Reproductive response to fluctuating lemming density and climate of the Long-tailed Skua *Stercorarius longicaudus* at Zackenberg, Northeast Greenland, 1996-2006

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(Med et dansk resumé: Reproduktiv respons på lemmingtæthed og klima hos Lille Kjove Stercorarius longicaudus *ved Zackenberg i Nordøstgrønland 1996-2006)*

Abstract Eleven years of monitoring at Zackenberg Research Station in high-arctic Northeast Greenland documented a relatively stable population of about 21-27 pairs of Long-tailed Skuas in a 17.1 km^2 study area. The average density, 1.2-1.6 pairs per km^2, was among the highest known. Territories were well spaced out with mean distances between nests/territory centres of 450-600 m, and situated very much in the same areas between years. The extent to which the skuas laid eggs was significantly correlated with lemming abundance at snowmelt, but at least some pairs initiated breeding even in lemming-poor years. Timing of egg-laying within each year was very synchronous, but the median date of egg-laying varied about 10 days between years. This variation was correlated neither with abiotic parameters like snowmelt nor with lemming abundance, but there was a weak correlation with early spring abundance of wolf spiders. Excluding supposed re-laid clutches, the annual mean clutch size ranged between 1.0 and 1.9 and was highly correlated with lemming abundance. Hatching success varied between 0 and 94%, but was neither correlated with fox nor lemming abundance. Likewise, the number of fledged young was not correlated with any abiotic or biotic parameter tested. By quantifying lost breeding potential during the different stages of reproduction, we identified the period between territory establishment and egg-laying as the most important for variation in reproductive success across years. Breeding potential lost during this stage was closely, but non-linearly related to lemming density at snowmelt. Juvenile production could be termed 'eruptive', in that only one year produced many juveniles (1.05 per pair) – a year both with many lemmings and many foxes. Based on estimates of mortality we suggest that reproduction during the study years in this population was not sufficient to maintain a stable population size.

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Introduction

Long-tailed Skuas breeding in Northeast Greenland arrive along the edge of the sea ice in the fourth week of May, whereupon they appear on the tundra during the last days of May and the first week of June (review by de Korte 1984). Here, they form a key component in one of the world's simplest vertebrate food-webs. The four most common predators, the Long-tailed Skua, the arctic fox *Alopex lagopus*, the stoat *Mustela erminea* and the Snowy Owl *Nyctea scandiaca*, share one common food resource, the collared lemming *Dicrostonyx groenlandicus*.

It has previously been documented that populations of collared lemming exhibit marked four-year cycles and that predator-prey interactions are probably the main reason for the existence of lemming cycles in Northeast Greenland (Gilg 2002, Gilg et al. 2006). Here, we focus on one of the lemming predators. Based on a long-term data set from central Northeast Greenland, we quantify inter-annual variation in breeding phenology and success and to what extent this variation can be explained by biotic and abiotic drivers. We specifically address which element of the breeding schedule is most important for total breeding potential, and how lemming density, alternative prey and snow affect each of these elements.

Material and methods

Study area and weather

The study took place as part of the BioBasis climate effect monitoring programme at Zackenberg Research Station in central Northeast Greenland (74º28'N; 20º34'W; Meltofte & Berg 2006). The climate is high-arctic with a mean (June through August) summer temperature of 4.2ºC (Sigsgaard et al. 2006), and timing of snowmelt (date of 50% snow-cover) varied more than a month from 5 June to 9 July during the last 17 years (Hinkler 2005).

The bird study area covers 19.3 km^2 of valley floor and slopes stretching from the coast of the fjord Young Sund and up to an elevation of 600 m (see map Fig. 1), but since all Long-tailed Skua territories were below 300 m a.s.l., we disregarded the part above this level, leaving a study area of 17.1 km^2. The vegetation is dominated by mesic dwarf shrub heaths mixed with abrasion plateaus, arctic willow *Salix arctica* snow-beds, grasslands and fens (Bay 1998).

The snow-cover on 10 June was chosen as an index of spring snow conditions, since this is close to the earliest median 1st-egg date of Long-tailed Skuas at Zackenberg (Table 1). 10 June snow-cover percentage during the years 1995-2006 was measured from satellite images (1995-1996) or photos (since 1997) taken from a height of 477 m a.s.l. overlooking the study area (Meltofte 2006, Sigsgaard et al. 2006). Air temperature was recorded continuously at a climate station centrally in the valley. Here, we used early spring mean temperatures for the period 21 May – 10 June as a measure of inter-annual variability of spring warmth. As an index of the advancement of snowmelt, we used the date of the first running water in the rivulets in the study area, which may correlate with the time when melt water forces lemmings out of their sub-nivean nests and tunnels.

