Timing of breeding and reproductive success in a Lapland Bunting *Calcarius lapponicus* population in Eqalungmiut Nunaat, West Greenland.

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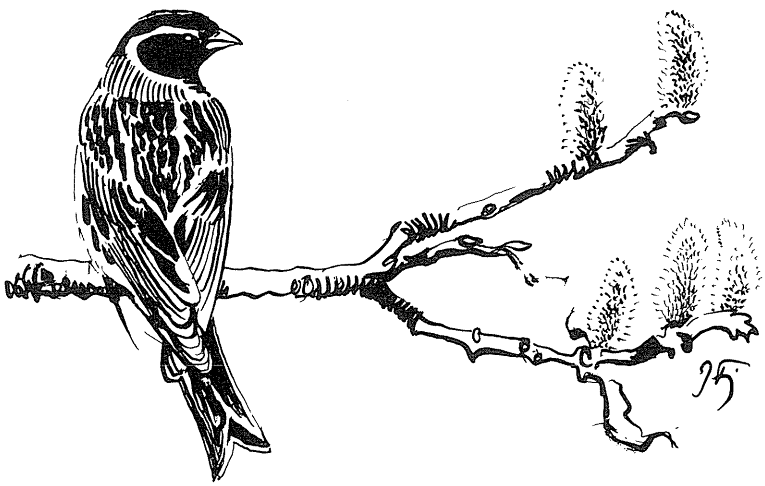
(Med dansk resumé: Laplandsværlingens tilrettelæggelse af ynglesæsonen og succes i Eqalungmiut Nunaat, Vestgrønland).



INTRODUCTION

Between 5 May and 20 August 1979, I took part in the »Greenland White-fronted Goose Study« expediton to Eqalungmiut Nunaat (67°32'N, 50°30'W) in the hinterlands of Nordre Srømfjord, West Greenland. During the 3½ month stay I studied the breeding of Lapland Buntings, the most numerous bird in the area.

Although the Lapland Bunting is one of the most common breeding passerines in the low arctic region of West Greenland (Salomonsen 1950) little is known of its breeding ecology here. Most studies of reproduction in arctic passerines have been carried out in Canada and Alaska (on Lapland Buntings, e.g. Williamson and Emison 1971, Hussell 1972, Custer and Pitelka 1977). The object of this paper is to present data on the timing of breeding and reproduction in the Eqalungmiut population of Lapland Buntings and to compare with results obtained in the North American populations. A description of nesting habitats is given in Madsen (1981a).

STUDY AREA

The study area was a low arctic, hilly, inland tundra, consisting of a broad south-facing valley system and surrounding plateau (above 3-400 m). In the valley the vegetation was fell heath with slopes of grass and widespread scrubs of *Betula nana* and *Salix* spp., the latter reaching a height of 1-2 m. On the plateau the fell heath vegetation was lower and often replaced by fell field and boulder field with patchy vegetation cover.

Table 1. Chronology of the breeding and moulting cycle. Moulting is measured by primary moult scores (P. Belman and D. A. Stroud pers. comm.). Dates give ranges.
Tabel 1. Kronologien af yngle- og fældecyklus. Fældningen er målt som håndsvingsfjerfældning. Datoerne angiver første og sidste dato.

14.–16. May	Peak arrival of ♂♂ *Største ankomst af ♂♂*
17.–18. May	Peak arrival of ♀♀ *Største ankomst af ♀♀*
24. May – 26. June	Laying of first egg *Lægning af første æg*
9. June – 8. July	Hatching *Klækning*
17. June – 17. July	Fledging *Udflyvning*
4. July – 2. August	Independent young *Uafhængige unger*
22. July – 8. August	Moulting *Fældning*

Positioned close to the ice cap and far from the coast, the area has a stable, continental weather. From May to mid June easterly winds predominated with bright and warm weather. A total of 16 days with snowfall were recorded from 5 May, the last day with snow being 13 June in the valley and 8 July on the plateau.

Precipitation was unevenly distributed: usually most of it fell on the heights. In the valley snow melted within hours after snowfall whereas the plateau remained snowcovered for days. From mid June to mid July winds from west to north predominated and this was the most rainy period with 14 days of rain from 20 June to 20 July. From then on easterly winds were again predominating with bright weather. For a full site description see Fox and Stroud (1981).

