Body mass dynamics of the Lapland Bunting *Calcarius lapponicus* in West Greenland

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(Med et dansk resumé: Kropsvægt og fedtpålejring hos Laplandsværlinger i Vestgrønland)

Introduction

The Lapland Bunting *Calcarius lapponicus* has a circumpolar distribution and is one of the most abundant of arctic-nesting passerines. In West Greenland it is a very numerous nesting species, the population wintering in southern Canada and northern USA (Salomonsen 1981). Although its breeding biology has been described by Madsen (1982) and Fox et al. (1987) and its moult by Francis et al. (1991), little has been written on the body mass dynamics and migration strategies of this ubiquitous arctic passerine species.

This paper summarises the changes in body mass observed amongst birds caught in two areas of Central West Greenland during 1984, with particular emphasis on changes during moult in adult Lapland Buntings and patterns of pre-migratory fattening in juvenile birds.

Methods

Lapland Buntings were caught in two different areas of Central West Greenland during summer 1984. One hundred and sixty three were caught in Eqalummiut Nunaat (67°32'N 50°30'W) between 24 May and 14 August (summer) with a combination of mist-nets and baited clap nets by a number of observers, whilst a further 434 were caught at two sites at Søndre Strømfjord (67°05'N 50°40'W) between 16 August and 11 September (autumn) by JM using mist-nets only (see Tab. 1).

All birds were sexed in the hand based on Svensson (1984); wing length, body mass and time of day were recorded for all birds; other measurements (bill length, bill depth, tail length, tarsus length) were taken when time permitted. Wing length was measured as the maximum straightened and flattened length to the nearest 0.5 mm; all hard-part measurements were made using calipers recorded to the nearest 0.1 mm. Fat scores were recorded when possible, from examination of fat de-

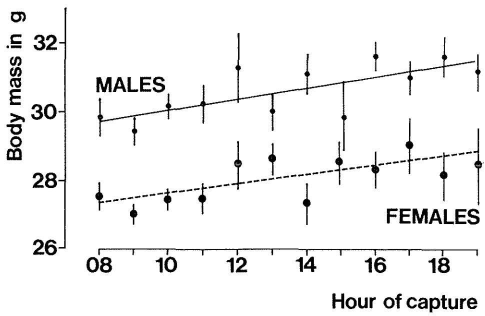


Fig. 1. Diurnal patterns of variation in weight of male (upper) and female (lower) Lapland Buntings captured at Søndre Strømfjord, West Greenland, summer 1984. Bars indicate ± one standard error.
Kropsvægt (± 1 SE) gennem dagen, juvenile Laplandsværlinger fanget ved Søndre Strømfjord aug.-sep. 1984. Tilvæksten (0,156 g/h for hanner (males), 0,132 g/h for hunner (females)) er signifikant forskellig fra nul.

Tab. 1. Details of site, age and sex of all Lapland Buntings caught in Central West Greenland in 1984.
Laplandsværlinger målt og vejet i Vestgrønland 1984. Netlings: redeunger; unsexed: køn ubestemt; males: hanner; females: hunner.

	Nestlings	Juveniles			Adults	
		unsexed	males	females	males	females
Eqalummiut Nunaat	46	49	–	–	28	40
Søndre Strømfjord	–	36	182	208	4	4

pots in the tracheal pit, based on a five point scale from 0 (no fat) to 4 (pit bulging and fat extending beyond pit).

Moult was examined on 51 adults (43 in Eqalummiut Nunaat, 8 in Søndre Strømfjord) and 297 juveniles (all except 8 from Søndre Strømfjord) between the end of June and 11 September. Primaries are numbered descendingly; the minute outermost (10th) primary was inconsistently recorded during fieldwork, and is not considered in this analysis, hence the maximum possible primary score was 45 (Ginn & Melville 1983).

We used the formula of McNeil & Cadieux (1972) and the improved version of Summers & Waltner (1979) (which accounts for weight loss in flight) to generate still air flight ranges for Greenland Lapland Buntings. Both formulae are based on given flight speed using 12 times basal metabolic rate as the energetic cost of flight used by Raveling & LeFebvre (1967). Two other methods, developed specifically for determination of still air flight ranges for wader species are also considered (Greenewalt 1975, Davidson 1984). We also use equations developed by Pennycuick (1989) using purely mechanical aerodynamic principals to independently estimate still air flight range based on fat loadings at the time of departure.