Long-tailed Skuas

Population size, number of clutches laid, breeding phenology and success of Long-tailed Skuas were recorded annually between June and August during 1996-2006 using standardised methods (Meltofte & Berg 2006). Birds appearing as pairs during a total survey of the study area during mid and late June were registered as pairs, and the total number of such pairs was considered the minimum number of territories for the year. Single, but local individuals recorded during the same period were considered to represent possible territories. Added to the minimum estimate, this provided the estimated maximum number of territories of the year. Skua pairs are relatively easy to record, but in years where few birds nested, the mapping of the population was problematic, since the birds were not as stationary and did not pair out as in other years (see Discussion). Skua nests are easy to find, but some nests may have been depredated before they could be found, so that our figures are minimum numbers. Still we expect that the number of clutches found provided a reasonable measure of breeding effort in the individual years. No chicks were ever found in areas where a nest had not been found earlier in the season.

To quantify the extent to which the territories/nests are found in the same locations in consecutive years, we produced a set of all possible territory centre/nest locations within the study area with a minimum distance of 50 m and randomly selected a subset of territory centre/nest locations equal to the number of territory centres/nests found in each year from this list. For each year we calculated the mean distance from each observed territory centre/nest location to the nearest territory centre/nest location from the list of random territory centre/nest locations for the previous year. We repeated this

Table 1. Long-tailed Skua breeding parameters in the 19.3 km² bird study area at Zackenberg 1996-2006 together with a number of selected biotic and abiotic parameters of relevance to the skuas (see section on material and methods for details), with weighted means where relevant. Clutch initiation dates and mean clutch sizes based on less than five nests were omitted (–), and nest successes based on less than 50 nest days are given in brackets. The number of immature Long-tailed Skuas is not corrected for potential re-sightings on multiple days. For parameters where a range is given we used the mean value in statistical tests.
Yngleparametre hos Lille Kjove i det 19,3 km² store fuglemoniteringsområde ved Zackenberg 1996-2006 sammen med udvalgte biotiske og abiotiske parametre.

Breeding parameter *Yngleparameter*	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**Mean**
No. of pairs/territories *Par/territorier*	25-29	22-25	21-24	19-24	21-28	22-25	23-26	25-29	21	24-29	21-30	22-26
Median 1st-egg date *Mediandato for 1. æg*	–	7.6	12.6	17.6	18.6	15.6	9.6	15.6	8.6	8.6	–	12.6
No. of nests (clutches) found *Fundne reder (kuld)*	8	18	23	8	5	21	14	7	21	8	2	12.3
Estimated to have been re-laid *Heraf omlagte*	–	4	6	1	0	4	4	1	1	1	0	2.2
Mean clutch size (initial clutches) *Gns. kuldstørrelse*	–	1.9	1.9	1.7	1.6	1.9	1.8	1.0	1.9	1.3	–	1.77
No. of young hatched *Klækkede unger*	1	25	16	2	2	18	14	5	36	6	1	11.5
Nest success (%) *Redesucces*	(0)	(81)	27	(18)	(18)	40	44	(76)	(94)	(52)	(50)	53.7
Estimated no. of young fledged *Flyvedygtige unger*	0	3-10	5-10	1	0	7-8	4-7	2	22	1	0	4.1-5.5
Chick survival (%) *Ungeoverlevelse*	0	26	47	50	0	42	39	40	61	17	0	42.1
Fledged young per nest *Flyvedygtige unger pr rede*	0.00	0.36	0.33	0.13	0.00	0.36	0.39	0.29	1.05	0.13	0.00	0.28
Fledged young per pair *Flyvedygtige unger pr par*	0.00	0.28	0.33	0.05	0.00	0.32	0.22	0.07	1.05	0.04	0.00	0.21
Records of immatures *Observationer af immature*	1	1	0	1	1	0	2	6	5	1	3	1.9
Lemmings per ha *Lemminger pr ha*	2.21	5.30	12.21	4.72	2.62	4.64	4.01	1.44	6.44	3.21	3.67	4.59
First lemming track or hole in snow *Første lemmingspor*	11.6	3.6	31.5	10.6	4.6	3.6	1.6	10.6	1.6	22.5	19.6	4.6
No. of lemmings seen June-July *Antal lemminger set*	0	1	43	9	1	11	4	1	23	1	3	8.8
Wolf spiders per 2 trap days *Jagtedderkopper pr 2 fældedage*	1.45	2.57	1.27	0	2.57	0.88	1.23	0.81	2.46	3.25	2.21	1.70
Snow free land 10 June (%) *Snefrit land 10. juni*	18.3	23.9	19.8	8.9	47.2	16.6	20.6	17.4	52.4	71.2	14.0	28.2
Mean temp. 21.5-10.6 *Middeltemperatur 21.5-10.6*	-0.15	-0.81	-0.90	-0.22	-1.25	-0.64	1.17	-1.06	-0.96	0.13	-0.31	-0.45
Break up of rivulets *Rindende vand i småelvene*	<6.6	11.6	11.6	15.6	4.6	10.6	4.6	3.6	31.5	4.6	13.6	<7.6
Fox encounters in June-July *Ræveobservationer i juni-juli*	14	5	7	13	11	14	21	11	16	18	22	13.8
Fox encounters per pct snow-free area *Ræveobs./pct snefrit areal*	0.77	0.21	0.35	1.46	0.23	0.84	1.02	0.63	0.31	0.25	1.57	0.70
Fox dens with pups *Rævegrave med hvalpe*	2	0	1	0	2	2	1-2	2	3	0	2	1.2
Fox dens per pct snow-free area *Rævegrave/pct snefrit areal*	0.11	0.00	0.05	0.00	0.04	0.12	0.07	0.11	0.06	0.00	0.14	0.04

selection procedure one hundred times and tested whether the difference in distance to the observed and the random nest locations differed from zero.

