z

Lee, W.Y. 2018: Bird observations in Siriuspasset, North Greenland, 2016 and 2017. – Dansk Orn. Foren. Tidsskr. 112: 53-58.

Lok, C.M. & J.A.J. Vink 2012: Trends and fluctuations in bird populations on the tundra at Cambridge Bay, Nunavut. – Can. Field-Nat. 126: 111-116.

Lyngs, P. 2003: Migration and winter ranges of birds in Greenland. An analysis of ringing recoveries. – Dansk Orn. Foren. Tidsskr. 97: 1-167.

MacKinnon, J., Y.I. Verkuil & N. Murray 2012: IUCN situation analysis on East and Southeast Asian intertidal habitats, with particular reference to the Yellow Sea (including the Bohai Sea). – Occasional Paper of the IUCN Species Survival Commission No. 47.

Martin, K. & K.L. Wiebe 2004: Coping Mechanisms of Alpine and Arctic Breeding Birds: Extreme Weather and Limitations to Reproductive Resilience. – Integr. Comp. Biol. 44: 177-185.

Meltofte, H. 1979: The population of waders Charadriidae at Danmarks Havn, Northeast Greenland, 1975. – Dansk Orn. Foren. Tidsskr. 73: 69-94.

Meltofte, H. 1985: Populations and breeding schedules of waders, Charadrii, in high arctic Greenland. – Meddr. Grønland / Monographs on Greenland, Bioscience 16.

Meltofte, H. 1998: Birds. Pp. 27-31 in: H. Meltofte & M. Rasch (eds): Zackenberg ecological research operations, 3rd annual report, 1997. – Danish Polar Center, Ministry of Research and Information Technology.

Meltofte, H. 2000: Birds. Pp. 32-39 in: K. Caning & M. Rasch (eds): Zackenberg ecological research operations, 5th annual report, 1999. – Danish Polar Center, Ministry of Research and Information Technology.

Meltofte, H. 2001: Wader population censuses in the Arctic: getting the timing right. – Arctic 54: 367-376.

Meltofte, H. 2003: Birds. Pp. 30-44 in: K. Caning & M. Rasch (eds): Zackenberg ecological research operations, 7th annual report, 2001. – Danish Polar Center, Ministry of Science, Technology and Innovation.

Meltofte, H. 2006a: Wader populations at Zackenberg, high-arctic Northeast Greenland, 1996-2005. – Dansk Orn. Foren. Tidsskr. 100: 16-28.

Meltofte, H. 2006b: Populations and breeding performance of divers, geese and ducks at Zackenberg, northeast Greenland, 1995-2005. – Wildfowl 56: 129-151.

Meltofte, H. (ed.) 2013: Arctic biodiversity assessment. Status and trends in Arctic biodiversity. – Conservation of Arctic Flora and Fauna, Akureyri.

Meltofte, H. & T.B. Berg 2004: Post-breeding phenology of waders in central NE Greenland. – Wader Study Group Bull. 104: 22-27.

Meltofte, H. & L. Dinesen 2010: Population densities of birds in Ørsted Dal, NE Greenland, 2009. – Dansk Orn. Foren. Tidsskr. 104: 59-72.

Meltofte, H. & T.T. Høye 2007: Reproductive response to fluctuating lemming density and climate of the Long-tailed Skua *Stercorarius longicaudus* at Zackenberg, Northeast Greenland, 1996-2006. – Dansk Orn. Foren. Tidsskr. 101: 109-119.

Meltofte, H. & M. Rasch 2008: The study area at Zackenberg. Pp. 101-110 in: H. Meltofte, T.R. Christensen, B. Elberling, M.C. Forchhammer & M. Rasch (eds): High-Arctic ecosystem dynamics in a changing climate. – Advances in Ecological Research 40, Academic Press.

Meltofte, H., T.T. Høye, N.M. Schmidt & M.C. Forchhammer 2007a: Differences in food abundance cause inter-annual variation in the breeding phenology of High Arctic waders. – Polar Biology 30: 601-606.

Meltofte, H., B. Sittler & J. Hansen 2007b: Breeding performance of tundra birds in High Arctic Northeast Greenland 1987-2007. Pp. 45-53 in: M.Y. Soloviev & P.S. Tomkovich: Arctic Birds. – Newsletter of International Breeding Conditions Survey, No. 9.

