

# Differences in food abundance cause inter-annual variation in the breeding phenology of High Arctic waders

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**Abstract** Previous work has shown that High Arctic waders in Greenland are “income breeders”, i.e. the resources used for egg formation are based almost entirely on biomass obtained on the breeding grounds. Thus, their breeding phenology is expected to be highly sensitive to inter-annual variation in food abundance during the pre-laying period. Early spring snow-cover may also influence timing of egg-laying either directly or mediated through food resources. Here, we report on the inter-annual variation in clutch initiation of three wader species breeding in High Arctic Greenland, Sanderling (*Calidris alba*), Dunlin (*Calidris alpina*) and Ruddy Turnstone (*Arenaria interpres*), in relation to spring snow-cover and spring arthropod abundance over ten breeding seasons at Zackenberg Research Station 1995–2005. Food abundance had the strongest effect on timing of clutch initiation, while the proportion of snow-free land had a weaker but still significant effect, i.e. more food and more snow-free land both result in earlier egg-laying. We hypothesize that food is most important when there is sufficient snow-free land to nest on, while snow-cover is of increasing importance in years with late snowmelt.

## Introduction

Spring snow-cover may delay clutch initiation in Arctic waders, Charadrii, to such an extent that waders in the northernmost land on Earth, the polar desert of Peary Land in northernmost Greenland, breed earlier than waders in many other parts of the Arctic, where spring snow-cover is deeper and more extensive (Meltofte 1976, 1985). In High Arctic Greenland, the difference in median laying dates between sites and years vary by up to 2–3 weeks, and the total laying period span more than 1 month (Green et al. 1977; Meltofte 1985, 2005). Since few studies have followed breeding Arctic wader populations over multiple years, the causal factors behind this variation have never been analysed. Hypotheses explaining this variation include: (1) snow-cover per se may prevent early egg-laying, (2) food abundance per se or (3) mediated through timing of snowmelt may be the governing factor (Meltofte 1985). Snow cover may have another indirect effect, since predation on eggs may be heavy on small snow-free patches, forcing the waders to wait (Byrkjedal 1980).

Since Arctic breeding waders are income breeders (Klaassen et al. 2001; Morrison and Hobson 2004) and, hence, highly sensitive to environmental changes in the pre-laying period, we examined concurrently, the relative importance of inter-annual variation in spring food abundance and spring snow-cover on clutch initiation during ten seasons at one site in High Arctic Greenland.

## Materials and methods

As part of the BioBasis monitoring programme at Zackenberg Research Station (74°30'N, 20°30'W) in

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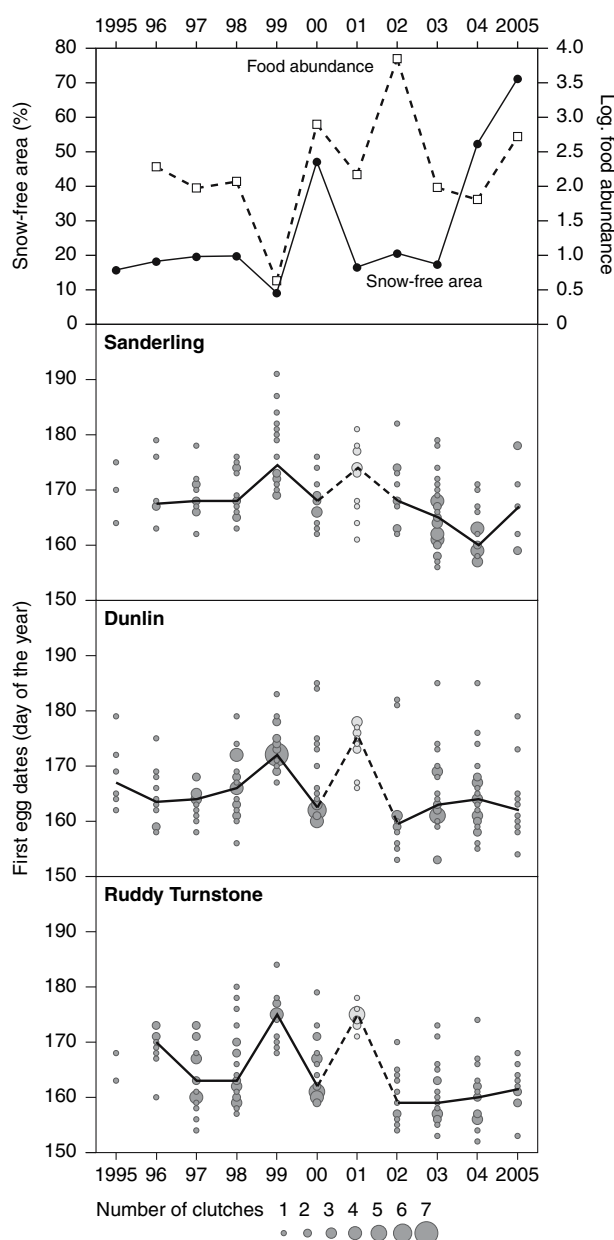
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central NE Greenland, the breeding phenology and success of waders have been monitored since 1995 (<http://biobasis.dmu.dk>). Based on records of incomplete clutches, egg-floating, hatching and weight of chicks found (Meltofte and Berg 2004), clutch initiation dates were estimated for a total of 477 clutches of Sanderling (*Calidris alba*), Dunlin (*Calidris alpina*) and Ruddy Turnstone (*Arenaria interpres*) between 1995 and 2005. Data from 2001 were omitted from the analyses, since almost all clutches recorded were relays after a snowstorm in mid June (Meltofte 2003). The remaining number of first egg dates available for the egg laying phenology analysis was 130 Sanderlings, 167 Dunlins and 143 Ruddy Turnstones (Fig. 1). Clutch size was known for 315 clutches from all seasons 1995–2005.