Results

Diurnal variation in body mass

Weights of autumn-captured juvenile Lapland Buntings increased through the day (Fig. 1), the mean gain in body mass being 0.156 g/h in males ($r=0.73$, $p < 0.01$) and 0.132 g/h in females ($r=0.70$, $p < 0.05$). There was no significant difference between these rates of increase ($p > 0.05$). In all subsequent analysis, body mass has been corrected to that predicted by these equations at 12:00 hr to standardise comparisons.

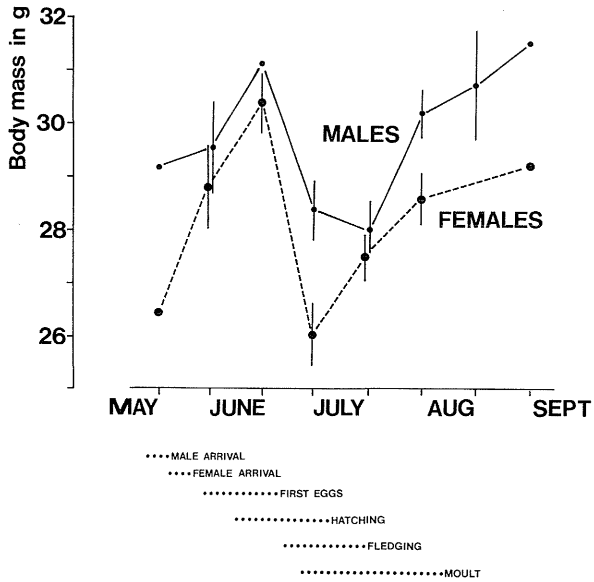


Fig. 2. Mean weights (adjusted for time of capture) of adult Lapland Buntings trapped in Eqalummiut Nunaat, West Greenland, summer 1984. Data are summarised by half-months and the figure shows nesting and moult phenology. Bars indicate ± one standard error.
Kropsvægt (± 1 SE), adulte Laplandsværlinger fanget i Eqalummiut Nunaat sommeren 1984. Males: hanner; females: hunner.

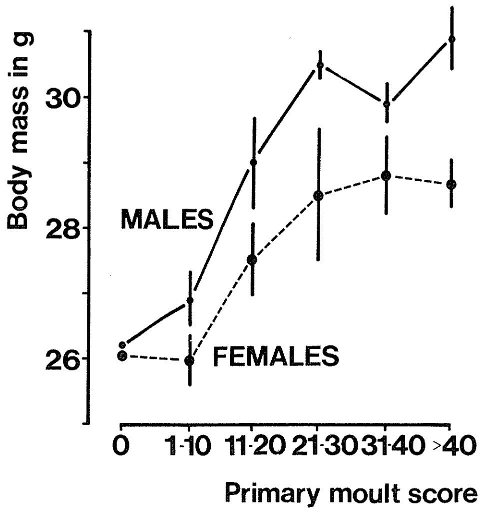


Fig. 3. Mean body weight (adjusted for time of capture) of adult male (upper) and female (lower) Lapland Buntings caught in post-nuptial moult, Søndre Strømfjord, West Greenland during August/September 1984. Bars indicate ± one standard error.

Kropsvægt (± 1 SE) og index for håndsvingfjerenes fældning (skala 0-45). Males: hanner; females: hunner.

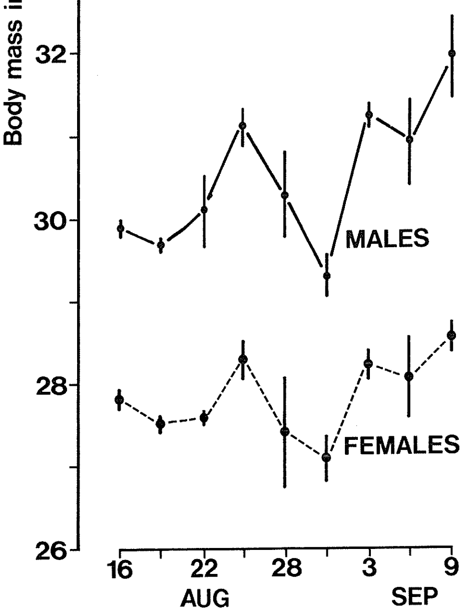


Fig. 4. Variation in mean body weight (adjusted for time of capture) of male (upper) and female (lower) juvenile Lapland Buntings caught at Søndre Strømfjord, West Greenland, August/September 1984. Bars indicate ± one standard error.