Based on records of incomplete clutches, egg-floating, hatching and weight of pulli found (see Meltofte & Berg 2006), clutch initiation dates were estimated for a total of 119 Long-tailed Skua nests between 1996 and 2006. Clutch size was recorded from the same 119 clutches. A further 12 1-egg clutches may have been incomplete and were excluded from the analyses. Clutches known or assumed to have been re-laid after the loss of the initial clutch were excluded from the calculation of 1st-egg dates. The remaining number of clutches available for calculation of annual median 1st-egg dates was 97. In the analysis of median 1st-egg date and clutch size variation, we further omitted years with less than five initial clutches.

Each nest was checked regularly during the incubation period to register predation and hatching success. In order to avoid that our visits increased the risk of fox predation, we normally checked from a distance if an incubating bird was present. Still, our activities may have increased fox predation to some extent. Hatching success was calculated using the modified Mayfield method (Johnson 1979). Following hatching, chick survival was recorded by regular visits at chick tending pairs, until the adults either left the area or fledged young were seen. In case the adults left the breeding site before chicks could have fledged, these were considered lost. Fledged young are tended by their parents for at least two weeks after fledging – often until departure (Maher 1970, Wiley & Lee 1998). However, our records of fledging success involved some uncertainty, since families could move away from the nest site (up to 400 m recorded prior to fledging, >500 m after fledging), and in some years the bird observer left Zackenberg before all chicks had fledged. In such years, other BioBasis personnel checked the remaining families.

Besides daily mapping of adult Long-tailed Skuas, we recorded all present 1-3 year old immatures. In Table 1 these are given as total records irrespective of possible re-sightings of the same individuals on more than one day.

In order to identify the stage of the breeding cycle that was most important for juvenile production, we calculated lost breeding potential before territory establishment, from establishment to egg-laying, during incubation, and from hatching to fledging. We assumed that the breeding potential before the season started was equal to the maximum number of recorded territories times two, the maximum clutch size. In each year, we calculated the proportion of this maximum breeding potential lost at each stage.

Prey species

During the study years, an index of end-of-winter lemming abundance was obtained from counts of lemming winter nests in a 2.05 km^2 study plot centrally in the bird study area. Using the relation between density of winter nests and actual density obtained from a study of lemming population ecology at Traill Island 220 km south of our study area, an estimate of lemming density at snowmelt was obtained (Schmidt et al. in press). We corrected this estimate for habitat differences between the lemming study area and the bird study area below 300 m a.s.l., providing an estimate of the overall lemming density available to the skuas. Furthermore, we recorded sightings of lemming tracks and holes in the snow and used the first dates of these records as an indication of timing of appearance of lemmings above the snow and thereby accessible to the skuas (Table 1). Finally, the number of live lemmings seen by one observer (the ornithologist) during June and July was recorded as a supplement to the nest recordings (Table 1). These lemmings were primarily seen on the snow during snowmelt, and the number therefore provides a measure of the availability of lemmings during this critical period.

We used the number of wolf spiders (only one species known from the area, *Pardosa glacialis*) caught per two trap days during 3-17 June in eight pitfall traps situated on an early snow-free heath (Plot no. 5; Meltofte & Berg 2006) as a measure of alternative food early in the season. *P. glacialis* is the largest abundant invertebrate available to skuas early in the season (Meltofte 2006), and early snow-free heaths are used extensively by the skuas for foraging (pers. obs.).

Arctic fox

Arctic fox is the main predator of Long-tailed Skua nests and young at Zackenberg, and encounters with foxes were recorded continuously during the bird monitoring period. In Table 1 these are given as number of observations of foxes in June and July. A few records of foxes attracted by the research station were omitted. Similarly, five fox dens within the bird study area were checked regularly for pups during June and July. To be able to analyse for possible relations between fox numbers per snow-free area and predation pressure, we established two indices by simply dividing the number of fox encounters and occupied fox dens by the percentage of snow-free area on 10 June (Table 1).

Results

In most years, the first Long-tailed Skuas were present at our arrival around 1 June. During arrival, flocks of up to about 10 individuals were recorded, but they soon dispersed and took up territories. The preferred habitat was early snow-free, mesic tundra together with gravelly and stony plateaus with mountain avens *Dryas* spp., arctic willow and white arctic bell-heather *Cassiope tetragona*. Fens and extensive abrasion areas were generally avoided, and a late snow-free area to the southeast was little used (Fig. 1).