MATERIAL AND METHODS

Nest records were compiled from the entire breeding season from end of May to mid July. 70 nests were found and revisited several times and their contents of eggs or young recorded on nest cards. In a number of nests young of known age were weighed with spring balances.

The start of breeding was defined as the date when the first egg in the clutch was layed. This date was determined from a) direct observation, b) calculation from dates of laying of subsequent eggs using one day's interval between the laying of an egg (Hussell 1972), c) the length of incubation, d) hatching date, and e) size and development of the young. The time from hatching to independence of the nestlings was set at 25 days, following Custer and Pitelka (1977).

In order to relate the timing of breeding to the potential food supply, arthropod activity and relative abundance was assessed. As Lapland Buntings almost exclusively feed on ground dwelling invertebrates pitfall trapping was chosen, supplemented with capture of flying insects above the vegetation by means of a sweep net. One transect of 10 pitfalls (white plastic tubes, diameter 12 cm, depth 12 cm) was located at an altitude of 200 m (emptied every 3-4 day), and another transect of five pitfalls at an altitude of 50 m (emptied every week). The pitfalls were placed on southfacing, gentle slopes at 20 m intervals, Sweepnetting was carried out along a fixed route with standardized strokes and only at noon on sunny, calm days (see Madsen 1981b for details).

Observation of prey items brought to the nestlings by the parents was only carried out through telescope. The method might bias the data towards the larger, more visible items, but can deduce whether nestling diet is dominated by caterpillars or imagos of various arthropod orders.

RESULTS

Chronology of the breeding season

The events of the breeding and moulting season are summarised in Table 1. The first pair was seen on 7 may, but the peak arrival was delayed by a week, the males arriving 2-3 days ahead of the females. By 20-22 May the sex ratio was estimated about equal and most birds in the lowland seemed already paired.

The incubation period was on average 11.5 days (0.3 S.E., n=17) and the mean nestling period 9.2 days (0.4 S.E., n=14).

The period of clutch initiation was extended over a month (Tab. 1). The lack of synchrony is due to differences in initiation dates between habitats, inside which a higher degree of synchrony is found (Fig. 1). In the majority of the lowland breeding population the clutch initi-

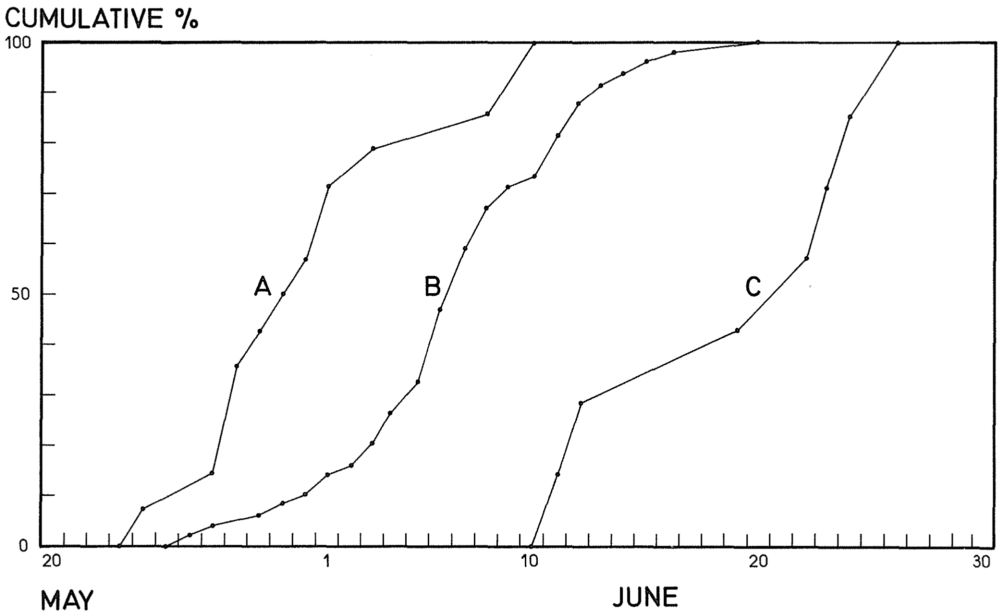


Figure 1. Seasonal egg laying dates in three subareas. A: a south east facing slope in the lowland, B: the rest of the lowland, and C: the plateau.
Figur 1. Sæsonens æglægningsdatoer i tre underområder. A: en sydøstvendt skråning i lavlandet, B: resten af lavlandet, og C: plateauet.

