Arrival and pre-nesting period of the snow bunting *Plectrophenax nivalis* in East Greenland

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The first snow bunting males arrive in Northeast Greenland in early April, 6–8 weeks before nesting and 2–4 weeks ahead of the females. At this time temperatures regularly reach −25 to −30°C and snow storms may rage for days. The living conditions during this long-lasting pre-nesting period and its possible function are described and discussed. Based on 781 birds caught, ringed, and measured, and on observations on phenology, diurnal rhythm, night roosts, etc., it is shown that the age ratio in males is close to 50/50 first living year/adults, that adult males arrive and occupy territories earlier than first year males, that first-year males have shorter wings and are leaner than adult males, that the birds lose weight during spells of inclement weather early in the season, that diurnal rhythm is apparently governed by direct insolation, that males apparently greatly outnumber females in the populations, and that competition for the optimal territories is probably the selective force behind the prolonged pre-nesting period in males.

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Introduction

The snow bunting *Plectrophenax nivalis* breeds virtually throughout the ice-free parts of Greenland. It is probably the most common bird and the only passerine breeding in any numbers in the high arctic. Although no racial differences within Greenland have been accepted (Salomonsen 1951), two distinct populations exist. The snow buntings of high arctic Northeast Greenland winter in central Eurasia, while those of low arctic Southeast and West Greenland spend the winter in central North America (Fig. 1) (Salomonsen 1967, 1981). This migratory pattern probably reflects the origin of the populations. The migratory divide in North Greenland is found somewhere between Thule and Peary Land (Meltofte 1976a), and in the southeast probably a little south of Scoresby Sund (Salomonsen 1981) (Fig. 2). Some snow buntings, mainly males, winter in Southeast and Southwest Greenland (Salomonsen 1967; Pihl 1976, and this paper).

The male snow buntings arrive in East Greenland very early in the spring, up to two months before nesting and 2–4 weeks before the females. They appear in high arctic Greenland at a time when temperatures regularly reach −25°C to −30°C, and when severe snow storms may rage for days. Based on data obtained from several hundred catches of snow buntings during their pre-nesting period and on observations on phenology, diurnal rhythm, etc., I attempt in this paper to evaluate the living conditions of the birds during this period, and to trace possible reasons for their extremely prolonged pre-nesting period.

Materials and methods

In addition to already published arrival data, I have used first observation dates collected by weather station crews in East Greenland in 1974 and 1975. Large numbers of snow buntings were caught for ringing at Angmagssalik by Stig Jürgensen in 1974–76 and Bjørn Christensen in 1975, at Kap Tobin (Scoresby Sund) by myself in 1974 and by Bjørn Christensen in 1976, and at Danmarks Havn by myself in 1975 (see Table 2). Most birds were caught in cage traps in the spring with grain and seed for bait. The birds were collected when a sufficient number had been trapped. Very often some hours passed between each inspection of the traps. As far as possible birds were sex and age determined on criteria given by Svensson (1975) (see further below),

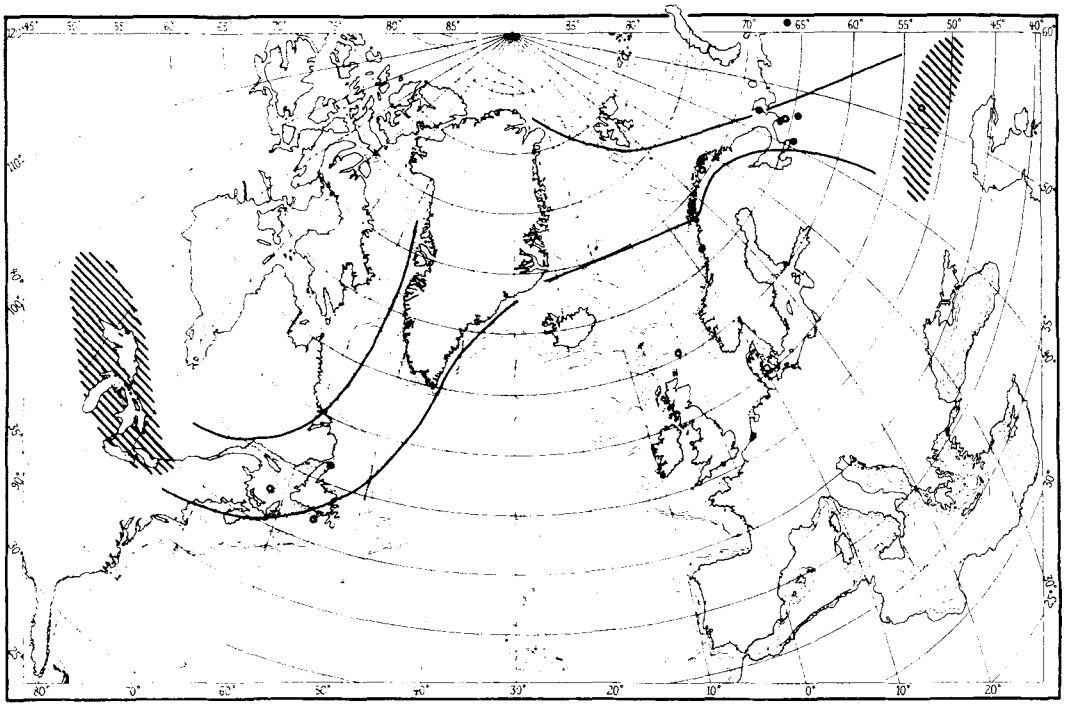

Fig. 1. Supposed wintering areas (hatched) and main migratory routes of Greenland snow buntings (after Salomonsen 1981). Recoveries of birds ringed in east Greenland are plotted. Open circles: autumn and winter; dots: recoveries during spring migration. All recoveries east of the Atlantic are of birds ringed at Danmarks Havn and Daneborg in Northeast Greenland. Those from Canada were ringed at Angmagssalik in Southeast Greenland.

and wings were measured flattened and straightened. At Danmarks Havn all birds, including retraps, were weighed with a 100 g spring balance. Observations were made on daily numbers, diurnal rhythm, roosting, etc., especially at Danmarks Havn in 1975.

