PRIMARY MOULT OF GREAT SKUAS ON THE BREEDING GROUNDS, WITH SPECIAL ATTENTION TO THE FAROE ISLANDS

Kees H.T. Schreven & Sjúrður Hammer

SUMMARY – Primary moult in birds demands energy and lowers flight ability. Therefore, timing of primary moult does usually not overlap with breeding or migration. Great skuas are exceptional, as they may start primary feather moult by the end of the breeding season and continue it during autumn migration. However, sixteen publications from 1921-2018 show variation in the timing and location of the onset of primary moult and it is unclear if this reflects geographical or temporal variation. Moreover, a quantification of the extent of primary moult on the breeding grounds is lacking. Here, we show for great skuas on the Faroe Islands, that they can moult the innermost four primaries (p1-4) on their breeding grounds. We collected 306 shed primaries in three areas: Skúvoy (2012 and 2013), Saksun and Svínoy (2013). We identified the primary types (p1-4) of these feathers based on morphometry and comparison with reference specimens, and found that shed feathers comprised 51% p1, 36% p2, 12% p3 and 1% p4. These frequencies did not differ significantly between the three areas, nor on Skúvoy between 2012 and 2013. Remarkably, they also did not differ between the breeding colony and the club site on Skúvoy, whereas this was expected as club sites are also visited by immatures, which start moult earlier than breeding adults. On Skúvoy, we trapped 19 adults on the nest, marked their inner 5 primaries on both wings (190 individual feathers), and retrieved 6 (3.2%) of these primaries in the field after shedding. Based on these marked feathers we estimate that at least 45% of the 300 breeding great skuas on Skúvoy moult at least p1 there. An inquiry among colleagues showed that primary moult occurs throughout the breeding range, and seemingly to a larger extent in the south (Iceland, Faroes, Shetland) than in the north (Norway, Jan Mayen, Bjørnøya, Svalbard) by mid-August. We discuss several possible explanations for these patterns: variation in the timing of the breeding season, the proportion of failed and non-breeders, and the food situation. Such variation could explain on the one hand the discrepancies between literature sources and on the other hand the wide range in reported start dates of primary moult.

figure 1. Great skuas at the club site at Vatndalsvatn, Skúvoy, Faroe Islands, 7 June 2013. Photo: Kees Schreven
Grote jagers op de soos bij Vatndalsvatn, Skúvoy, Faeröer, op 7 juni 2013.

	source	1st cycle		2nd cycle		≥3 cycle		location of moult	location of specimens	yr of specimens/sample size
	bron	start	end	start	end	start	end	*ruiplaats*	*herkomst van exemplaren*	*jaar & steekproefgrootte*
A	Bent 1921	-	>1 year old	-	-	8	-	-	-	-
B	Witherby *et al.* 1944	-	-	<9	>9	not in 6–9, but <12	>12	-	-	a few
C	Dement'ev & Gladkov 1951	-	>1 year old	-	-	8	12	-	based on A and B	based on A and B
D	Stresemann & Stresemann 1966	< 7	late 7	-	-	8	late 1	start before leaving breeding area, continue at sea	Iceland, Faroes, Shetland, England	1886-1916 (5)
E	Glutz von Blotzheim & Bauer 1982	3	7	-	-	(8)9–10	1	mainly at sea, only with or after taking pelagic lifestyle	-	-
F	Cramp & Simmons 1983	early 3–early 4	late 7–mid 8	as adult, some late 5	as adult	BR: 8–early 10. FN: some early 7	BR: 2–mid 3. FN: some in 1	-	-	
G	Ginn & Melville 1983	-	-	-	-	8	1–3	in winter area	based on B, C, D	based on B, C, D
H	Bezzel 1985	early 3	late 7 (–mid 8)	-	-	8–10	2–3	-	-	-
I	Furness 1987	-	-	-	-	early autumn	winter	during and after moving to winter area	-	-
J	Baker 1993	early 3–4	7–mid 8	5–6	after autumn	BR: 8-early 10. FN: from 7	BR: 2–mid 3. FN: 1	-	-	-
K	Del Hoyo *et al.* 1996	-	-	-	-	autumn	winter	-	-	-
L	Olsen & Larsson 1997	3–early 4	early 6–late 8	5–6	2–3	BR: 8-early 10. FN: some from 7	BR: 1–mid 3/4. FN: some in 12-1	-	based on F, G, J	based on F, G, J
M	Newell et al. 2013	early 2–early 4	late 5–late 8	probably as adult	probably as adult	early 8–mid 10	early 2–late 5	-	North Atlantic, North sea	unknown (139)
N	Demongin 2016	(2)3–early 4	(early 6)late 7–mid 8(10)	(late 5)9–10	3–5	BR: 8-early 10. FN: some from 7	BR: (1)2–mid 3(4). FN: 12-1	may start in breeding area, end in winter area		various literature sources
O	Baker 2016	early 3–4	7–mid 8	5–6	8–10(11)	BR: 8–early 10, FN: from 7	BR: 2–mid 3. FN: 1	in winter area	based on J	based on J
P	Van Bemmelen *et al.* 2018	2–5	(late 6)7–8(9)	as adult	as adult	(7)8–mid 10(11)	(late 12)1–2 (–early 4)	breeding area, migration, wintering	Norwegian Sea, North Sea, Bay of Biscay	partly based on D, M (259)