The population of Long-tailed Skuas in our bird study area was relatively stable around mean values of 21-27 pairs in all years (Table 1). All territories were found below 300 m a.s.l., and territories were established at very much the same places from year to year – mean distance to the nearest territory/nest of the previous year was less than 300 m in most

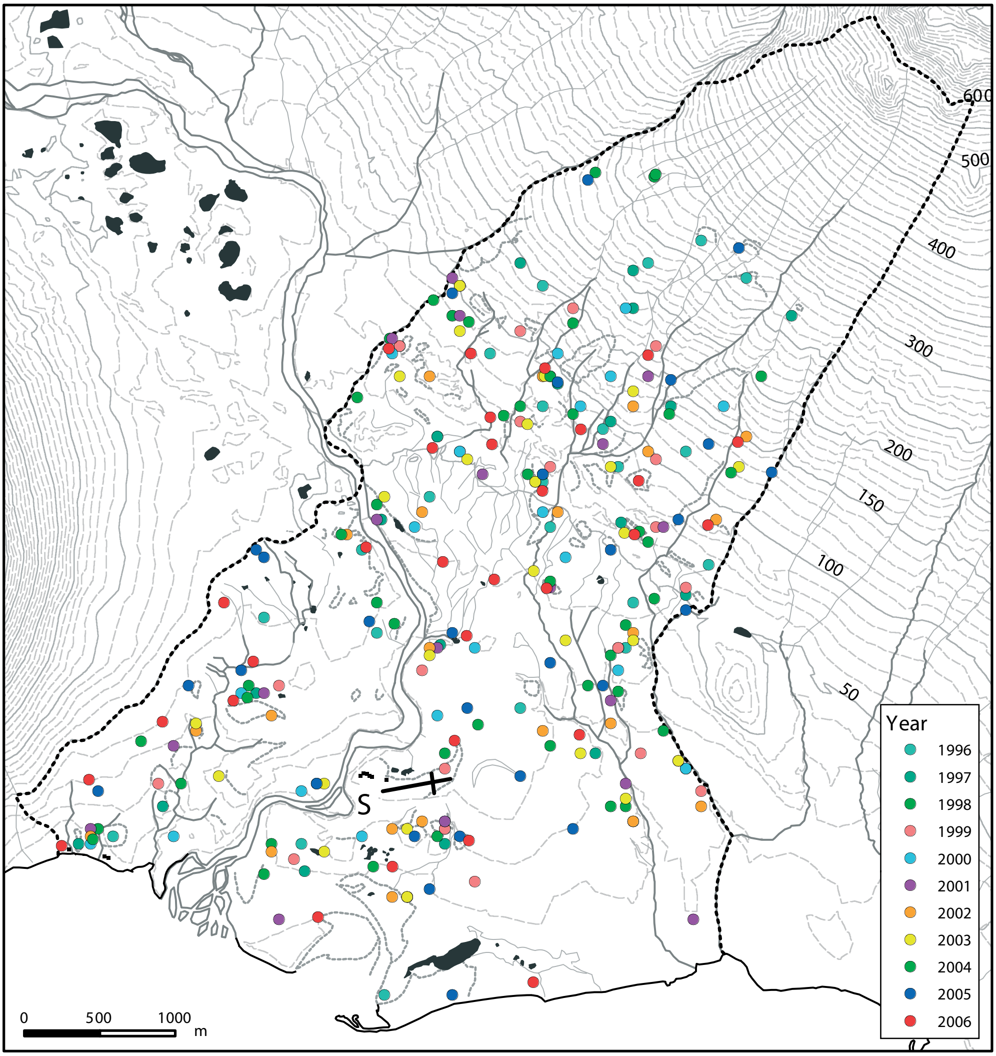

Fig. 1. Map of the bird study area at Zackenberg with Long-tailed Skua territories/nests indicated. The position of the research station (S) and the runway is marked.
Kort over undersøgelsesområdet ved Zackenberg med sikre Lille Kjove-territorier/reder.

years (Fig. 2). Only 2004 and 2005, with the lowest extent of snow-cover and thereby more room for spacing out nests, deviated from this pattern. The mean distance from observed nest locations to the nearest observed nest in the previous year was significantly lower than the mean distance from observed nest locations to the nearest nest from the list of random nest locations (average difference = 118.71 m; t = 6,63, df = 8, P = 0.0001).

Eggs were produced every year, but the number of clutches found varied considerably and was strongly correlated with the number of lemmings at snowmelt (r = 0.73, N = 11, P = 0.01).

Egg-laying took place during early and mid June, with the earliest egg laid on 4 June and the latest (apparently re-laid) on 2 July (Fig. 3; see below). Breeding phenology as expressed by median 1st-egg dates was correlated neither with lemming abundance, snow-cover, rivulet break-up or spring temperature, but there was a correlation with the abundance of wolf spiders, provided that the outlaying data point from 2000 was omitted (r = -0.89, N = 8, P = 0.003). Furthermore, although not significant, the correlation coefficient between 1st-egg dates and total numbers of clutches found was negative (r = -0.58, N = 10, P = 0.08), perhaps