According to Svensson (1975), snow buntings in their first year of life can be age determined by the extent of black or dark colour of the longest primary coverts. However, this applies to European populations, and according to Salomonsen (1931, 1951), the extent of dark colour on primary coverts differs much in subspecies. Therefore 22 adult and 130 juvenile and immature specimens in the Zoological Museum of Copenhagen, collected in Greenland in the autumn (adults after 1 August), were analysed with respect to this characteristic. The primary coverts are not moulted until the post-nuptial moult of the first summer, so birds showing juvenile characters in the autumn should be representative of first-year birds the next spring too, while first-summer birds have attained adult plumage after 1 August. All of the 94 males, except one adult and ten juveniles, were clearly distinguishable. Thirteen adults showed white or almost white primary coverts, and eighty juveniles had more or less black longest coverts. One adult male and ten juveniles had broad black tips on the longest primary coverts.

Thus, in accordance with Svensson (1975), there is a little overlap (about 10% being intermediate). The criteria given are valid for males in Greenland populations, too. In females, eight adults and fifty juveniles all showed dark or predominantly dark longest primary coverts. Although a certain difference could be seen between the two groups, the primary coverts could not be used for age determination of female snow buntings in Greenland. According to the European criteria, nearly all Greenland females should be in their first living year.

A certain number of errors, or at least differences, may be involved in the present material in the observers' separation of adult, first-year, and unageable males.

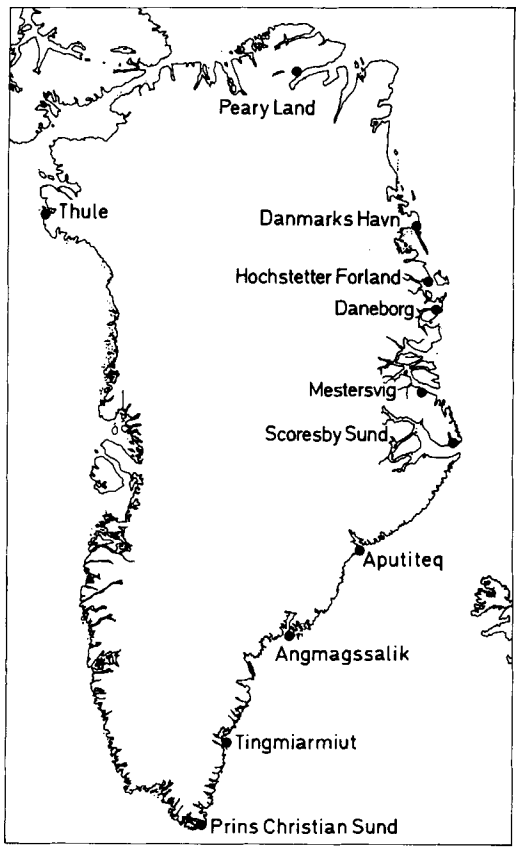

Fig. 2. Map of Greenland showing main localities mentioned in the text and in Table 1.

Results

Arrival

The first snow buntings arrive in South and West Greenland in late March and early April, earlier now than in the last century (Salomonsen 1951, 1967). In East Greenland, from Scoresby Sund and northwards, the first observations are usually made in the first or second week of April (Table 1), but in areas with few birds (e.g. Peary Land) or in late seasons (e.g. Germania Land 1939) no birds are seen until late April or even early May. The snow buntings in Southeast Greenland belong to the West Greenland population, and arrive a little earlier than those further north. Except for possible wintering individuals, the first birds at Angmagssalik are usually seen in March (Table 1). The early arrival at this place compared to most other areas in Greenland (Salomonsen 1951) could be caused by migrants to Iceland over-shooting their goal during spring migration.

The only reported observation of direct immigration was that of four birds arriving from the east-northeast at Havgårds Ø (80°N) in Northeast Greenland on 25 April 1970 (Sirius pers. comm.).

The first arrivals are males; the first females are not seen until late April or early May. At Danmarks Havn (Fig. 3) and Daneborg, the main influx of males takes place in late April and of females in early or mid May (Rosenberg et al. 1970; Meltofte 1975, 1977).

According to recoveries of birds ringed mainly during this study, spring migration is speedy. Four recoveries from the Archangelsk region in the northern Soviet Union are dated 8–20 April, and four recoveries from northern Norway are dated 6–25 April (see Fig. 1). Southeast Greenland birds have been recorded on Newfoundland until 20 April (see Luttik & Wattel 1979; Orr et al. 1980). At Bodø, northern Norway, flocks of several hundred (perhaps up to 10,000) individuals occur in April (J. Fjeldså, unpubl. data; see Vincent & Bédard 1976). The first flocks appear in late March. They reach a peak just after mid April and disappear in early May. This is closely in accordance with the arrival pattern for high arctic Greenland.

Annual time variation in first arrivals cannot be determined by weather conditions in high arctic Greenland itself, as the birds have to fly more than 1500 km non-stop across the sea from northern Norway; only the climate in the winter quarters and along the route can influence the progress of migration.

Danmarks Havn is located in an extremely favourable kettle-hole where flocks of snow buntings gather, particularly around the weather station, in April and May during the pre-nesting period. Pre-nesting concentrations in April were also observed at Daneborg (Conradsen 1957; Rosenberg et al. 1970), but in less favourable areas like Peary Land (Johnsen 1953) and Kap Tobin (Meltofte 1976b), only few birds were seen in April and larger numbers were not observed until early or mid May.