table 1. Information about the timing and location of primary moult in great skuas, as given in 16 publications from 1921-2018. Numbers indicate months, BR=breeders, FN=failed and non-breeders.

Overzicht van timing and plek van handpenrui van grote jagers volgens 16 publicaties (1921-2018). Getallen geven maanden weer, BR=broedvogels, FN=niet-broeders en mislukte broeders

Flight feather moult requires energy (Lindström *et al.* 1993) and reduces flight ability (Swaddle *et al.* 1996). Therefore, in most species, flight feather moult usually does not overlap with other energy- and flight-demanding activities, such as breeding and migration (Payne 1972). Among the exceptions to this generality, adult great skuas (*Stercorarius skua*) may start their primary feather moult by the end of the breeding season, continue during autumn migration and finish in winter (see references in table 1). However, estimates of the timing of primary moult, published in 1921-2018, differ (table 1). The reported earliest and latest starting dates vary by respectively two and three months between sources. With regards to where the onset of moult takes place, some authors state that adult primary moult may start on the breeding grounds (Demongin 2016, Stresemann & Stresemann 1966, Van Bemmelen *et al.* 2018), while others state that adult great skuas moult their primaries essentially at sea, with or after taking on their pelagic lifestyle (Glutz von Blotzheim & Bauer 1982), only during migration and wintering (Furness 1987), or even only in the wintering area (Baker 2016, Ginn & Melville 1983). It is unclear whether these different statements describe geographical or temporal variation. In the earliest publications, the material was limited and descriptions were based on only a few museum specimens. Also, the origin of the samples is rarely mentioned explicitly in literature. Another complication may be that the timing of primary moult is plastic in great skuas, being dependent on age (already recognised by Bent 1921) and breeding status of an individual (only recognised from Cramp & Simmons (1983) onwards). Adult great skuas moult their primaries descendantly (from the innermost primary outwards) from July-October until December-April, with failed and non-breeders starting about a month earlier than breeders (table 1).

To put the different statements about primary moult on breeding grounds to the test, we investigated primay moult of great skuas by collecting feathers on Skúvoy (2012 and 2013), Saskun and Svínoy (both in 2013), Faroe Islands. We compared breeding colonies with club sites and marked feathers of adults trapped on their nests. We also contacted colleagues across the breeding range of great skuas to see how widespread primary moult on the breeding grounds is today. Finally, we discuss possible explanations for the apparent geographical patterns.