ation commenced 2-3 weeks upon arrival, mean date being 7 June (0.7 S.E., n=49). In one particular area, a south facing, gentle slope covered with *Salix glauca* scrubs an earlier start was found, mean date being 1 June (1.4 S.E., n=14), significantly earlier than the rest of the lowland population (chi-square test, p ⟨ 0.001). The early start here was probably favoured by weather conditions (here the earliest foliage of *Salix* and *Betula nana* was found) and an early mass emergence of *Eurois occulta* caterpillars (see later), which gave the egg producing females a high-protein food-supply and might have enabled them to start egg laying as quickly as physiologically possible after mating on arrival. The latest pairs to start egg laying were found on the plateau, mean date being 20 June (0.8 S.E., n=7), which was significantly later than the majority of the lowland breeders (p ⟨ 0.0001). Colder weather probably forced these birds to a long pre-nesting period.

Clutch size

It is evident that the Lapland Buntings only produced a single clutch. However, second nesting attempts following nest losses might have occurred and have been included in the sample.

The overall mean clutch size was 5.18 (0.12 S.E., range 3-7, n=70). If the total period of clutch initiation is divided into three periods of equal length it is found that clutch size decreased as the season progressed (chi-square test, p ⟨ 0.001), reflecting also (Tab. 2) that the plateau breeders had smaller clutches than the lowland breeders. The decrease could be a result of a) later breeders having smaller clutches than earlier breeders or b) plateau breeders having smaller clutches than lowland birds. However this complexity cannot be tested for dependence due to the small sample of plateau nests.

Nest success

The nest success in the three habitats is summarised in Table 2. The pooled success was 4.13 young/female. In all respects (both absolute and relative terms) the *Salix* covered slope was the most opportune place to nest and rear young in, followed by the rest of the lowland and the plateau. The higher success in the lowland was probably a result of both a more plentiful food supply there compared to the

Table 2. Clutch sizes and reproductive success in relation to the breeding habitat. Dates give the mean time of clutch initiation. Clutch size, number of eggs hatched and number of young fledged declined significantly from the *Salix* slope to the plateau (chi-square test, $p < 0.05$).
*Tabel 2. Kuldstørrelser og ynglesucces i relation til ynglelokaliteten (*Salix*-skråning, resten af lavlandet, plateau). Datoer angiver det gennemsnitlige tidspunkt for lægning af det første æg inden for lokaliteten. Kuldstørrelser, antal af klækkede æg og antallet af udfløjne unger aftog fra pileskråningen* (Salix) *til plateauet.*

	Salix slope 1 June	*Rest of lowland* 7 June	*Plateau* 20 June
Clutch size (S. E.) *Kuldstørrelse* N	5.62 (0.17) 14	5.27 (0.14) 48	4.00 (0.33) 8
Eggs hatched (S. E.) *Klækkede æg* N	4.75 (0.32) 13	4.26 (0.28) 37	3.38 (0.53) 8
Young fledged/female (S. E.) *Udfløjne unger/hun* N	4.67 (0.34) 13	4.19 (0.28) 37	3.13 (0.48) 8
Percent 'fledged' eggs *Procent 'udfløjne' æg* N	83.1	79.5	78.3
Percent succesful nests *Procent succesrige reder* N	100.0	89.5	75.0

plateau as well as a more favourable weather (higher temperatures and less precipitation) during the lowland breeding period.

Nest losses

Of 254 eggs layed the total loss was 31.1%. Hatching failures contributed 11.8%, predation by Ravens *Corvus corax* and Arctic Foxes *Alopex lagopus* 7.5%, abandonment 6.3%, flooding of nests 3.9% and starvation of young 1.6%. All observed cases of predation was on eggs. This might be explained by the behaviour of the incubating female when a predator (human beings included) approaches the nest. At a distance of 1-2 m the female flushes and leaves the nest uncovered and easily detected (in this way 90% of all nests in this study were found). When young are present in the nest the female keeps some distance away when a predator approaches, and the nest is only found with difficulty in the vegetation.

Growth of young

Growth of young from four nests from the lowland and two nests from the plateau was followed (all hatched between 24 and 28 June). The mean growth rate from hatching till the age of eight days was 2.8 g/day (0.1 S.E., n=20) and 2.4 g/day (0.1 S.E., n=10) in the lowland and on the plateau, respectively, the difference being statistically significant (Mann-Whitney U-test, $p < 0.05$), two of the nests being »fast« ones, the two others having approximately the same growth rates as the plateau nests.