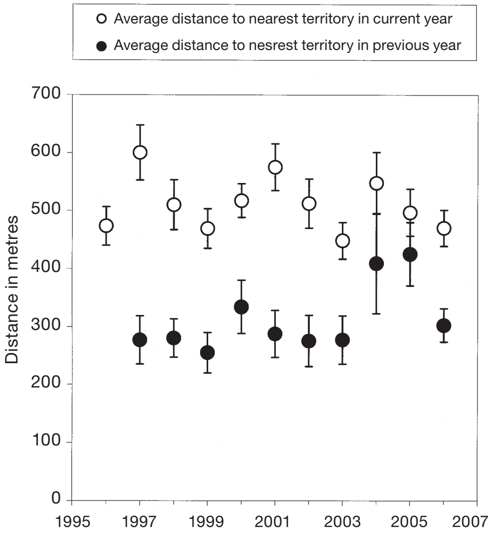

Fig. 2. Mean distance from Long-tailed Skua territory centres/nests to the nearest (neighbour) territory centre/nest of the current and the previous year. Error bars show SDs.
Middelafstanden (med standardafvigelse) fra territoriecenter/rede til nærmeste territoriecenter/rede samme år (cirkler) og det foregående år (sorte prikker).

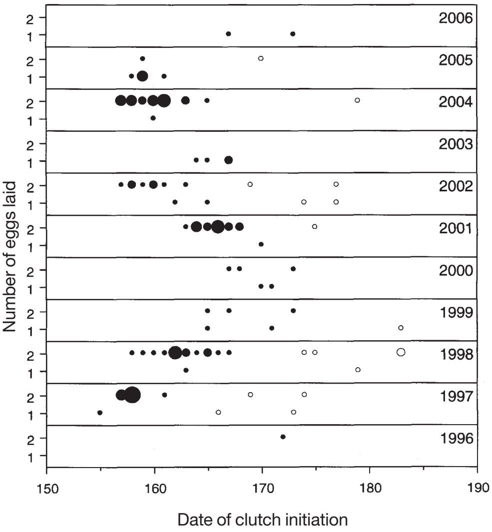

Fig. 3. Laying dates of first-eggs (day of the year) of Long-tailed Skua at Zackenberg 1996–2006. One-egg and two-egg clutches shown separately. Day 150 is 30 May. The largest dot represents six clutches.
Datoer for første-æg hos Lille Kjove ved Zackenberg 1996–2006, med et-ægskuld og to-ægskuld vist hver for sig. Dag 150 er den 30. maj. Den største prik repræsenterer seks kuld.

suggesting an association between high breeding density and early egg-laying.

In most years, egg-laying was very synchronized (Fig. 3), but the peak was often followed by a few 'stray' clutches. In a number of cases we found new-laid clutches in territories, where the original clutch had been predated. Replacement clutches may be produced from 8 days after the loss of the original clutch (Wiley & Lee 1998), and based on this we estimated that several clutches were most likely replacements. These are marked in Fig. 3.

Annual mean size of first clutches varied between 1.0 and 1.9 (Table 1) and was positively correlated with the number of nests found (r = 0.81, N = 9, P = 0.008). No difference was apparent between the size of initial and replacement clutches (initial 1.75, N = 97; replacement 1.68, N = 22; t = 0.68, P = 0.50). However, the number of 1-egg clutches may have been underestimated since 12 such clutches were excluded from analysis because they might have been incomplete (see Material and methods), but since these included both initial clutches and supposed replacements, their exclusion should not alter the conclusion. Of nine clutches that we are confident were re-lays, three had two eggs, five had one, and one had at least one egg. There was no significant correlation between clutch size of initial clutches and laying date (r = 0.22, N = 9, P = 0.57).

Hatching success was correlated neither with lemming abundance nor number of fox encounters, fox dens with pups, or fox encounters or fox dens with pups divided by percent snow-free land (see Table 1). However, there was a significant correlation between number of young hatched and median 1st-egg date (r = -0.71, N = 10, P = 0.02), so that early egg-laying was associated with higher numbers of hatched young. The correlation coefficient between skua nest success and wader nest success was positive but not significant (r = 0.30, N = 10, P = 0.10 (wader data from Meltofte 2006)).

In total, 56% of the 225 eggs recorded in this study hatched, whereas 38% probably were predated by arctic foxes. Using the modified Mayfield method (Johnson 1979), the overall nest success was 53.7% (Table 1). Of non-predated eggs, 7% were deserted (including clutches damaged during a snow-storm, see below), and one egg with a fully developed embryo was abandoned after