The snow-cover on June 10 was chosen as an index of spring snow conditions, since this is close to the earliest median 1st egg dates in waders in High Arctic Greenland (Meltofte 1985). In an area of 17 km<sup>2</sup> below 300 m a.s.l. in the bird monitoring area at Zackenberg (cf. Meltofte 2006), June 10 snow-cover percentage during the years 1995–2005 was measured from satellite images 1995–1997 and photos taken from a height of 480 m a.s.l. overlooking the study area 1998–2005 (Meltofte 2005 and unpubl.; Sigsgaard et al. 2005). Across 1995–2005, the mean snow-cover on June 10 was 72% and ranged between 29 and 91% (Fig. 1).

During the years 1996 through 2005 an index of arthropod food abundance was obtained from catches of Diptera (mainly Chironomidae and Muscidae) and spiders (mainly Linyphiidae and Lycosidae) in eight yellow pitfall traps, each 10 cm in diameter, situated in a fen centrally in the study area, which was extensively used as a communal pre-breeding feeding area by all three wader species and hence, considered representative for their feeding conditions before egg-laying. Traps were emptied once a week and the sum of the two weekly catches per trap day between June 3 and 17 were used (Fig. 1; Meltofte and Berg 2004).

In order to examine the potential change in the relative statistical importance of the various model predictors as the breeding season progresses, we used five response measures of clutch initiation for each species and year, reflecting the phenology in clutch initiation dates: the earliest date of clutch initiation observed in a given year (MIN), the date at which 25% of the birds had initiated their clutch (1QUART), the median (MEDIAN) where 50% of all clutches had been initiated, third quartile (3QUART) where 75% of the clutches had been initiated, and finally the latest observed clutch initiation date (MAX). Each response measure of clutch initiation was analysed in a General



**Fig. 1** Annual snow free proportion of land on June 10 and food abundance (natural log, transformed abundance (ind/2d) of Diptera and spiders caught between June 3 and 17) together with 1st egg dates (day of the year, incl. median 1st egg dates) of three species of waders at Zackenberg, Northeast Greenland, 1995–2005. Note the *dashed lines* in the three lower panels, indicating the omitted 2001 data

Linear Model (GLM) with species, log-transformed arthropod food abundance (FOOD), percentage snow-free land (SNOW-FREE), together with all their interactions as model predictors. To avoid pseudo-replication, we included YEAR as random factor in the analyses. These initial full models were reduced by successive removal of non-significant parameters, starting with the higher order interactions. As post hoc test we used Tukey HSD (honestly significant differenced) with

$\alpha = 0.05$  (Quinn and Keough 2002). We tested for collinearity among predictor variables (FOOD and SNOW-FREE) by Pearson correlation analysis.