Meltofte, H., T. Piersma, H. Boyd, B. McCaffery, B. Ganter *et al.* 2007c: Effects of climate variation on the breeding ecology of Arctic shorebirds. – Meddr. Grønland / Monographs on Greenland, Biosci. 59: 1-48.

Meltofte, H., T.T. Høye & N.M. Schmidt 2008: Effects of food availability, snow and predation on breeding performance of waders at Zackenberg. Pp. 325-343 in: H. Meltofte, T.R. Christensen, B. Elberling, M.C. Forchhammer & M. Rasch (eds): High-Arctic ecosystem dynamics in a changing climate. – Advances in Ecological Research 40, Academic Press.

Meltofte, H., J. Durinck, B. Jakobsen, C. Nordstrøm & F.F. Rigét 2019: Trends in the autumn passage numbers of Arctic and boreal waders in W Denmark 1964-2017 as a contribution to East Atlantic Flyway population trends. – Ardea 107: 197-211.

Meltofte, H., J. Hansen & F. Rigét submitted: Trends in breeding performance in wader populations at Zackenberg, high Arctic Greenland, in relation to environmental drivers 1996-2018.

Mortensen, C.E. 2000: Population densities of breeding birds in Jameson Land, East Greenland, 1984-1988. – Dansk Orn. Foren. Tidsskr. 94: 29-41. (Danish, with English summary)

Pattie, D.L. 1990: A 16-Year Record of Summer Birds on Truelove Lowland, Devon Island, Northwest Territories, Canada. – Arctic 43: 275-283.

Pellissier, L., H. Meltofte, J. Hansen, N.M. Schmidt, M.P. Tamstorf *et al.* 2013: Suitability, success and sinks: how do predictions of nesting distributions relate to fitness parameters in high arctic waders? – Diversity and Distribution 19: 1496-1505.

Piersma, T., H. Meltofte, J. Jukema, J. Reneerkens, P. De Goeij & W. Ekster 2006: A single year comparison of two methods of censusing breeding Red Knot and Sanderling in High Arctic Greenland. – Wader Study Group Bull. 109: 83-87.

Piersma, T., T. Lok, Y. Chen, C.J. Hassell, H.-Y. Yang *et al.* 2016: Simultaneous declines in survival of three shorebird species signals a flyway at risk. – J. Appl. Ecol. 53: 479-490.

Rauch, J. & V. Johnston 2012: Yukon North Slope and Mackenzie Delta. Pp. 97-111 in: J. Bart & V. Johnston (eds.): Arctic shorebirds in North America: a decade of Monitoring. – Studies in Avian Biology no. 44, University of California Press, Berkeley.

Reneerkens, J., A. Benhoussa, H. Boland, M. Collier, K. Grond *et al.* 2009: Sanderlings using African-Eurasian flyways: a review of current knowledge. – Wader Study Group Bull. 116: 2-20.

Reneerkens, J., P. van Veelen, M. van der Velde, P. Luttikhuizen & T. Piersma 2014: Within-population variation in mating system and parental care patterns in the Sanderling (Calidris alba) in northeast Greenland. – Auk 131: 235-247.

Robinson, R.A., S.R. Baillie & H.Q.P. Crick 2007: Weather-dependent survival: Implications of climate change for passerine population processes. – Ibis 149: 357-364.

Ryabitsev, V.K. & N.S. Alekseeva 1998: Nesting density dynamics and site fidelity of waders on the middle and northern Yamal. – International Wader Studies 10: 195-200.

Saalfeld, S.T. & R.B. Lanctot 2015: Conservative and opportunistic settlement strategies in Arctic-breeding shorebirds. – Auk 132: 212-234.

Salomonsen, F. 1950: Grønlands Fugle The Birds of Greenland. – Einar Munksgaard, København.

Schmidt, N.M., T.B. Berg, M.C. Forchhammer, D.K. Hendrichsen, L.A. Kyhn *et al.* 2008: Vertebrate predator-prey interactions in a seasonal environment. Pp. 345-370 in: H. Meltofte, T.R. Christensen, B. Elberling, M.C. Forchhammer & M. Rasch (eds): High-Arctic ecosystem dynamics in a changing climate. – Advances in Ecological Research 40, Academic Press.

Schmidt, N.M., R.A. Ims, T.T. Høye, O. Gilg, L.H. Hansen *et al.* 2012a: Response of an arctic predator guild to collapsing lemming cycles. – Proc. Royal Soc. B: Biol. Sci. 279: 4417-4422.