Kropsvægt (± 1 SE) for juvenile Laplandsværlinger, Søndre Strømfjord 1984. Males: hanner; females: hunner.

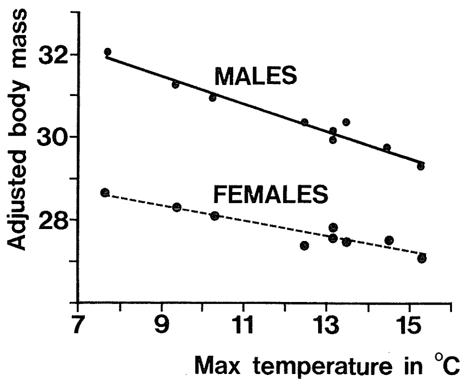


Fig. 5. Variation in mean weight (adjusted for time of capture) of juvenile Lapland Buntings with mean daily maximum temperature, Søndre Strømfjord, West Greenland, August/September 1984. Data points represent three-day means. The decreases are significant (males, upper, 0.33 g increase per degree decrease, $r=0.97$, $p < 0.001$; females, lower, 0.18 g increase per degree decrease, $r=0.90$, $p < 0.001$).

Sammenhæng mellem middelvægt for juvenile Laplandsværlinger og gennemsnitlig daglig maksimumtemperatur, Søndre Strømfjord aug.-sep. 1984. Punkterne repræsenterer gennemsnit over tre dage. Males: hanner; females: hunner. Hældning: -0,33 g pr °C (hanner), -0,18 g pr °C (hunner); p < 0,001 i begge tilfælde.

Seasonal variation in adult body mass

Insufficient numbers of adults were caught at regular intervals to give more than an overall picture of change in body mass throughout the entire summer. Data summarised by two-week periods are shown in Fig. 2.

The pattern of moult in this sample of birds has already been considered by Francis et al. (1991), but Fig. 3 shows the progressive increase in body mass of both sexes.

Seasonal variation in juvenile body mass

Body mass increases in nestling birds have already been documented by Fox et al. (1987). Post-fledging weights showed a general trend of increase amongst juveniles through August and September (Fig. 4), with males remaining heavier than females at all stages. These changes showed a highly significant inverse relationship to the mean maximum daily temperature (Fig. 5). Of the 17 retrapped birds for which data are available, 5 caught between 16 and 18 August had lost body mass by their subsequent recapture, those caught after 19 August showed an average of 0.223 g/day increase, 0.175 g/day for males (n=8), 0.425 g/day for females (n=4).

Fat scores of juveniles

Fat scores of captured juveniles increased throughout August, except during the onset of night-time sub-zero temperatures towards the end of the month (Fig. 6), when overall body mass also declined (Figs 4 and 7). Fat score correlated well with body mass during the period (Fig. 8). Only two males were caught with fat score 4, both of which weighed 35.2 g. A single female, scored in excess of 3, weighed 31.9 g. The differences between these weights and the mean weights for birds with a fat score of 0 are 6.25 g and 4.85 g respectively. Assuming that weights of birds with a fat score of 0 approximate to lean body mass, and that the entire difference in mass between the two states equates to accumulated fat deposits, this represents 22% and 17% fat loadings (as a percentage of lean body mass) in males and females respectively, accumulated over three to four weeks.

Still air flight ranges of juveniles

From 11 September onwards, the numbers of Lapland Buntings began to decline as birds moved south on migration. We assume that the fat deposition observed was accumulated immediately prior to departure and that birds caught with high fat scores and maximal summer weights were about to depart for wintering areas. We have then used several different formulae to estimate the still air flight ranges of these birds based on the observed fat loadings. These results are shown in Tab. 2.