At Danmarkshavn Weather Station, the numbers of birds vary with the weather conditions

Table 1. Dates of first observation of snow buntings at localities in East Greenland (see Fig. 2). A. 1892–1965. B. 1969–1983.

A. Locality	1892–1965
Peary Land	1907 05 07, 1921 05 03, 1949 04 26, 1950 04 15
Germania Land (Danmarks Havn)	1907 04 05, 1908 04 05, 1939 05 02, 1951 04 13
Hochstetter Forland	1930 04 30
Wollaston Forland (Danesborg)	1954 04 07, c. 1955 04 21, 1964 04 11, 1965 04 16
Mestersvig	1964 04 11
Scoresby Sund	1892 04 21, pri. April 1925, 1928 03 26, 1929 04 05, 1933 04 12, 1935 04 06
Angmagssalik	Mean 1895–1915: 03 23[1] (range 03 13 – 04 04, N = 13), 1924 03 15, 1931 03 11

B. Locality	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
Peary Land					04 25	04 26								
Germania Land (Danmarks Havn)	04 13	04 05	04 18	04 07[2]	04 14	04 06	04 09	04 05	04 11	04 09	04 05	04 09	04 14	04 15
Wallaston Forland (Danesborg)	03 19	04 04				04 21	04 15[3]	03 22		04 11				
Mestersvig						04 16	04 25							
Scoresby Sund (Kap Tobin)						04 03	04 08[4]							
Aputiteq						04 02	04 02							
Angmagssalik						03 09[5]	[6]	04 02						
Tingmiarmiut						04 08	04 02							
Prins Christian Sund						04 08	[7]							

1. A few birds present all through winters 1913/14 and 1914/15.
2. Hvalrosodden 28 March.
3. Jackson Ø 9 April.
4. Stewart Ø c. 25 March.
5. Three birds all through winter.
6. Seven birds all through winter.
7. Some birds all through winter.

Data from Bay (1894), Manniche (1910), Koch (1925), Helms (1926), Pedersen (1926, 1930, 1942), Chapman (1932), Tcherniakofsky (1939), Petersen (1941), Johnsen (1953), Conradsen (1957), Rosenberg et al. (1970), Meltofte (1975), and this study.

(Fig. 3). On days with new snow and/or strong wind, large numbers of birds are attracted by the favourable feeding conditions near the houses where a very lush vegetation is found. In 1975 there was even plenty of food in the traps. On some days the number of individuals ringed outnumbered the number of birds counted. On 23 April 1975, for instance, up to 85 snow buntings were counted at one time, while 109 individuals were caught in the traps. After this date, most of the birds caught already carried rings, but after a new snow storm on 12–14 May, many new individuals appeared (Fig. 3).

Age composition in males

Table 2 shows that about half of the age-determined males were first-year individuals, and that the proportion of adults apparently decreased from April to May (only statistically significant for Angmagssalik: χ^2-test: $p < 0.01$). This may indicate both an earlier arrival of the adults, as already suggested by Salomonsen (1951) and Conradsen (1957), and an earlier dispersal (see below). The proportion of unidentified individuals includes both intermediately coloured birds and birds not age-determined. The sampling may not be fully representative, however, as first-year

Table 2. Sex and age composition of snow buntings caught for ringing at Danmarks Havn, Kap Tobin, and Angmagssalik in April and May 1974–76.

	April	%	May	%	Total	%
Danmarks Havn						
♂♂ adult	65	51	25	41	90	48
♂♂ 1st year	62	49	36	59	98	52
♂♂ total	180		64		244	
♀♀	6		12		18	
♂♂/♀♀ undet.	2		1		3	
Kap Tobin:						
♂♂ adult			56	44	56	44
♂♂ 1st year			72	56	72	56
♂♂ total			149		149	
♀♀			97		97	
♂♂/♀♀ undet.						
Angmagssalik:						
♂♂ adult	85	71	59	51	144	61
♂♂ 1st year	35	29	57	49	92	39
♂♂ total	120		130		250	
♀♀	2		12		14	
♂♂/♀♀ undet.	3		3		6	

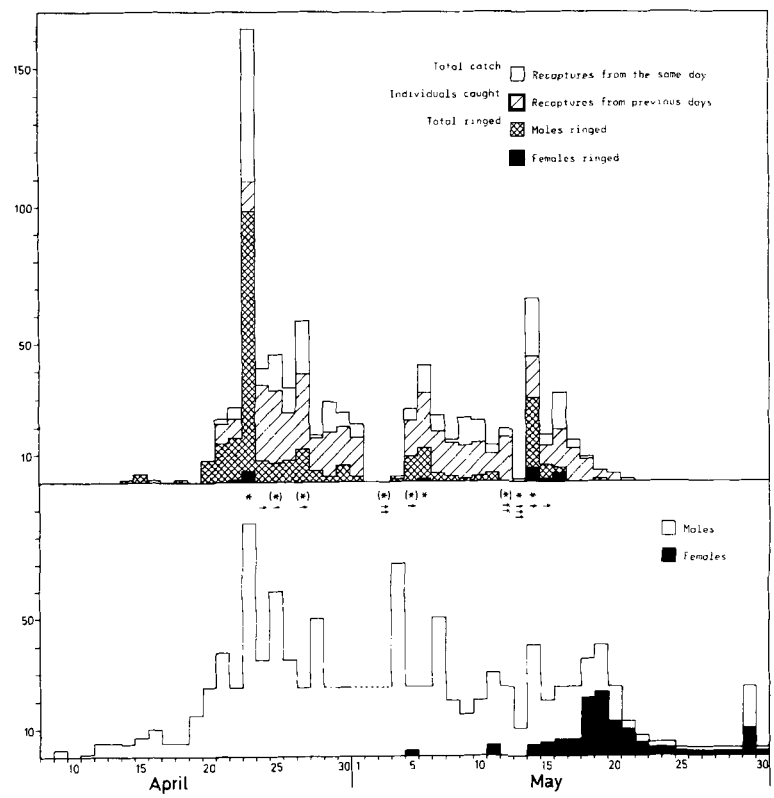

Fig. 3. Snow buntings at Danmarkshavn Weather Station in April and May 1975. *Lower part:* daily numbers of birds recorded. Snow fall and heavy wind are indicated. *: snow, (*): showers of snow, snow fall part of the day, or drifting snow,: →: about 15 knot wind per arrow. The proportion of females to males was estimated only, and females prior to mid May were clearly not sufficiently recorded, as individual females were caught from 22 April (see upper part). In 1970 the main immigration of females started about 5 May (Meltofte 1975).