Schmidt, N.M., D.K. Kristensen, A. Michelsen & C. Bay 2012b: High Arctic plant community responses to a decade of ambient warming. – Biodiv 13: 191-199.

Schmidt, N.M., L.H. Hansen, J. Hansen, T.B. Berg & H. Meltofte 2019a: BioBasis. Conceptual design and sampling procedures of the biological monitoring programme within Zackenberg Basic, 22th edition. – Department of Bioscience, Aarhus University.

Schmidt, N.M., J. Reneerkens, J.H. Christensen, M. Olesen & T. Roslin 2019b: An ecosystem-wide reproductive failure with more snow in the Arctic. – PLoS Biol https://doi.org/10.1371/journal.pbio.3000392

Seneviratne, S.I., N. Nicholls, D. Easterling, C.M. Goodess, S. Kanae *et al.* 2012: Changes in climate extremes and their impacts on the natural physical environment. Pp. 109-230 in: C.B. Field, V. Barros, T.F. Stocker, D. Qin, D.J. Dokken *et al.* (eds): Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. – Cambridge University Press.

Skov, K., C. Sigsgaard, M.R. Mylius & M. Lund 2018: GeoBasis. Guidelines and sampling procedures for the geographical monitoring programme of Zackenberg Basic. – Department of Bioscience, Aarhus University & Department of Geosciences and Natural Resource Management, University of Copenhagen.

Smith, P.A., L. McKinnon, H. Meltofte, R.B. Lanctot, A.D. Fox *et al.* 2020: Status and trends of tundra birds across the circumpolar Arctic. – Ambio 49: 732-748.

Stewart, L., C.E. Simonsen, J.-C. Svenning, N.M. Schmidt & L. Pellissier 2018: Forecasted homogenization of high Arctic vegetation communities under climate change. – Journal of Biogeography 45: 2576-2587.

Studds, C.E., B.E. Kendall, N.J. Murray, H.B. Wilson, D.I. Rogers *et al.* 2017: Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. – Nature Com. 8: 14895.

Szabo, J.K., P.F. Battley, K.L. Buchanan & D.I. Rogers 2016: What does the future hold for shorebirds in the East Asian–Australasian Flyway? – Emu 116: 95-99.

Tagesson, T., M. Mastepanov, M. Tamstorf, L. Eklundh, P. Schubert *et al.* 2012: High-resolution satellite data reveal an increase in peak growing season gross primary production in a high-Arctic wet tundra ecosystem 1992-2008. – Int. J. Appl. Earth Obs. 18: 407-416.

Taylor, A.R., R.B. Lanctot & R.T. Holmes 2018: An evaluation of 60 years of shorebird response to environmental change at Utqiagvik (Barrow), Alaska. Pp. 312-330 in: W.D. Shuford, R.E. Gill Jr. & C.M. Handel (eds): Studies of Western Birds 3. – Western Field Ornithologists, Camarillo, CA.

van Gils, J.A., S. Lisovski, T. Lok, W. Meissner, A. Ożarowska *et al.* 2016: Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. – Science 352(6287): 819-821.

van Roomen, M., S. Nagy, G. Citegetse & H. Schekkerman 2018: East Atlantic Flyway Assessment 2017: the status of coastal waterbird populations and their sites. – CWSS, Wilhelmshaven, Wetlands International, Wageningen, BirdLife International, Cambridge.

Ward, M.P., K.W. Stodola, J.W. Walk, T.J. Benson, J.L. Deppe & J.D. Brawn 2018: Changes in bird distributions in Illinois, USA, over the 20th century were driven by use of alternative rather than primary habitats. – Condor 120: 622-631.

Wauchope, H.S., J.D. Shaw, Ø. Varpe, E.G. Lappo, D. Boertmann *et al*. 2017: Rapid climate-driven loss of breeding habitat for Arctic migratory birds. – Global Change Biology 23: 1085-1094.

Weiser, E.L., R.B. Lanctot, S.C. Brown, H.R. Gates, R.L. Bentzen *et al.* 2018: Environmental and ecological conditions at Arctic breeding sites have limited effects on true survival rates of adult shorebirds. – Auk 135: 29-43.

Yoccoz, N.G. 1991: Use, overuse, and misuse of significance tests in evolutionary biology and ecology. – Bulletin of the Ecological Society of America 72: 106-111.

Authors' address
Department of Bioscience (mel@bios.au.dk), Aarhus University,
Frederiksborgvej 399, DK-4000 Roskilde, Denmark