METHODS

STUDY AREAS AND BREEDING PHENOLOGY ON THE FAROE ISLANDS

The extent of primary moult was assessed in the three locations with the largest great skua colonies on the Faroe Islands (Hammer *et al.* 2014): Skúvoy (N 61°45′, W 6°48′), Saksun, specifically Svínaskoradalur (N 62°15′, W 7°12′) and Svínoy (N 62°16′ W 6°21′). On Skúvoy, around 150 pairs breed annually (Hammer 2017). Of these, around 100 breed in a colony on the south-eastern part, Bergið, whereas isolated pairs breed scattered across the rest of the island. Central on the island is the lake Vatndalsvatn, which holds a club site, where a group of on average 45 skuas (range 5–112) can be seen daily in the breeding season (figures 1 and 2). The club site is visited by breeders and non-breeders. In Saksun, 100-200 pairs breed annually. On the local club site 50-70 skuas can be seen daily in summer. On Svínoy, 100-200 pairs breed annually. There is a club site, but it is unknown how many birds visit it. Information on phenology and success of breeding is only available for Bergið, Skúvoy. Here, great skuas arrive in late April and disappear around late September (pers. obs. SH and local birdwatchers). In 2012, first eggs were laid on average on 21 May (range 4 May–16 June, unpubl. data) and in 2013 on 25 May (range 7 May–22 June, Schreven

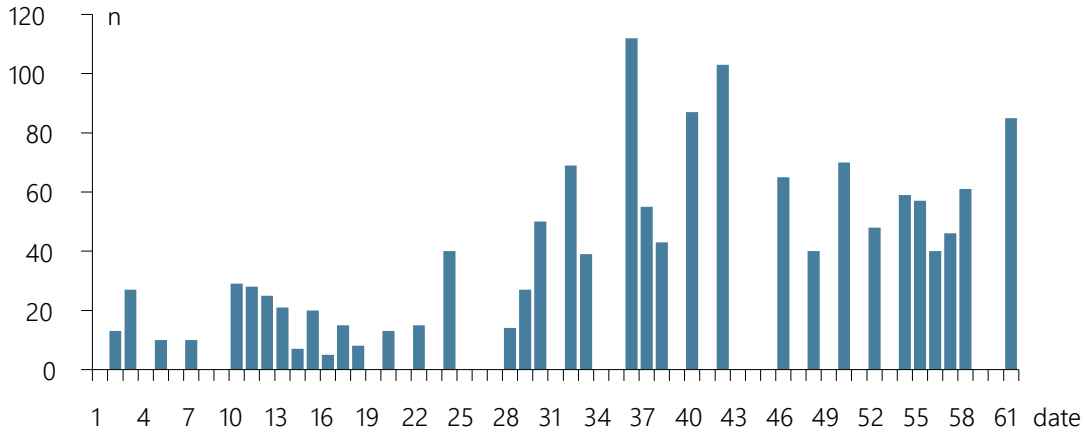

figure 2. Daily maximum number of great skuas observed at the club site at Vatndalsvatn, Skúvoy, Faroe Islands, between 2 May - 30 June 2013. Counts were made in the late morning and evening. If there is no bar, the club site was not counted. Day number 1 = 1 May

Aantallen grote jagers in ochtend en avond op de soos bij Vatndalsvatn, Skúvoy, Faröer, tussen 2 mei - 30 juni 2013. Dagnummer 1 = 1 mei

& Hammer 2018). The number of territories in which eggs were found was 114 in 2012 and 133 in 2013. Chicks were found in 66 of these territories in 2012 and 84 in 2013. In addition, in 2012, another 35 territories were found only at the chick stage. In 2012, 89 large chicks could be ringed, and 82 in 2013. Chicks fledge after 42-56 days and the parental care stops in the two following weeks, when the parents depart (Perry 1948).

FEATHER MARKING

On Skúvoy, from 29 May–7 July 2013, we caught 51 adults, all on different nests (mostly in the Bergið colony, a few on the rest of the island), with a wire-trap that was released remotely (Hammer 2017). Because we started marking feathers only from halfway the season onwards, the first 31 individuals were not marked. Also the last individual was not marked. So, of 19 birds, caught on 15–27 June 2013, we marked the inner five primaries of both wings (in total 190 feathers) on the underside with a Sharpie® black waterproof marker (figure 3). The other feathers were not marked because we presumed they are never moulted on the Faroes. We used a unique combination of long and short stripes on the shaft to indicate the individual, and a number (1–5) on the inner vane to indicate the primary type. The sex was

figure 3. Primary marks on a trapped adult in the field. Photo: Kees Schreven

Adulte grote jager met genummerde handpennen.