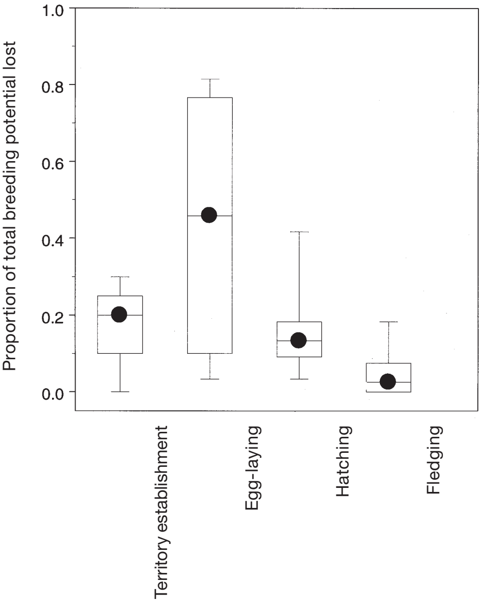

Fig. 4. The proportion of breeding potential lost at different stages of the reproductive period in Long-tailed Skua at Zackenberg for the years 1996–2006. Estimates are given for the proportion of the maximum breeding potential that remained at the beginning of a stage but was lost before the beginning of the following stage. The initial potential (before territory establishment) was 54, twice the maximum number of territories observed in the study area.
Andelen af tabt ynglepotentiale i de forskellige stadier i ynglecyklus hos Lille Kjove ved Zackenberg i årene 1996-2006.

its sibling hatched and left the nest. A single egg was probably laid by a pair already having a nest with two eggs 20 m away. Direct information on chick mortality is limited to the observations that 3-4 chicks from two broods apparently died or were deserted shortly after hatching, and in 1995 an apparently deserted chick at least two weeks old starved to death.

In contrast to the waders, of which almost all clutches were lost during a snow-storm in mid June 2001 (Meltofte et al. 2007), only two out of at least 15 skua clutches laid before or during the snow-storm were damaged (the adults kept incubating them for at least 37 and 40 days, respectively, until they were abandoned (Meltofte 2003)). However, the snow-storm may have hit neighbouring skua populations harder, since a flock of 14 individuals was seen during the snow-storm, at a time when flocks were never seen in other years.

Fledging success was low. Expressed as the percentage of hatched young surviving to fledging (mean of minimum and maximum estimate), it was correlated neither with lemming abundance, fox encounters or fox dens with pups. Neither was the number of fledged young correlated with any of the external biotic or abiotic parameters, or the number of young fledged per nest with fox encounters or fox dens with pups.

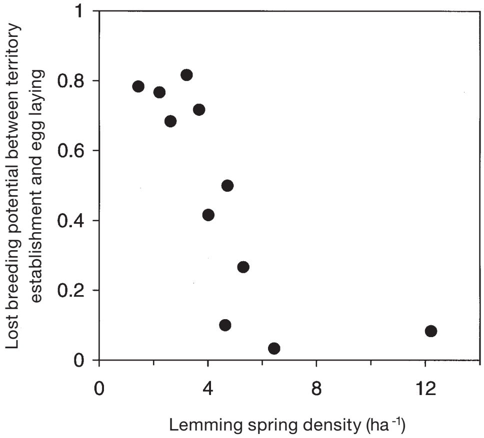

Fig. 5. The relationship between the lemming density (estimated from counts of winter nests) and the proportion of breeding potential lost between establishment of territories and egg laying of Long-tailed Skuas at Zackenberg, 1996–2006.
Forholdet mellem tætheden af lemminger og tabet af ynglepotentiale mellem territorieetablering og æglægning hos Lille Kjove ved Zackenberg 1996–2006.

The loss of breeding potential was largest and most variable between territory establishment and egg-laying (Fig. 4). The lost breeding potential during this period was non-linearly related to the lemming density (Fig. 5).

From late June, non-breeders and failed breeders begin to form loose groups of up to 15 individuals, often performing aerial group displays (de Korte 1984, this study). Depending on lemming abundance, these birds begin to leave the tundra from mid July, but failed breeders may reappear on their territories more or less regularly until mid August (de Korte 1984, this study). In most years, however, birds remaining after early August are mainly successful breeders (this study). The first flying juveniles were seen at Zackenberg in late July, and the last family groups were seen in late August.

Opposite to findings by de Korte & Wattel (1988) at Scoresby Sund further south in Northeast Greenland, where Long-tailed Skuas fed extensively in the fjord in lemming-poor years, we hardly ever saw skuas feeding over Young Sund. The exception was about 10 birds feeding together with about 125 Glaucous Gulls *Larus hyperboreus* at a pod of about 50 narwhals *Monodon monoceros* in Young Sund off Zackenberg on 20 July 2002.

Most years, a few immature Long-tailed Skuas appeared in the study area between mid June and late July (Table 1). They either roamed the area or joined the loose groups of post-breeding adults. Most were seen in 2003 and 2004, 1-3 years after the productive years 2001 and 2002, and to some extent in 2006, two years after the extraordinarily successful year 2004 (see also Wiley & Lee 1998). The relatively good breeding seasons of 1997 and 1998 were not followed by such visits, however. Most immatures were estimated to have been at least two years old, but a few apparently one-year-old individuals were recorded (cf. Olsen 2000; see also Meltofte 2007).

Mortality of adult Long-tailed Skuas during the breeding season was only witnessed twice, one bird apparently taken by a Gyrfalcon *Falco rusticolus* and the other found dead of unknown causes.

Discussion

Densities of Long-tailed Skua territories at Zackenberg – 1.2-1.6 pairs per km^2 – were among the highest found in a modern quantitative study (cf. Andersson 1976, de Korte 1977, Elander & Blomqvist 1986, Boertmann et al. 1991, Wiley & Lee 1998, Mortensen 2000, Gilg et al. 2006).