In Fig. 3 the growth of young from the lowland and the plateau is compared. On the ninth day after hatching weights on the plateau as a whole decreased. This was caused by a snow fall on the plateau (no snow in the lowland) where two of the young in one nest starved to death. In this nest it was noticed that in good weather the biggest young were always on the top of the nest (the young were individually marked) where they presumably would be fed first, whilst in bad weather they were placed in the bottom of the nest cup where they would be sheltered from chilling. During the snow fall only the three biggest young survived.

Potential food resources and prey items

Figure 4 gives an gross impression of activity and relative abundance of arthropods observed to be prey items of the Lapland Buntings. The results indicate that 1) already on arrival of

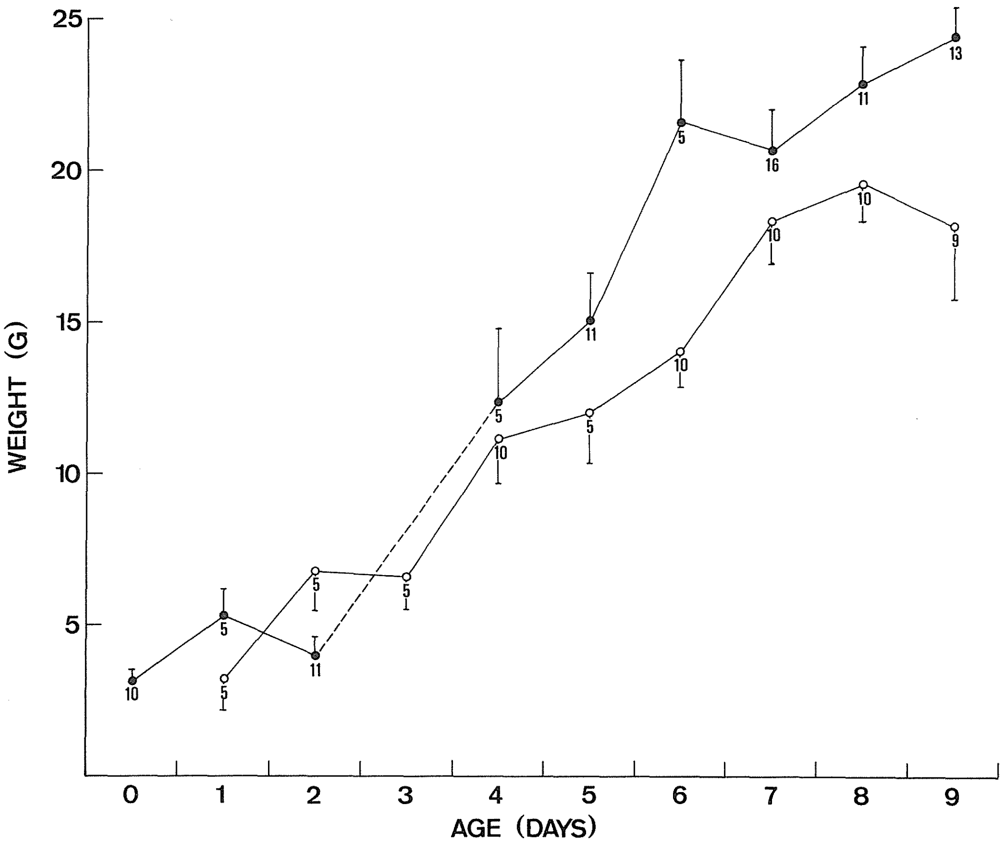


Figure 2. Mean weights of Lapland Bunting young from hatching to fledging in the lowland (filled circles) and on the plateau (open circles). Small letters adjacent to circles indicate sample size, bars give one standard deviation.

Figur 2. Gennemsnitlige vægte af Laplandsværlingernes unger fra klækning til udflyvning i lavlandet (fyldte cirkler) og på plateauet (åbne cirkler). Små tal ved cirklerne angiver prøvestørrelse. Lodrette streger angiver én standardafvigelse.

the Lapland Buntings arthropods were abundant, 2) most arthropod orders were abundant during the whole sampling period – also after the time when the last raised young had reached independence –, and 3) although there was some degree of concordance in captures of some orders between the two sampling sites, there is no overall seasonal trend in the patterns of activity (full details given in Madsen 1981b). No quantitative sampling of arthropods was performed on the plateau but obviously the arthropods were scarcer there and the active season delayed and limited due to the colder conditions.