To quantify the intra-annual variation in clutch initiation dates we calculated the standard deviation (SD) in all clutch initiation dates for each species per year. Low SD indicates more synchronous clutch initiation within season and vice versa. We analysed these SD's as a response variable in GLM's with species, MEDIAN and their interaction as predictors. Finally, we investigated the possible consequences of late breeding on clutch size. We did this by categorizing the clutches as either full (four eggs) or partial (less than four eggs—most often three). We tested whether the proportion of these two groups were dependent on nest initiation date or year for each species. We constructed a logistic model for each species with the predictors: clutch initiation date, year and their interaction; as in other analyses, full GLMs were reduced by removing non-significant terms successively.

**Results**

The very earliest egg-laying recorded was around June 1 and the latest in early July in all three species (Fig. 1). Median laying dates varied from around June 8 in the earliest breeding seasons until around June 22 in the latest, also in all three species. On average, Ruddy Turnstones were earliest, with Dunlins less than 1 day later and Sanderlings the latest with up to 5 days later egg-laying than Dunlins in the five measures of laying phenology (Table 1).

Across years, increasing arthropod food abundance and increasing proportion of snow-free land in early

June led to significantly earlier clutch initiation dates in all three species (Table 1; Fig. 2). Food abundance, snow-free land and their interaction all had significant influence, except on the very latest clutches (MAX). The random factor YEAR was never present in the final models. The significant and positive interaction term in the reduced models indicates that their effects are not independent. At high levels of food abundance and early snowmelt nest initiation dates are not as early, and at low levels of food abundance and late snowmelt nest initiation dates are not as late as a model with the same values of the main effects but without the interaction term would predict. The models without the interaction term and models without both the interaction term and snow-free land as main effect had similar AIC<sub>c</sub>. Both of these models had consistently lower AIC<sub>c</sub> than models without both the interaction term and food abundance as main effect (Table 1). This indicates that food abundance was better at explaining variation in clutch initiation dates than both snow-free land and the interaction between food abundance and snow-free land. The proportion of snow-free land and food abundance were not correlated ( $r = 0.319$ ;  $P = 0.404$ ).

During the study period, the standard deviation (SD) in clutch initiation dates decreased with median date for the Dunlin (0.383 per day;  $F_{1,8} = 7.260$ ;  $P = 0.027$ ), but not significantly so for Ruddy Turnstone (0.093 per day;  $F_{1,8} = 2.60$ ;  $P = 0.146$ ). For Sanderling the SD in clutch initiation date increased non-significantly with median date (0.126 per day;  $F_{1,8} = 1.03$ ;  $P = 0.339$ ). There were no differences in average SD across years for the three species ( $F_{2,27} = 1.444$ ;  $P = 0.254$ ).

In both Sanderling and Dunlin, clutch size decreased significantly with clutch initiation date (Sanderling:

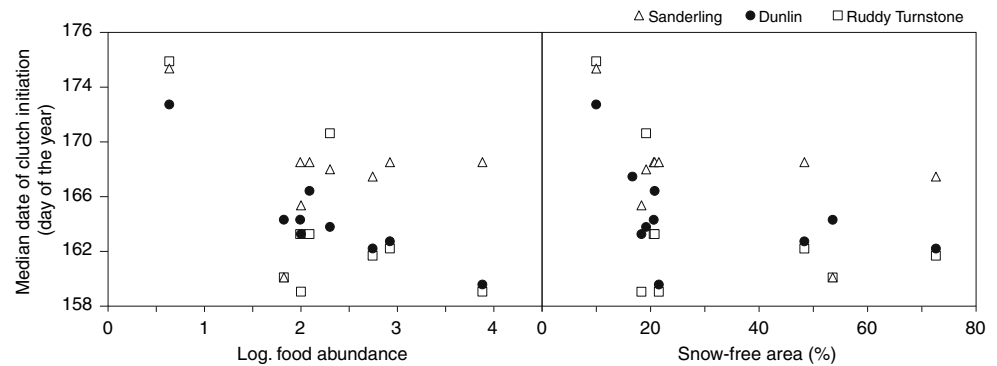
**Table 1** Model statistics and parameter estimates of final reduced linear models of clutch initiation dates (presented as day of the year) in five stages of egg-laying: the earliest date of clutch initiation observed in a given year (MIN), the date at which 25% of

the birds had initiated their clutch (1QUART), the median (MEDIAN) where 50% of all clutches had been initiated, third quartile (3QUART) where 75% of the clutches had been initiated, and finally the latest observed clutch initiation date (MAX)