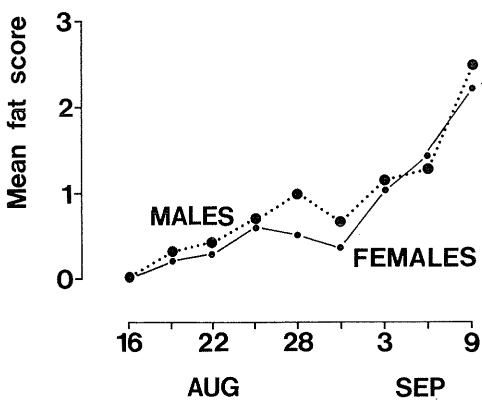


Fig. 6. Variation in mean fat score measurements from juvenile male (upper) and female (lower) Lapland Buntings caught at Søndre Strømfjord, West Greenland, August/September 1984.
Gennemsnitligt fedtindex (skala 0-4) for juvenile Lapландsværlinger, Søndre Strømfjord 1984. Males: hanner; females: hunner.

Discussion

Most studies of passerines have demonstrated daily variation in body mass in temperate passerines which is generally accepted to represent a diurnal fat accumulation/utilisation cycle (e.g. Evans 1969, King 1972, Lehikoinen 1987). Birds utilise fat deposits to meet nightly thermoregulatory demands, these deposits being replaced during subsequent daytime feeding. The loss of fat and overall body mass amongst birds captured late on in the season may be a function of fatter birds departing the study area (a fact not borne out by the retrap of birds throughout the period of catching) or the first frosts of the autumn imposing greater demands on the overnight metabolism of accumulated reserves. The latter supports the general diurnal model of the accumulation/utilisation cycle. Our findings of 0.13-0.16 g/h gain in body mass by Lapland Buntings through the day prior to autumn migration (0.44% body mass gain/h in males, 0.41% in females) are less than amongst spring migrating Snow Buntings *Plectrophenax nivalis* (0.98% and 1.23% respectively, Banks et al. 1989), although this may be a function of diminished thermoregulatory demands during the warmer arctic summer and the shorter hours of darkness.

Having corrected for time of capture, patterns of adult mass through the breeding season compare with other such studies (e.g. Boddy 1984). Males were significantly heavier than females in all months. Males showed extremely low weights on arrival from wintering areas in southern Canada and the United States. However, both sexes showed a rapid increase in mass prior to nesting in May 1984, when despite deep snow and low temperatures, birds were able to feed on snow surface arthropods (Fox & Stroud 1986, Fox et al. 1987) and, during prolonged periods of daylight for foraging, were able to accumulate new body reserves prior to breeding. Weights of adults fell dramatically during the feeding of young, and male weights continued to fall into late July, in contrast to females; otherwise, there was close correspondance between the change in body mass in both sexes.

Both sexes showed an increase in mass during wing and body moult, a common feature of passerine weight dynamics (e.g. Newton 1966, Orell & Ojanen 1980, Boddy 1984) partly due to the growth of new feathers and an increase in water content (Evans 1969). During the moult, adults are reluctant to fly as they lose some remiges and most rectrices simultaneously and may even become

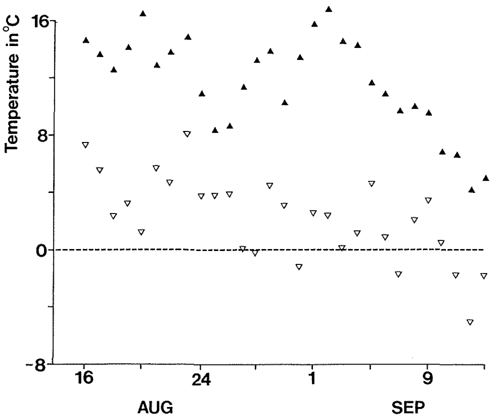


Fig. 7. Daily maximum and minimum recorded temperature from Søndre Strømfjord Air Base, West Greenland, August/September 1984.
Daglig maksimum- og minimumtemperatur ved Søndre Strømfjord lufthavn, aug.-sep. 1984.

Tab. 2. Basic physical parameters of male and female juvenile Lapland Buntings caught at Søndre Strømfjord, West Greenland, August/September 1984. Still air flight range determinations have been calculated using these parameters based on different formulae referred to in the Methods.
Parametre for juvenile Laplandsværlinger fanget ved Søndre Strømfjord august-september 1984, og maksimal flyvedistance estimeret vha. formler givet i de angivne kilder. Male: hanner; female: hunner.