This general impression from the plateau is reinforced by the composition of prey items brought to the nestlings (Table 3), which is believed to reflect the abundance of arthropods (Custer and Pitelka 1977). The main nestling diet on the plateau consisted of adult *Diptera* and relatively few caterpillars, while the main diet in the lowland was caterpillars throughout the season. The *Eurois* caterpillar was particularly dominant. In a randomly chosen plot in the area with early breeding 100 *Eurois occulta* caterpillars were counted in 9 m^2 on 16 June (mean biomass 6.7 g/m^2 f.w.). They constituted the only prey in the area, and Lapland Buntings were seen flying to the area with the highest density of caterpillars to forage. At several nests small piles of killed or half-dead caterpillars were seen.

DISCUSSION

It is an often cited hypothesis that food supply is the ultimate factor determining the timing of birds' breeding season. In order to maximise

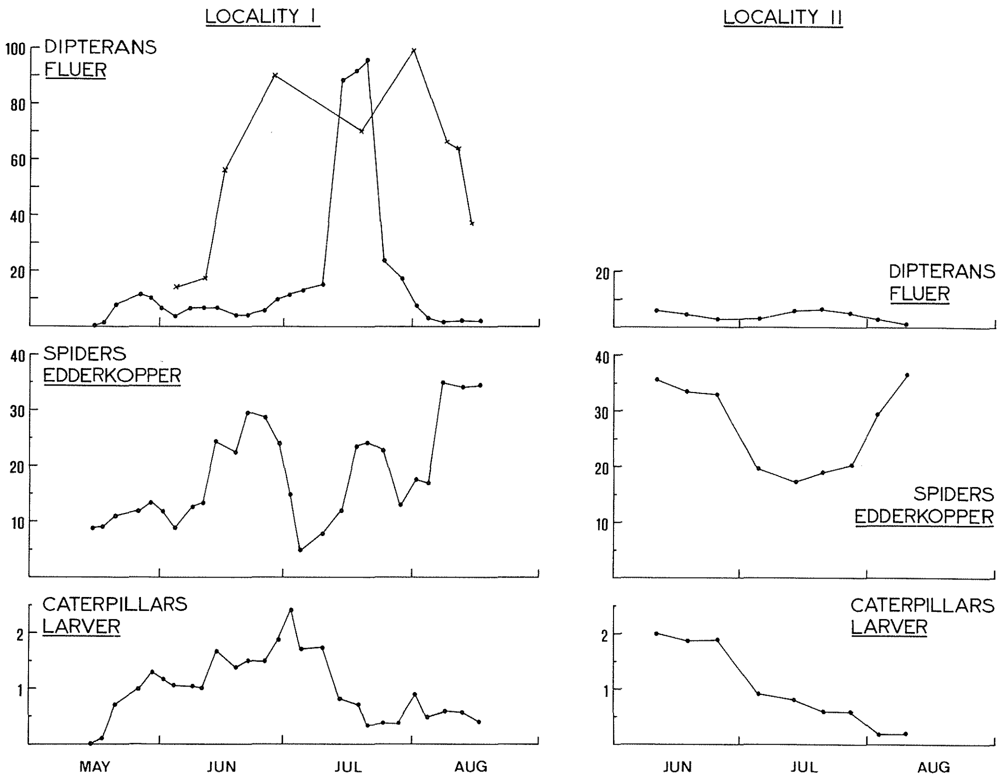


Figure 3. Seasonal abundance and activity of potential prey items measured by pitfall trapping and sweep netting (crosses in upper diagramme at Locality I). Locality I: 10 pitfalls at 200 m, and Locality II: 5 pitfalls at 50 m. Numbers give individuals/day/10 pitfalls. Running means of three samples.
Figur 3. Sæsonmæssig hyppighed og aktivitet af potentielle fødeemner målt ved fangst i fangglas og insektnet (krydser i øverste diagram på Lokalitet I). Lokalitet I: 10 fangglas i 200 m's højde og Lokalitet II: 5 fangglas i 50 m's højde. Antallet vist som antal individer/dag/10 fangglas. Løbende gennemsnit af tre prøver.

the reproductive outcome, the young are raised when sufficient food is available, although this relationship often is modified by the physiological capacity of the egg laying female and the neccessity to finish the breeding season before moult (Lack 1968, Perrins 1970).