Table 3. Age composition of snow buntings caught in good and inclement weather at Danmarks Havn in April and May 1975. (Days with inclement weather shown in Fig. 3. Only first-time caught individuals included.)

		April	(N)	May	(N)
Good weather	Adults	46	(39)	22	(18)
	1st y.	54		78	
Inclement weather	Adults	53	(88)	49	(43)
	1st y.	47		51	

birds may be trapped more readily than older individuals; first-year birds were retrapped more often and over longer periods than adults.

Table 3 shows that the proportion of adults increased in inclement weather, especially in May, and that the proportion of adults was much lower in good weather periods in May than in April, further confirming that adults disperse earlier than first-year birds but may gather into flocks again during spells of bad weather. However, due to the limited materials, these differences do not reach full statistical significance (χ^2-test). As Table 3 only includes first-time caught birds, the inclement weather sample may be the most representative for the age composition in male snow buntings in general, indicating a close to fifty-fifty first-year/adult ratio for males in the spring. This ratio fits in well with the age composition of 34 snow buntings ringed as pulli in Greenland and recovered the following year in Greenland (Salomonsen 1967). Fifteen were found as one-year olds and nineteen as older birds, indicating that roughly 40–50% of the summer population are one-year old birds. Custer & Pitelka (1977) present similar values for the Lapland bunting *Calcarius lapponicus* in arctic Alaska.

Apparently the single trap catches at Danmarks Havn were predominated by either first-year or adult birds, indicating that the two age groups stayed in more or less separate flocks. Unfortunately this was not tested.

Wing measurements

Wing measurements of 927 snow buntings from East Greenland are presented in Table 4. Males have significantly longer wings than females (Student's t-test: $p < 0.01$), and adult males have significantly longer wings than first-year males ($p < 0.01$). The material shows no statistically significant differences between the three trapping sites.

Body weights

Mean body weights of 259 first-time caught snow buntings at Danmarks Havn are presented in Table 5. Males were heavier than females (Student's t-test: $p < 0.01$), adult males were heavier than first-year males ($p < 0.05$), males caught in April were 4.8% lighter than males caught in May, and males caught during spells of inclement weather in April were 3.9% lighter than those caught in good weather periods. This was obviously not the case in May, and the difference between males in April and May is less pronounced (1.9%), when considering only birds caught in good-weather periods.

While the differences in body weight of adult males, first-year males, and females are statistically significant, the differences between April and May and between good and inclement weather due to great variance and small samples do not reach full statistical significance. These weights cannot be said to be fully representative, however, as lean and hungry individuals may be more easily caught; on the other hand, they had access to large amounts of food once inside the traps. But the relative differences should at least be indicative. The snow buntings seemed nervous and fed very eagerly in poor-weather periods.

Table 4. Wing measurements (in mm) of snow buntings caught at Danmarks Havn, Kap Tobin, and Angmagssalik during 1974–76. (At Danmarks Havn and Kap Tobin only birds from spring months April to June included, while material from Angmagssalik includes spring and autumn, July to September, measurements.)

	Danmarks Havn			Kap Tobin			Angmagssalik		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
♂♂ adult	113.4	2.9	92	113.3	2.4	56			
♂♂ 1st y.	110.7	2.5	100	110.3	2.5	72			
♂♂ total	112.1	3.0	247	111.3	2.9	148	111.3	2.8	348
♀♀	107.0	2.4	20	104.8	2.7	96	105.7	2.2	68

Table 5. Body weights (in g) of snow buntings caught in good and inclement weather (see Fig. 3) at Danmarks Havn in April and May 1975. Only first-time caught individuals included. For sample size, see Tables 2 and 3.

Sex	Weather	Age	April Mean	April S.D.	May Mean	May S.D.
♂♂	Good	Adult	41.9	4.9	(42.8)	
		1st y.	40.4	5.1	40.9	4.0
		Total	40.7	4.9	41.5	4.4
♂♂	Inclement	Adult	40.0	4.9	42.0	4.7
		1st y.	38.5	4.7	41.5	4.6
		Total	39.1	4.8	41.7	4.5
♂♂	Total		39.6	4.9	41.7	4.4
♀♀	Total			34.6	4.9	

Of the 259 snow buntings caught at Danmarks Havn during the pre-nesting period in 1975, 144 were retrapped 572 times. Individual birds were retrapped up to 33 times and up to 26 days after ringing, many being caught several times (maximum seven) in one day, especially during inclement weather. But the different age and weight groups showed large differences in this respect. Including retraps on the day of ringing, 71% of the first-year males were retrapped, but only 50% of the adults (χ^2-test: $p < 0.01$). When initially caught, adults and first-year birds retrapped later on weighed respectively 5% and 9% less than birds caught only once ($p < 0.05$ and $p < 0.01$, respectively, t-test).