	Male	Female
Fat weight *Vægt, maks. fedt* (g)	35.20	31.90
Lean weight *Vægt, intet fedt* (g)	28.95	27.05
Fat loading *Maks. fedtvægt* (g)	6.25	4.85
Proportion fat *Maks. andel fedt*	0.22	0.17
Flight speed *Flyvehastighed* (km/h)	34.5	34.5
Still air flight range *Maksimal flyvedistance* (km)		
McNeil & Cadieux (1972)	640	530
Summers & Waltner (1979)	680	570
Greenewalt (1975)	1370	1130
Davidson (1984)	550	460
Pennycuick (1989)	1000	810

flightless for short periods (Francis et al. 1991). Flightlessness may make the adults difficult to catch prior to migration, hence, the analysis of premigratory fattening is restricted to first-year birds which only undergo a partial post-juvenile body moult in autumn prior to migration.

Visual fat scores are considered good estimators of fat deposits (e.g. Rogers & Rogers 1990) and the build-up of fat deposit scores in juvenile Lapland Buntings correlates well with overall increase in body mass. It may be that this increase is not all due to changes in fat content of the body, since changes in protein, water and crop/gut contents (e.g. Newton 1969, Jenni & Jenni-Eiermann 1987, Piersma & van Brederode 1990) can also influence overall body mass. However, most of these changes are of low orders of magnitude, and other studies suggest that most of the premigratory increase is due to fat deposition. Hence, in the absence of carcass analysis, we have assumed that all of the change is due to fat accumulation.

Many Lapland Buntings have left West Greenland by mid-September (Salomonsen 1950, pers. obs.) and whilst further fattening may occur further south and west of our study areas, departure to these areas would involve some energetic cost to balance additional periods of feeding. Hence, the data used in modelling flight ranges, whilst not ideal, give some useful determinations of the potential of birds to reach near coasts for ultimate passage to wintering ranges. These data

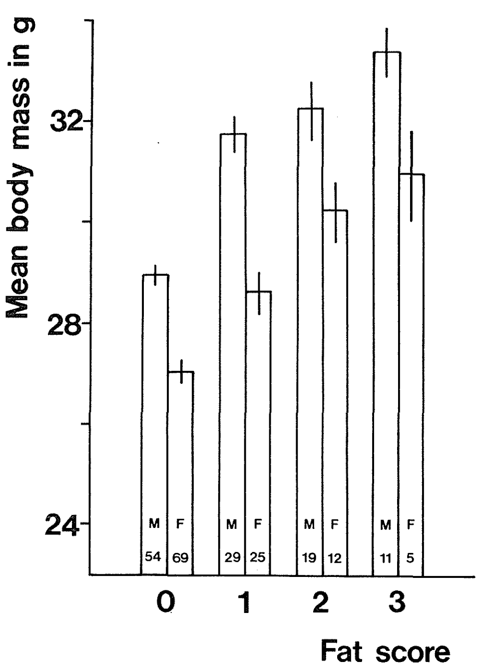


Fig. 8. Variation in weight with regard to fat score in juvenile Lapland Buntings, Søndre Strømfjord, West Greenland, August/September 1984. Note that too few birds were caught in fat score class 4 to include their data. Bars indicate ± one standard error.
Sammenhæng mellem kropsvægt (± 1 SE) og fedtindex for juvenile Laplandsværlinger, Søndre Strømfjord aug.-sep. 1984. M: hanner; F: hunner.

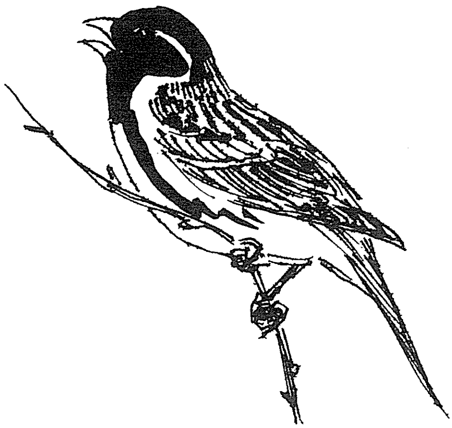
Juvenile Lapland Bunting. Photo: Per Schiermacher Hansen.
Ved Søndre Strømfjord i Vestgrønland kunne det påvises, at juvenile Laplandsværlinger opbygger fedtdepoter på 20% af kropsvægten eller mere før borttrækket om efteråret.