In the arctic the timing of breeding is often controlled by the time of thaw. This is pronounced in the North American tundras where the onset of breeding is highly synchronised. The thaw is late and the invertebrate season is short with a significant peak in the patterns of abundance and an abrupt end to the season (Holmes 1966, MacLean and Pitelka 1971, Seastedt and MacLean 1979). Custer and Pitelka (1977) argue that it is not only necessary to the Lapland Buntings that the eggs hatch while food is plentiful (as suggested by Lack 1968) but also that the young must reach independence of their parents before the disappearence of the food supply.

The Greenland tundra differs from the North American in being more mountainous and heterogeneous, with differing snow cover, precipitation and thaw even within areas a short distance apart. When the Canadian-Alaskan and the Greenland study areas are compared the essential difference in factors which seem to influence the timing of breeding in the Lapland Buntings is the date of thaw – and ultimately the duration of available food supply. In Eqalungmiut Nunaat snow was not a serious controlling factor (at least not in the lowlands), the invertebrate season had a longer duration compared to north American areas, and ultimately the egg laying was synchronised to a lesser degree. A similar pattern has been found in the timing of breeding in waders in North East Greenland (Green, Greenwood and Lloyd 1977).

The pooled seasonal fledging success of 4.13 young/female in Eqalungmiut Nunaat is high compared to what has been found on the north American continent. Williamson and Emison (1971) found 1.7-3.0 young/female on Amchitka Island (51°5'N) and Cape Thompson (68°6'N), and Custer and Pitelka (1977) found on average 2.31 young/female at Barrow (71°20'N) (this mean is not corrected for nest losses and second breeding attempts). The higher success in Greenland is partly due to a lower predation rate, since on the continent Arctic Skuas *Stercorarius parasiticus* are severe predators upon the Lapland Bunting young (Custer and Pitelka 1977). Probably the higher success rate is also explained by a smaller risk of breeding, since the Greenland birds have a higher flexibility in timing of breeding (and perhaps a higher chance of producing replacement clutches) due to the longer breeding season as well as a more pentiful food supply reducing nestling mortality.

As has been indicated in this study a correlation was found between food availability in the breeding habitats and the onset of breeding. On the *Salix* covered slopes breeding was advanced through the superabundance of caterpillars, contrasted by the plateau, where the colder weather probably caused a delay in the arthropod season and ultimately led to a long prenesting period. In other studies additional food which was provided to various Tit species *Parus ssp.* led to advancement of egg laying (Källander 1974, Brömssen and Jansson 1980). These observations are in support of a hypothesis of Perrins (1970) which states that birds start breeding as soon as food is abundant enough for egg formation. Early breeders gain fitness by producing larger clutches than later breeders (Klomp 1970) and having a longer breeding season where to rear young in an optimal feeding condition.

At least in the lowland the prolonged breeding season and the associated arthropod abundance ensured that food supplies at hatching and probably at the age of independence were not critical to the young. Likewise, moulting seemed to occur when arthropods were still active in the lowland. On the plateau, however, this period might have been critical.

Especially on the *Salix* covered slope in the lowland the reproductive success was improved, not only because of larger clutches but also because of a better nestling survival. This was probably a result of less susceptibility of the young as the time devoted to food gathering by the parents was minimised as the caterpillars were easy prey. Hildén (1977) observed an analogous example of mass occurrence of caterpillars associated with an improved reproductive outcome in a forest community of passerines in Finland. He assumed this was a result of the superabundant food that made it possible for the females to brood the nestlings while the males performed the parental feeding duties alone.

Low productivity and reduced growth rates on the plateau indicate that food gathering here was combined with high effort. The lighter fledgling weights might even lower post-fledging survival (Lack 1966).

In conclusion, it is my impression that the critical factors which affected the timing of the breeding season were the food supplies in the territories during pre-nesting, the birds breeding as quickly as physiologically possible but met by the constraints of decreasing clutch size as the season progressed. In addition, but less critical, the breeding cycle (the independence of young) and moulting cycle had to be finished before the end of the active arthropod season.

Table 3. Observed nestling food items.
Tabel 3. Observerede fødeemner bragt til redeungerne.

Prey *Bytte*	Valley *Dal* (%)	Plateau (%)
Dipterans *Tovingede fluer*	11.8	79.0
Caterpillars *Larver*	76.5	9.7
Spiders *Edderkopper*	11.8	8.1
Plant material *Plantemateriale*	0.0	3.2
N	58	62

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Lapland Bunting *Calcarius lapponicus*. Foto: JM.