Fig. 4 shows that retrapped males rapidly gained weight during the week after ringing, but lost weight during the first day. Initial weight loss was probably due to the severe weather prevailing when the majority of these birds were caught, and the succeeding increase reflects the better conditions during the following days, and especially perhaps the optimal feeding possibilities inside the traps. Twenty-one first-year males retrapped more than eight days after ringing ended up with a mean weight of 46.6 g (range 36-56 g), or 17% more than all first-time caught first-year males ($p < 0.01$). This final weight seems to be the maximum mean weight for first-year snow bunting males during this period, but may perhaps only be attained by birds having access to unlimited food resources (see below). These individuals specialized in feeding in the traps, and were only caught when taken by surprise. Otherwise they easily found their way out of the traps again.

A few birds were so exhausted when caught, that they probably did not survive; no males weighing less than 27 g were retrapped.

Diurnal rhythm and night roosts

Fig. 5 shows that during the pre-nesting period at Danmarks Havn in 1975, the snow buntings arrived and left the feeding area around the weather station and the traps almost symmetrically around solar zenith. No correlation was found with the daily air temperature cycle two metres above the ground. Thus probably the

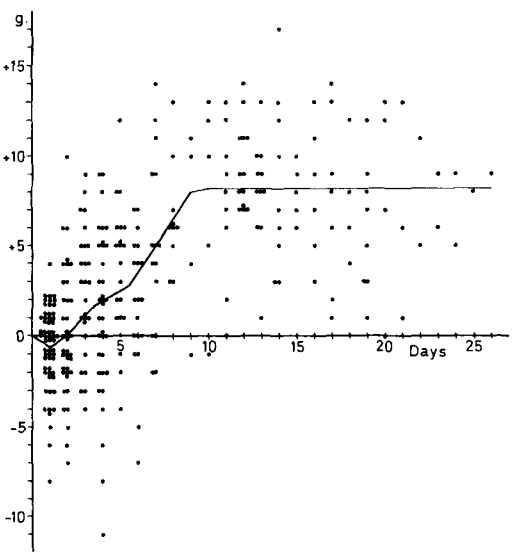

Fig. 4. Changes in body weight in male snow buntings after ringing at Danmarkshavn Weather Station, based on 381 recaptures of 110 individuals during April-May 1975. Only first captures each day used. Mean change shown as a solid line. After nine days the data were pooled for calculation of the mean.

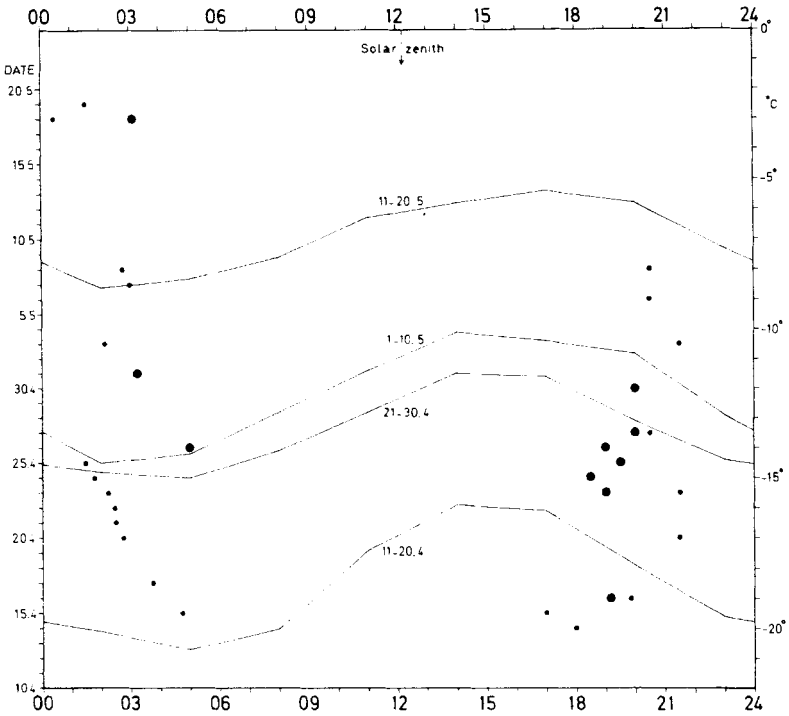

Fig. 5. Time of first and last observations of snow buntings on a number of days between 14 April and 19 May 1975 at the feeding areas around Danmarkshavn Weather Station (solid dots) together with the mean daily temperature oscillation per ten-day period (solid lines). Small dots indicate a few birds present, large dots more than ten birds present. Times given are local solar times, i.e. one hour after GMT. During period 11 April to 20 May maximum sun height increased from 21.5° to 33.2° over the horizon and the minimum height from −4.9° to 6.8°.

Fig. 6. Termometerfjeldet (138 m above sea level) at Danmarks Havn with the main night roost circled (26 April 1975). Even the cliffs a little higher to the right were sometimes used. Note the 'semi-snow-cover' on the plain in the foreground.

Fig. 7. The main night roost on Termometerfjeldet with ten snow buntings sitting in cracks and on the snow ridge in front of the cliff (see Fig. 8). Most birds flew off as I approached the cliff (26 April 1975).

direct insolation and thereby the conditions near the ground are the most decisive factors for the diurnal rhythm of the birds. At Danmarks Havn the sun is in the sky for 24 hours a day from 25 April; the average daily temperature oscillation in 1975 decreased from only 5°C in mid April to about 3°C in mid May, reaching a maximum during the afternoon and a minimum during the early morning hours (Fig. 5). Unfortunately, no measurements of the microclimate are available, but the daily oscillations are much more pronounced near the ground.