In accordance with the high population density found at Zackenberg, skua pairs were relatively close to each other. While our mean closest neighbour distances varied between c. 450 and 600 m, mean distances in Alaska were between 900 and 1300 m, both to Long-tailed Skua nests and to Pomarine Skua *Stercorarius pomarinus* nests (Maher 1974).

Although Long-tailed Skua, in contrats to the Pomarine Skua, may breed at low lemming densities – or no lemmings at all (Kampp 1982, Furness 1987) – the species is well known to exhibit a numerical response to fluctuating lemming abundance, so that many pairs refrain from breeding or fail to fledge young in years of low lemming densities (Wiley & Lee 1998). This is confirmed in our study, where we found that numbers of eggs laid was closely coupled to lemming density (Fig. 5). At lemming densities above about 6 lemmings/ha, almost all established pairs laid a full clutch of two eggs, whereas at lower lemming densities fewer nests and smaller clutches were produced. However, the breeding outcome was also influenced by other factors. Predation on nests and young, and availability of alternative prey of the predators, interact with lemming occurrence, so that even in years with maximum breeding effort, i.e. in lemming peak years, foxes may take virtually all skua eggs and young (Meltofte et al. 1981, Hansen 1984).

In Jameson Land, south of our study area, where snow-cover is often more extensive than at Zackenberg, de Korte (1985) found that timing of egg-laying in three study years was correlated with progress of snowmelt and experience of the pair, but not with body reserves. The importance of snowmelt was not confirmed by our nine years of usable data. Instead we found that timing of egg-laying was correlated with the abundance of alternative prey early in the season, in the form of wolf spiders, although the correlation was only significant when an outlaying year was omitted. Whether this effect reflects a real response to arthropod food availability, or spider abundance varied in parallel with some other significant factor(s), is not known. During the Arctic summer, however, arthropods make up 8–10% of Long-tailed Skua food biomass (de Korte & Wattel 1988), with breeding female Long-tailed Skuas feeding more on arthropods than males (Wiley & Lee 1998). This could mean that arthropod prey is important, at least during the pre-laying and laying period, when other food is scarce, i.e. before lemmings appear above the snow (cf. Table 1). Long-tailed Skuas initiated egg-laying about 10 days earlier in years with many spiders than in years with few. A similar role of arthropods was found for waders at Zackenberg (Meltofte et al. 2007). An important difference between the two avian taxa, however, is that waders have to acquire most of the nutrients for egg-production after arrival at the breeding grounds (Klaassen et al. 2001), while Long-tailed Skuas arrive on the breeding grounds with large body stores accumulated at sea immediately before arrival (de Korte 1985). After arrival, sufficiently large densities of lemmings are a precondition for maintaining the body stores and produce eggs, and the more weight the females lose, the smaller clutches and eggs (de Korte 1985). Alternative prey, e.g. invertebrates, might trigger the onset of egg-laying, provided that lemmings are available as well. Since skuas arrive before lemmings appear above the snow, we suggest that skuas have the ability to assess the abundance of lemmings under the snow, perhaps from auditory clues.

Early breeding could benefit chick survival in that lemming numbers often decline during the

The population of Long-tailed Skuas at Zackenberg was relatively stable at about 21-27 pairs during the 11 study years, but reproduction was apparently insuficient to maintain the population without immigration. Photo: Erik Thomsen.

summer (Gilg 2002). In lemming-poor years, parents may abandon their eggs or leave their chicks to die from starvation, and even in successful breeding years, the youngest chick often dies (Wiley & Lee 1998). Furthermore, in our study early egg-laying was associated with high hatching success, but we see no obvious explanation for this, and more data are needed for firm conclusions.

Opposite to de Korte (1985 plus references therein), but in accordance with Andersson (1976) and Meltofte et al. (1981), we found a high degree of synchrony in the laying dates of Long-tailed Skuas at Zackenberg (Fig. 3). This synchrony may have been exaggerated by our procedure to classify all late clutches as replacement clutches (see Material and methods), but this does not change the general finding that the vast majority of clutches were laid within about one week in all study years; in some years actually within a few days. Furthermore, late clutches were so few that they would not have changed the median date by more than one or two days if they had all been included as initial clutches.

In accordance with de Korte (1985), who found that clutch (and egg) size was closely correlated with body stores of the female, we found the size of original clutches to correlate significantly with lemming abundance.

There is some controversy as to whether replacement clutches always have only one egg (Wiley & Lee 1998), but Maher (1970) found two eggs in a replacement clutch, and we found several re-laid two-egg clutches at Zackenberg. Meltofte et al. (1981) and Hansen (1984) each reported a case where Long-tailed Skuas laid two successive replacement clutches (both of one egg).