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DANSK RESUMÉ:

Laplandsværlingens tilrettelæggelse af ynglesæsonen og succes i Eqalungmiut Nunaat, Vestgrønland.
I foråret og sommeren 1979 undersøgte jeg aspekter af Laplandsværlingens yngleøkologi i Eqalungmiut Nunaat (67°32'N, 50°30'W) i bunden af Nordre Strømfjord, Vestgrønland. Undersøgelsesområdet var en sydvendt, frodig dal med udbredte græsheder og pile- og birkekrat og over 3-400 m et plateau med mere sparsom vegetation. Fra dalen til plateauet forløb en vejrmæssig gradient med mindre nedbør og tidligere sneafsmeltning i dalen end på plateauet.

Ialt 70 reder blev fulgt fra æglægning til udflyvning af unger, og antallet af æg og udfløjne unger noteredes. I Tabel 1 er kronologien i ynglesæsonen og fældeperioden vist. Den tidligste ynglestart blev fundet på en sydøstvendt skråning, hvor der var en masseforekomst af sommerfuglelarver, som Laplandsværlingerne levede af og dannede små lagre af ved rederne. I den øvrige dal var ynglestarten gennemsnitligt en uge senere (se Figur 1), og på plateauet forsinket med endnu to uger. For området som helhed var den gennemsnitlige kuldstørrelse 5,18, men faldt i løbet af sæsonen og fra lavlandet til plateauet (Tabel 2). Den samlede ynglesucces var 4,13 udfløjne unger pr. hun. Den første halvdel af ynglesæsonen havde størst succes (Tabel 2), og af de tidligst ynglende par havde fuglene på den sydøstvendte skråning størst succes. Ialt gik 31,1% af de lagte æg tabt. Manglende klækning, predation, forladte reder, oversvømmede reder og ungedød var de observerede årsager hertil. Ravne og Arktiske Ræve var predatorer. Redeungernes tilvækst var størst i dalen, 2,8 g/dag mod 2,4 g/dag på plateauet (Figur 2). I Figur 3 er sæsonvariationen i Laplandsværlingernes potentielle fødeemner vist. Allerede ved ankomsten var der stor arthropodaktivitet, og denne varede ved til det tidspunkt, hvor Laplandsværlingernes unger havde opnået forældreuafhængighed. Der er ingen gennemgående tendens i arthropodernes aktivitet igennem sæsonen. Målingerne blev kun foretaget i dalområdet, men aktiviteten har sandsynligvis været forsinket på plateauet. I dalen var redeungernes vigtigste føde larver (Tabel 3), mens deres vigtigste føde på plateauet var fluer.

I arktisk Nordamerika er fuglenes ynglesæson kort og kontrolleret af tøtidspunktet og en kort aktivitetsperiode for arthropoder. Dette er i kontrast til denne undersøgelse, hvor ynglesæsonen var lang, lige som den potentielle føde havde længere varighed. Yngle-successen i det grønlandske område var højere end på den nordamerikanske tundra. Dels var predationsraten lavere, og dels må det formodes at den længere ynglesæson gav større flexibilitet m.h.t. yngletidspunkt og mulighed for omlæg.

Fuglenes tilrettelæggelse af ynglesæsonen er i

overensstemmelse med en hypotese om, at tilrettelæggelsen er en interaktion mellem en selektiv fordel af at yngle tidligt og den fysiologiske tilstand hos den æglæggende hun. Ud fra ynglesuccessen sås der at være fordel ved at yngle tidligt. Specielt på den sydøstvendte skråning var det favorabelt, idet omkostningerne ved at samle føden var minimal. Her kunne æglægningen starte umiddelbart efter ankomsten, fordi føden var rigelig. På plateauet var fødeudbuddet ringere og omkostningerne ved at indsamle føden større p.g.a. det koldere vejr (ses indirekte ud fra ungernes tilvækst), og fuglene her har sandsynligvis været fysiologisk tvunget til en længere periode, inden æglægningen kunne starte.

Det konkluderes, at de kritiske faktorer, som indvirkede på Laplandsværlingernes yngletidspunkt, var fødeudbuddet i territorierne inden æglægning. Endvidere måtte sæsonen tilrettelægges således, at ungerne opnåede uafhængighed og fældningen blev afsluttet, inden fødeudbuddet ville forsvinde.

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