Response	Predictor coefficients							AIC <sub>c</sub>			
	Intercept	Species			Food	Snow-free	Food × Snow-free	Final model	Food × Snow-free	Food	Snow-free
		Sanderling	Dunlin	Turnstone							
MIN	176.85	0 <sup>c</sup>	-4.333 <sup>b</sup>	-4.778 <sup>a</sup>	-5.981	-0.5555	0.2033	134.5	142.2	148.7	140.1
1QUART	180.11	0 <sup>c</sup>	-2.917 <sup>b</sup>	-3.806 <sup>a</sup>	-5.845	-0.5176	0.1840	131.8	138.7	146.9	137.7
MEDIAN	182.12	0 <sup>c</sup>	-3.278 <sup>b</sup>	-3.722 <sup>a</sup>	-5.814	-0.4841	0.1769	131.0	137.5	146.5	135.2
3QUART	187.76	0 <sup>c</sup>	-4.556 <sup>b</sup>	-4.917 <sup>a</sup>	-6.089	-0.5444	0.1974	135.8	142.5	149.9	140.6
MAX	178.50	0 <sup>c</sup>	1.500 <sup>b</sup>	-4.300 <sup>a</sup>	-	-	-	158.0	-	-	-

Full models included the effects of species, food abundance, the proportion of snow-free land and all their interactions and year as random factor. For the three species, different letters denote significant differences among species. Parameter estimates are given for significant predictors only and tests are based on type III sums of squares. AIC<sub>c</sub> estimates are given for final models and for models where each of the significant predictors was excluded. The excluded predictor is given as heading. For models without main effects the interaction term was not included

**Fig. 2** The relationship between median 1st egg dates (day of the year) of three species of waders and annual food abundance (natural log. transformed abundance (ind/2d) of Diptera and spiders caught between June 3 and 17) and snow free proportion of land on June 10, respectively



Wald Chi-square = 4.524;  $P = 0.033$ ; Dunlin: Wald Chi-square = 5.132;  $P = 0.024$ ), while this was not so in Ruddy Turnstone (Wald Chi-square = 2.732;  $P = 0.098$ ). For Dunlins, the probability of a full clutch approximately halved from earliest to latest clutch initiation date.

## Discussion

Spring snow cover has been considered the prime determinant of initiation of egg-laying in Arctic waders (Meltofte 1976, 1985; Green et al. 1977). While this may be true in areas and years with much snow, our results suggest that inter-annual variation in timing of egg-laying is determined mainly by food availability during the pre-laying period. Already Högstedt (1974) showed that the length of the period from arrival until egg-laying was negatively correlated with the abundance of earthworms in a temperate breeding wader, the Northern Lapwing (*Vanellus vanellus*). Likewise, Nol et al. (1997) found that clutch completion dates in sub-Arctic nesting Semipalmated Plovers (*Charadrius semipalmatus*) were negatively correlated with average temperatures during pre-laying and attributed this to food abundance. Supplementary food provided experimentally prior to breeding significantly advances egg-laying in a large number of bird species (see review by Meijer and Drent 1999). That Arctic-breeding waders could be under influence of similar constraints became even more obvious after the discovery—among others based on material from Zackenberg—that they rely on local arthropod resources for production of eggs (Klaassen et al. 2001; Morrison and Hobson 2004).

In most years at Zackenberg, many territories are inaccessible early in the season due to snow-cover, and the earlier arriving individuals nest on the earliest snow-free patches, which are much the same from year to year. Hence, it seems likely that late snowmelt would postpone breeding over extensive areas, whereas in years where snow-free areas are widespread

by the time birds arrive on the breeding grounds, the availability of food resources will be the limiting factor for timing of egg-laying.