The snow buntings from the area at Danmarks Havn roosted on southwest exposed cliffs on Termometerfjeldet about 900 m northeast of the weather station (Figs. 6 and 7). The cliffs were exposed to the sun until 09:15 p.m. and again from 09:15 a.m. (local solar times). The prevailing winds (and storms) at Danmarks Havn blow from northern and northwesterly directions. The birds sat in narrow cracks in the cliffs (Fig. 7) and in scrapes made by the birds in the snow just behind the ridge of a snow fan half a metre in front of one of the cliffs (Fig. 8). The amount of droppings indicates that these sites were used regularly. From Quebec in Canada, Vincent & Bédard (1976) report similar night roost scrapes made by snow buntings on the lee side of snow drifts in the winter, but only when temperatures fell below −7°C. Here the distance between each scrape was about 2.5 m, however, and rarely less than 30 cm. Huddling did not occur even under extreme physical conditions.

During snow storms, snow buntings, like tetraonids, may let themselves be nearly covered with snow (in Norwegian: dokke) behind the edge of snow drifts (Meltofte 1975; see also Bagg 1943; Parmelee 1968; Marjakangas 1981; Thiede 1982). The very low number of birds present on the weather station during the severe snow storm (45 knots) on 13 May was thus caused by the fact that most birds would be seeking shelter and many probably remained on night roost throughout the day.

The birds flew to and from the roosts in groups of up to ten, and very often fed nearby for some time after arrival. Song, flight pursuits, and other antagonistic displays were often performed at the roost. On 24 April 40–50 individuals were present, about 35 on 26 April, and about 20 on 8 May;

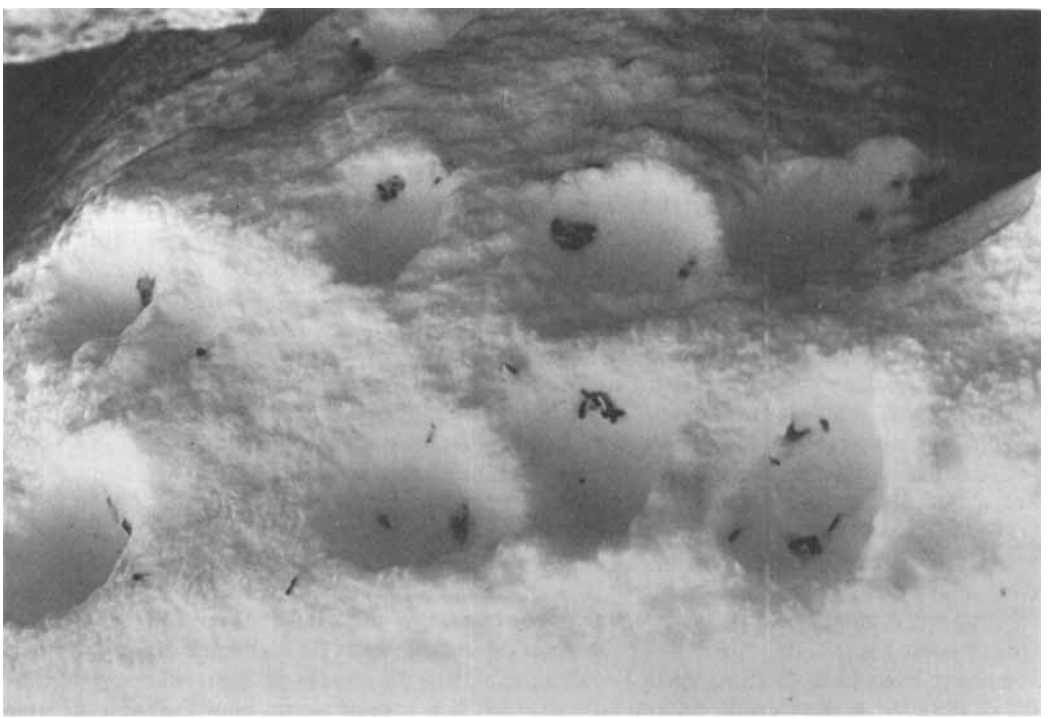

Fig. 8. Vertical photo of the scrapes behind the edge of the snow drift in front of the main night roost on Termometerfjeldet on 26 April 1975.

about the same numbers as estimated at the weather station on the corresponding days. By 21 May no birds were present at the roosts; thus, after dispersal and mating, the snow buntings did not roost there any more. Similarly, a communal roost on Rathbone Ø near Scoresby Sund, occupied by 80 snow buntings on 12 May, was left by 26 May (Ko de Korte in litt.). Parmelee & MacDonald (1960) made similar observations on Ellesmere Island, but elsewhere communal roosting, especially involving males, has been reported throughout the breeding season (Summers 1971, 1973; Swann 1975).

Dispersal and breeding phenology

Snow buntings were heard singing sporadically from arrival at Danmarks Havn in mid April 1975 and encounters took place on the feeding sites, especially around the traps. At Angmagssalik, where the first birds usually appear as early as March, singing does not start until mid April (Petersen 1908). Song intensified from the last days of April, as the males approached full nuptial plumage. It was my impression that newly arrived (unringed) males had a less developed nuptial plumage than 'residents'. Age differences may also be involved here. By mid May most males were in nuptial plumage, the bills having turned from yellow to dark grey. But a few were still more or less in winter plumage. From then on loose flocks were more frequent in the lowland around the weather station. Males highly outnumbered females in these flocks, while females increased to more than 50% of the birds present at the weather station (Fig. 3). Pairs appeared from about 20 May when the males had attained almost full nuptial plumage with only narrow light edges on black feathers. In late May the number of birds present in the lowland at Danmarks Havn reached a peak with more than one hundred individuals. Most birds still stayed in loose flocks, of which 76% of 165 sex-determined individuals were males. During the last few days of May flocks decreased in size and number; most birds appeared in pairs, and many males sang intensively.

During spells of bad weather, however, flocks formed again. Thus, during three days of severe snow storm from 16 to 18 June, up to 100 individuals gathered at the weather station; 80% of these were males. The birds sought shelter, some were nearly covered by snow, and others fed intensively. One fresh egg was found on the ground in open terrain.