Even though all eggs and young were lost to predators in some years and the majority in most others, we found no correlation between skua hatching or fledging success and fox abundance (or two measures of fox abundance per snow-free area). This is opposite to findings by Gilg et al. (2006) and most likely the result of an intricate relation between skua breeding effort, fox activity and lemming abundance. Fox predation on skua eggs and young vary from year to year depending on numbers of foxes and fox pups, and on abundance of other prey, especially lemmings; in addition, factors like individual foxes's search images may play a role. Even a difference in the susceptibility of individual foxes to mobbing by skuas could influence predation rates. In consequence of such interplays, skua breeding success is relatively high in years with many lemmings and few foxes (such as 1997 and 1998; Table 1) and very low in years with few lemmings and/or many foxes (such as 1996, 2000, 2003 and 2006), but may also be relatively high in years with good numbers both of lemmings and foxes (such as 2001, 2002 and particularly 2004), which is well known in arctic birds in general (Underhill et al. 1993). Overall, the breeding success of Long-tailed Skuas at Zackenberg have been low or medium in most years, with only 2004 standing out with a very high productivity, resulting in what could be termed an 'eruptive' breeding output (see also Wiley & Lee 1998).

Long-tailed Skuas are long-lived birds and are faithful to breeding sites (Wiley & Lee 1998). We found that territories were established in very much the same places between years, and a number of observations of marked birds support results from elsewhere, that individuals most often breed in or near the same territories from year to year (Wiley & Lee 1998). Our study documented a relatively constant potential breeding population each year.

With a total production of 45-61 fledglings during 11 study years (Table 1), the average annual production was only 4.1-5.5 juveniles, or about 0.2 per territorial pair per year (Table 1). This is less than half the number (0.53) found by Andersson (1976) and assumed only to balance losses among adults if their mortality was fairly low, 9-16% annually. Since actual mortality of adults in two other studies was estimated at 10% (Andersson 1981, de Korte 1986), productivity in the present study was well below the level needed to maintain the population. Hence, provided that we did not underestimate the number of fledged young, recruitment from other areas was necessary to maintain the extraordinarily dense population in our study area.

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Resumé

Reproduktiv respons på lemmingtæthed og klima hos Lille Kjove *Stercorarius longicaudus* ved Zackenberg i Nordøstgrønland 1996-2006

Elleve års monitering (1996-2006) ved Zackenberg Forskningsstation i højarktisk Nordøstgrønland dokumenterede en relativt stabil bestand på omkring 21-27 par Lille Kjove i et 19.3 km^2 undersøgelsesområde (Tabel 1). Alle kjoveterritorier og reder fandtes i de 17,1 km^2, der lå under 300 m højde (Fig. 1), og den gennemsnitlige tæthed her var 1.2-1.6 par pr km^2, hvilket er en af de største kendte tætheder. Territorierne var jævnt fordelt med en gennemsnitlig afstand mellem territoriecentre (og reder) på 450-600 m, og de lå nogenlunde de samme steder fra år til år (Fig. 2).

Om kjoverne lagde æg de enkelte år var signifikant korreleret med mængden af lemminger ved snesmeltningen, men selv i år med få lemminger var der kjovepar, der forsøgte at yngle. Æglægningen var vel synkroniseret mellem de fleste par, men mediandatoen for æglægningen (1. æg i hvert kuld) varierede med omkring 10 dage fra år til år (Fig. 3). Denne variation var hverken korreleret med abiotiske parametre (snedække, temperatur, snesmeltning) eller med forekomsten af lemminger. Den eneste signifikante korrelation var med antallet af jagtedderkopper i det tidlige forår, som enten må udgøre en vigtig supplerende føderessource inden lemmingerne bliver tilgængelige under snesmeltningen, eller svinge parallelt med andre forhold, der er vigtige for kjoverne. Korrelationen var dog kun signifikant, når et enkelt afvigende år blev udeladt.

Når der ses bort fra omlagte kuld, varierede den gennemsnitlige kuldstørrelse mellem 1.0 og 1.9 fra år til år (Tabel 1), og den var i høj grad korreleret med antallet af lemminger. Redesuccesen varierede mellem 0 og 94%, men den var hverken korreleret med ræveforekomster eller med antallet af lemminger. Tilsvarende var antallet af unger, der kom på vingerne, hverken korreleret med abiotiske eller biotiske parametre.

Ved at kvantificere tabet af ynglepotentiale mellem de forskellige stadier i ynglecyklus, viste det sig som forventet, at perioden mellem territorieetablering og æglægning var mest afgørende for kjovernes ynglesucces (Fig. 4). Det tabte ynglepotentiale i denne periode var tæt relateret til tætheden af lemminger ved starten på snesmeltningen, sådan at en tæthed på over seks lemminger pr ha resulterede i, at næsten alle kjoverne lagde kuld på to æg (Fig. 5).

Kjovernes ynglesucces kunne betegnes som "eruptiv", idet et enkelt år (2004), hvor der både var mange lemminger og mange ræve, resulterede i 22 flyvedygtige unger mod 0-10 i de andre år. Den samlede ynglesucces i undersøgelsesårene var formentlig ikke høj nok til at opretholde en stabil bestand, så enten var vores registrering af flyvedygtige ungfugle mangelfuld, eller der skete rekruttering fra andre områder.

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