Arctic waders have limited ability to predict conditions on the breeding grounds prior to arrival. In High Arctic Greenland, they arrive during late May and early June each year, and many do not arrive until after the initial laying dates in years with early breeding (Rosenberg et al. 1970; Meltofte 1985, 2001). Since waders need a minimum of 5–8 days after arrival to produce eggs (Roudybush et al. 1979), egg-laying before June 1 (median around June 8) is probably not physiologically possible no matter how early the snow melts and how abundant food is. This also fits our interpretation of the significant and positive interaction term between snow-free area and food abundance in the models of clutch initiation date. It indicates that in years of favourable food and snow conditions clutch initiation is later than a model with no interaction term would predict.

The multi-annual life cycles of Arctic arthropods means that the abundance of invertebrate prey on the Arctic tundra in spring is a function of both current weather conditions and the population size of arthropod cohorts in the previous seasons (Hodkinson et al. 1996). This may be the reason why snow cover and food abundance were not correlated in our study. We found that food abundance is more important than snow cover for timing of egg-laying throughout the laying period. However, snow cover may be important for timing of egg-laying at Zackenberg in years of late snowmelt (Fig. 2). Indeed, if we restrict our analyses of clutch initiation date to years where the proportion of snow-free land falls below 25%, snow cover is the only significant predictor in models of all measures of timing of clutch initiation except the very last nest (MAX). Following this, we hypothesize that food is the most important factor, when there is sufficiently snow-free land to nest on, while the effect of snow-cover increases in years of late snowmelt. Despite a relatively long study period, we still have too limited data for rigorous tests of such non-linear responses.

Additional factors not included in our analyses may be responsible for variation in clutch initiation date. For example, only “species” affected the termination of egg-laying (MAX), indicating species-specific evolutionary constraints to production of replacement clutches laid after loss of the initial clutch. Hence, the termination of egg-laying is probably set by ecological constraints resulting from the inability for late hatching young to grow sufficiently strong before autumn migration. Apparently, the biggest of the three species, the Ruddy Turnstone, has the earliest termination date. The result is that the total laying period is longer in early snow-free areas and years, since re-laying after loss of the initial clutch can take place longer after the initial clutch in such years (Green et al. 1977; Meltofte 1985). That we only found a significantly shorter laying period in late breeding seasons for Dunlin is probably the result of fewer replacement clutches found in the other species, simply because of smaller sample sizes.

Arthropod food abundance is important for breeding success of Arctic waders through its influence on resource limitation not only for the adults during egg formation, but also for chick growth (Nettleship 1973, 1974; Schekkerman et al. 2004). The timing of peak abundance of arthropod food for the chicks during summer is at least partly unpredictable for the adult waders at the time of egg-laying. Hence, it seems advantageous for them to initiate egg-laying as soon as conditions allow. There are several advantages of early breeding: the earlier an individual can breed, (1) the bigger chance of producing a full clutch of four eggs, (2) the more chances it has for re-nesting, if the initial clutch is lost, (3) the earlier it can leave the tundra and migrate to the temperate and tropical staging, moulting and wintering areas, and (4) the more time is available for its young to gain mass and skills prior to autumn migration, since winter in northern Greenland begins in September (e.g. Meltofte 1985, 2000; Nol et al. 1997; Sandercock et al. 1999; this study).

In addition, a large fraction of the wader populations may give up breeding at all in years with late snowmelt. At Zackenberg, we estimated that between one half and two thirds of the Ruddy Turnstones refrained from breeding in the very snow rich year of 1999 (Meltofte 2000). The critical value for the Zackenberg study area seems to around 15–20% snow free land in early June. This fraction will vary considerably between sites and regions, probably depending on average conditions.

Early breeding also incurs risks. Severe weather is more frequent and predation on eggs may be higher early in the season, when the extent of snow-free land is limited and thus easier for the foxes and other preda-

tors to scrutinize (Byrkjedal 1980; Meltofte et al. 1981). The effect of the relation between snowmelt and predation on timing of egg-laying is most likely inherited in the nest site selection behaviour of the birds, and it may be difficult to separate from the effect of snow cover per se. Timing of breeding in Arctic waders is clearly balanced between several factors, of which food abundance and snow-cover early in the season seem to be of great importance. Consequently, the expected changes in snow precipitation, spring temperatures and thereby spring snow-cover following climate change (Kattsov et al. 2005) may have pronounced and complex effects on wader breeding performance.

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