show that juvenile Lapland Buntings can attain sufficient fat reserves to cross the 450 km to Baffin Island, the nearest part of the Canadian arctic archipelago to Søndre Strømfjord. The direct flight lines involve just under 1000 km to the Labrador coast and 1100 km to northern Quebec, regions en route to their wintering areas as shown by ringing recoveries summarised by Francis et al. (1991). However, generally, most of the West Greenland coast lies within 700 to 900 km of the Canadian side of the Davis Strait, so assuming the Pennycuick (1989) model to be the best applicable to our study, this small passerine can accumulate sufficient fat reserves in West Greenland in autumn for the direct migration towards the wintering continent rather than make a shorter sea-crossing involving a longer ultimate route.

There are two recoveries of Lapland Buntings ringed at Ammassalik in southeast Greenland (65°36'N) from Quebec (Canada) and Minnesota (USA) showing that at least some east coast birds pass southwestwards to winter in North America. If these birds traverse the Greenland ice-cap, the distance (500-600 km) is less than the journey to Iceland (600-700 km) for an onward passage to Europe. Since there are feeding opportunities along the southeast coast of Greenland to the southern tip where birds are known to concentrate in autumn (cf. Salomonsen 1950), they may be able to feed and migrate in short hops southwards, accumulating reserves as they go. Energetically, therefore, it would make sense for birds breeding as far north as Ammassalik to winter in the New World.

Further north in East Greenland, the species is absent from the Blosseville coast, but has occurred with increasing frequency around the Scoresby Sund area, with breeding proven in 1962 and perhaps other recent years (Ferns 1978). From here, it is 1000-1100 km to West Greenland over the ice-cap and far more down the east coast. In contrast, it is 400-500 km to Iceland before the final 900 km to Britain. Small numbers of Lapland Buntings occur regularly in western and southern Iceland, and the specimens of those taken show closer similarity in measurements to Greenlandic birds than Scandinavian birds, although these may also occur (A. D. Fox & Æ. Petersen unpubl.). Similarly, there are records of birds showing size ranges characteristic of Greenlandic birds in Britain, Ireland, the Netherlands and France (see discussion in Francis et al. 1991), particularly in early autumn before the arrival of Scandinavian birds. Small numbers of Lapland Buntings nesting in northeastern Greenland may thus winter in the Old World in contrast to the remainder of the Greenland population which winters in Canada and the United States of America.

Our study shows that not only is fat stored on an accumulating basis in preparation for migration, but that it is also utilised to sustain energy loss incurred at night. By early September, the study area was enduring over four hours of darkness when birds were forced to roost (although even in continuous daylight, the species does roost during the "night"). For this reason, the effects of cold weather and/or the timing of breeding in Lapland Buntings may have a profound impact on the autumn migration dispersal and survival of the species as has been demonstrated amongst arctic nesting geese (Owen & Black 1989).



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Resumé

Kropsvægt og fedtpålejring hos Laplandsværlinger i Vestgrønland

Omkring 600 Laplandsværlinger blev målt og vejet i to områder i Vestgrønland i 1984. Fuglenes vægt voksede i løbet af dagen og faldt om natten. Vægten korrigeret for klokkeslet voksede fra ankomsten om foråret indtil klækningen, men faldt betydeligt i ungetiden; dette gjaldt begge køn. De adulte fugles vægt øgedes siden under fældningen og nåede et maksimum pri. september, kort før borttrækket. Juvenile Laplandsværlinger opbyggede fedtdepoter i tiden med. august - pri. september. Fedtdepoternes størrelse skønnedes ud fra sammenhængen mellem fedtindex og kropsvægt hos levende fugle, og nåede mindst 17-22% af kropsvægten straks før borttrækket. Skønnede maksimale flyvedistancer indikerer, at disse fedtreserver er tilstrækkelige til, at fuglene uden yderligere fedtpålejring er i stand til at krydse Davisstrædet på vej til vinterkvarteret i Nordamerika. For den lille bestand i NØ Grønland er det muligvis en bedre strategi at overvintre i Europa, hvor Laplandsværlinger af formodet grønlandsk oprindelse af og til er registreret.

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