In 1975, egg laying took place about mid June at Danmarks Havn. The first fledglings left the nests 12–13 July, the bulk of them about 16 July. This is in good accordance with statements from most of the high arctic Greenland, while most young in South and West Greenland fledge in late June (Salomonsen 1951).

Given a fledging period of 10–12 days, an incubation period of 12–13 days (Manniche 1910; Parmelee & MacDonald 1960), and one egg laid per day (Tinbergen 1939), most clutches were initiated in mid June and most young hatched during the last days of June and the first days of July. Earlier breeding has been found on a number of occasions in Northeast and North Greenland. Pairs have been seen several times from early May, and nest building has been observed in mid May. At Scoresby Sund an egg was found on 1 June and hatched pulli seen on 22 June (Pedersen 1930). At Daneborg, a clutch was hatched on 19 June, 1975 (Meltofte 1977), and newly hatched young were found on 20 June 1969 at Danmarks Havn (Meltofte 1975). In Peary Land, the northernmost land area in the world, fledglings have been seen as early as on 1, 4, 6, and 7 July of 1964, 1968, 1912, and 1949, respectively (Freuchen 1915; Johnsen 1953; Røen 1965; Andersen 1970).

Breeding may be considerably delayed under extreme conditions. In 1939, Pedersen (1942) found that the snow bunting flocks did not break up until the second half of June, and many individuals died during the pre-nesting period.

Discussion

The most striking feature of the snow bunting's pre-nesting period is the fact that the males arrive 2–4 weeks in advance of the females. They appear in high arctic Greenland at a time when temperatures regularly reach −25 to −30°C, when severe snow storms are common and most of the ground is snow covered. Not until late May do maximum temperatures regularly exceed zero. The main reason why snow buntings are able to survive at all in these extreme high arctic environments is probably the same as for many other animals: the fact that regular storms blow the snow off large areas, so that vegetable food is available throughout the year. Large areas are only covered with

what could be called a semi-snowcover, through which the seed spikes of grasses and sedges appear. From the time the first snow buntings arrive early in April, the heavy insolation causes much of the thin snow cover to evaporate. By absorbing the insolation the exposed seed spikes and other tall vegetation create snow free holes in the snow around them, which further increases the feeding possibilities for snow buntings.

After all, the climate is 'milder' in April than in March. Spring actually starts in early April when mean temperatures rise to above −20°C compared with −20 to −30°C throughout March.

Many authors have speculated about the function of the long-lasting pre-nesting period of the snow bunting (Salomonsen 1972). I am unable to provide anything but speculations either. Great differences in population densities exist, varying from more than five pairs per square kilometre in highly favourable areas, to nearly none or at least exceedingly thin populations in large, barren, 'rock-less', or late thawing areas. There is probably hard competition for the most favourable breeding sites. The males start to sing and occupy territories soon after arrival and long before the arrival of females. No doubt the optimal territories are occupied first, the competition for them being perfectly illustrated by the well developed display and fight system described in detail by Tinbergen (1939); some males even succeed in getting more than one female. During all of the pre-nesting period the birds gather into flocks again as soon as unfavourable weather conditions prevail. The birds often alternate between territorial and flock behaviour in the course of one single day (Tinbergen 1939; Rosenberg et al. 1970).

The majority of the less favourable breeding areas are not populated until early, mid or even late May, when the majority of the birds having spent the pre-nesting period in favourable areas like the kettlehole at Danmarks Havn, leave for other breeding areas. Only a small proportion of the locally breeding birds carried rings.

Thus it seems advantageous for the male snow buntings to arrive and occupy the most favourable territories as early as possible, but not so early that the advantage of optimal territories is counteracted by a too heavily increased mortality risk. The lacking pre-nuptial moult of the snow buntings (Salomonsen 1951) may be part of the adaption features making this strategy possible.

For female snow buntings the pre-nesting period lasts 2–5 weeks. In addition to time for competition for favourable breeding territories, for mating, etc., this period may be needed to give the females time to adjust the onset of breeding to the diversified local and annual environmental conditions, i.e. the progress of spring (Meltofte 1976a). This can hardly be the reason for the 6–8 weeks pre-nesting period for males, however, especially as they are prepared to copulate during a much longer period than the females (Tinbergen 1939).

Still another feature is striking. There are several indicia that males outnumber females in snow bunting populations. Bay (1894) observed that the great majority of birds seen at Scoresby Sund were males, and similarly Pedersen (1926) noted 'Eine gewisse Überzahl bei den Männchen'. These statements might have been based on observations during early spring when many snow buntings congregate around houses, etc., and only few females are present. But Summers (1973) found this obliquity even in late summer. Out of twenty snow buntings feeding scattered on the tundra, fourteen were males. In late May 1975, at a time when all females had arrived and most males should be defending territories, 76% of 165 sex-determined individuals feeding in loose flocks at Danmarks Havn were males. Among the juveniles kept in the Zoological Museum of Copenhagen, collected in Greenland in the autumn, when biased sampling among juveniles is less likely than in the spring, 64% are males. Of 38 Northeast Greenland juveniles 26 are males. In Peary Land (Meltofte 1976a) and on Hochstetter Forland (Meltofte et al. 1981) several male snow buntings have been heard singing in territories where females were never seen. The males left by late June or early July without any sign of breeding. Even on Baffin Island in Canada single and small groups of unmated males were seen in unfavourable areas (Watson 1957). All of this indicates a certain surplus of males in the populations, and that they establish territories in marginal areas. This further supports the idea that strong competition exists between the males both for favourable territories and for a mate at all.

Salomonsen (1951) states that one-year old males breed. Their later arrival, however, and dispersal and poorer physical condition in general (lower weight and shorter wings), make it likely that they constitute the main part of the marginal unmated males.

Similarly Custer & Pitelka (1977) found that

'floating' males of Lapland buntings were a conspicous sight at Point Barrow after about 20 June, and that they included an unknown proportion of non-breeders believed to have been mainly first-year individuals.

The males are bigger and heavier than the females and should thus be better equipped to sustain periods of inclement weather during their early pre-nesting period. Apparently they are able to maintain close to normal body weight even in April, but only under good weather conditions. During spells of bad weather in April weights drop, illustrating the unfavourable living conditions that male snow buntings have to face after arrival.

The body weights found for pre-nesting males are quite similar to weights found in July-September at Mestersvig (Green & Summers 1975), and also fit in well with weights given for both May and August in Peary Land (Møhl-Hansen 1947; Johnsen 1953).

Bentz (in litt.) recently studied staging snow buntings before their departure from northern Norway. A total of 151 males and 49 females weighed at Andøya on 19–25 April 1982 averaged 51.5 g and 44.7 g, respectively. Compared to the arrival weights in Northeast Greenland, this shows a pre-migratory fat gain of at least 30% in both sexes. The pre-migratory weights found by Bentz are closely in agreement with those found during the same period in the spring in captive (outdoor) snow buntings at Quebec in Canada (Vincent & Bédard 1976). Here the body weights increased very abruptly in March and April, from below 40 g to above 50 g (all birds grouped). Mean post migration weight in Canada was about 48 g, i.e. very close to the final weights of the snow buntings in the traps at Danmarks Havn.

Even though differences may be found from year to year and from place to place, the snow bunting populations breed highly synchronously. The main part of the broods hatch within a week or so (Meltofte 1977; Asbirk et al. manuscript). Onset of breeding may be triggered by the disappearance of the snow, i.e. when the feeding conditions (on arthropod prey) are improved for the females prior to and during egg laying (see Custer & Pitelka 1977; Morton 1978; Madsen 1982). This is further supported by the fact that pre-nesting snow buntings weigh significantly less than artificially fed birds during the same period (Vincent & Bédard 1976). Ultimately onset of breeding may even be governed by the time required for development including post-juvenile moult by the young before autumn migration (Asbirk et al. manuscript). Furthermore, most young hatch and are fed at the time of the season when arthropod prey is superabundant, i.e. from late June until the second half of July (Hussell 1972; Meltofte, unpubl.).

In Northeast Greenland song and other territorial behaviour cease at the time of hatching by early July. After fledging, family flocks stay together for about 10–12 days when the young are still fed (Asbirk et al. manuscript). The males leave, often to more mountainous areas for a very rapid moult during the second half of July and early August. During this period they may be almost flightless (see Green & Summers 1975). Females moult a little later. Flocks of up to 250 individuals may gather in August, the first appearing in late July, and numbers reach a peak in late August and early September. Most adults leave during the first half of September (Manniche 1910) and most immatures follow before the end of the month (Meltofte 1975). Single individuals are seen, however, until late October or even in November and December (Bird & Bird 1941).

Population densities in favourable areas have been estimated to about three pairs per square kilometre at Mestersvig (Vibe 1954; Ferns 1978), and more accurately censused to 4.7 pairs per square kilometer at Daneborg in 1964 (Rosenberg et al. 1970) and 5.6–5.8 pairs per square kilometre at Danmarks Havn in 1975 (Meltofte 1977). At Danmarks Havn, however, only 3.3–3.6 pairs per square kilometre were recorded breeding. Optimal breeding sites are rocky 'islands' or boulder screes near early thawing, moist, well vegetated areas.

The diurnal rhythm registered fits in well with observations made at the same time of the year on Ellesmere Island (Parmelee & MacDonald 1960) and is in relatively good agreement with the diurnal rhythm found in snow buntings during the nesting period at Mestersvig farther south in Northeast Greenland (Asbirk & Franzmann 1979). The daily activity pattern there was highly synchronized with the ground temperature oscillations, and thereby with arthropod activity.

The apparent seasonal increase in duration of daily activity seen in Fig. 5 may partly be a result of the increased number of birds present in April (Fig. 3). On a few occasions birds were actually at the weather station throughout the 'night'.

At Ny-Ålesund on Spitsbergen the snow bunt-

ings were found to roost during the afternoon and evening hours in June and July, and to leave the roosts around midnight (Swann 1975). These results indicate that both the endogenous rhythm and environmental stimuli, such as insolation intensity, weather, temperature and feeding conditions, may govern the diurnal rhythm (see Lennerstedt 1973).

Summary

Based on 781 snow buntings caught, ringed, and measured on three different sites in East Greenland in the spring, and on observations on phenology, diurnal rhythm, night roosts, etc., the characteristics and function of the pre-nesting period (that is the period from arrival until start of nesting) are described and discussed. The following main points are emphasized:

1. Two different populations exist in East Greenland: one in the high arctic northeastern part, wintering in central Eurasia, and one in the low arctic southeastern part wintering in central North America together with the West Greenland birds. These differences probably reflect the geographic origin of the two populations.
2. Males arrive 2–4 weeks ahead of females, and have a total pre-nesting period of 6–8 weeks.
3. Among the males there is a close to fifty-fifty adult/first-year ratio.
4. Adult males arrive and disperse, i.e. occupy territories earlier than first-year males.
5. First-year males have shorter wings and are generally leaner than adult males.
6. The birds lose weight during spells of inclement weather in April.
7. Communal roosting takes place during the pre-nesting period.
8. The diurnal rhythm is probably governed by direct insolation and not by air temperature.
9. The prolonged pre-nesting period of the males is probably a result of strong competition between males for the most favourable territories.
10. There are strong indications that males highly out-number females in the populations. The surplus of males probably occupy marginal territories and constitute mainly first-year birds.

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