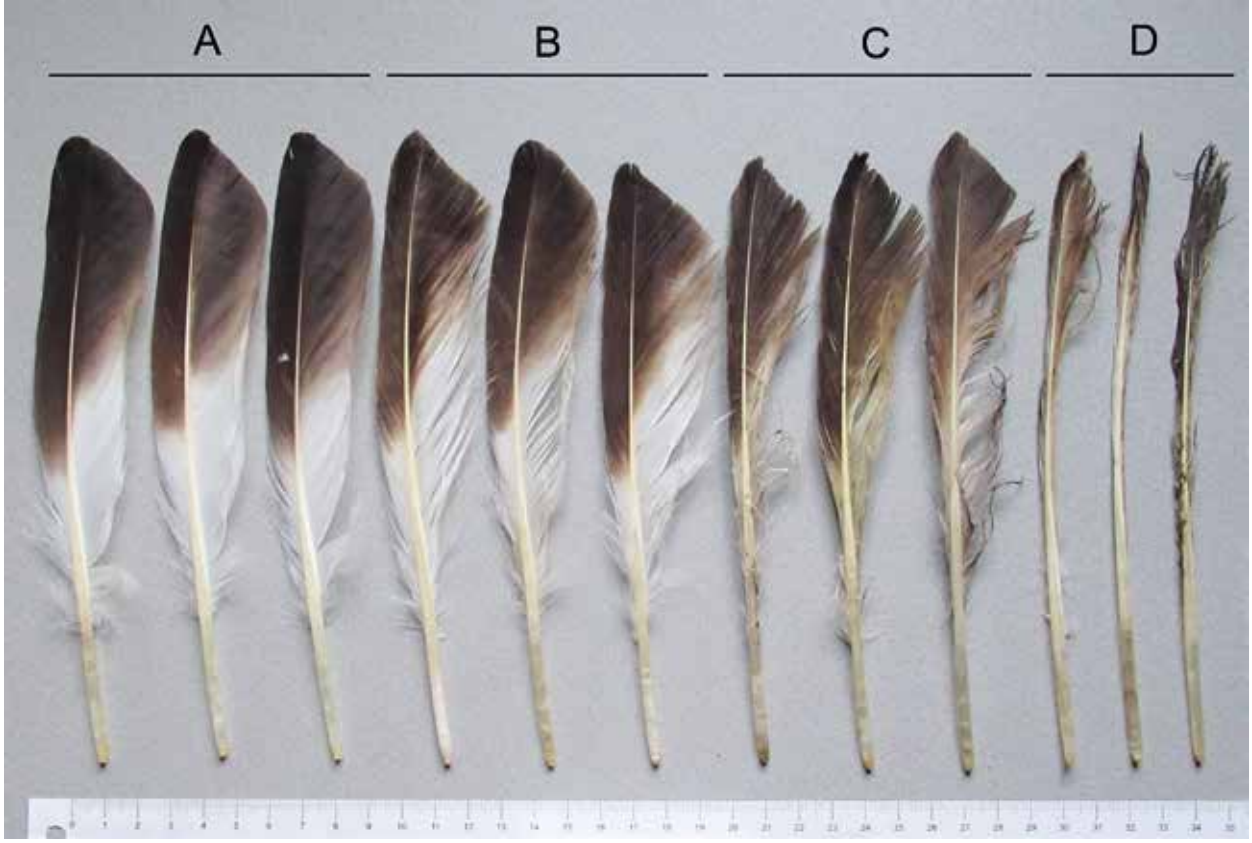

figure 4. Freshness of found shed feathers (here, p1). A: fresh, B: presumably from the previous season, in good condition, C: presumably from the previous season, in more abraded condition (*e.g*. when laying in a ditch), D: presumably from two years ago.

Versheid van gevonden handpennen (hier alle p1). A: vers, B: vermoedelijk van vorig jaar maar in goede staat, C: vermoedelijk van vorig jaar maar meer gesleten, D: vermoedelijk van twee jaar geleden.

figure 5. Reference feathers from a large individual (A) and a small individual (B).

Referentiehandpennen van een groot (A) en een klein exemplaar (B).

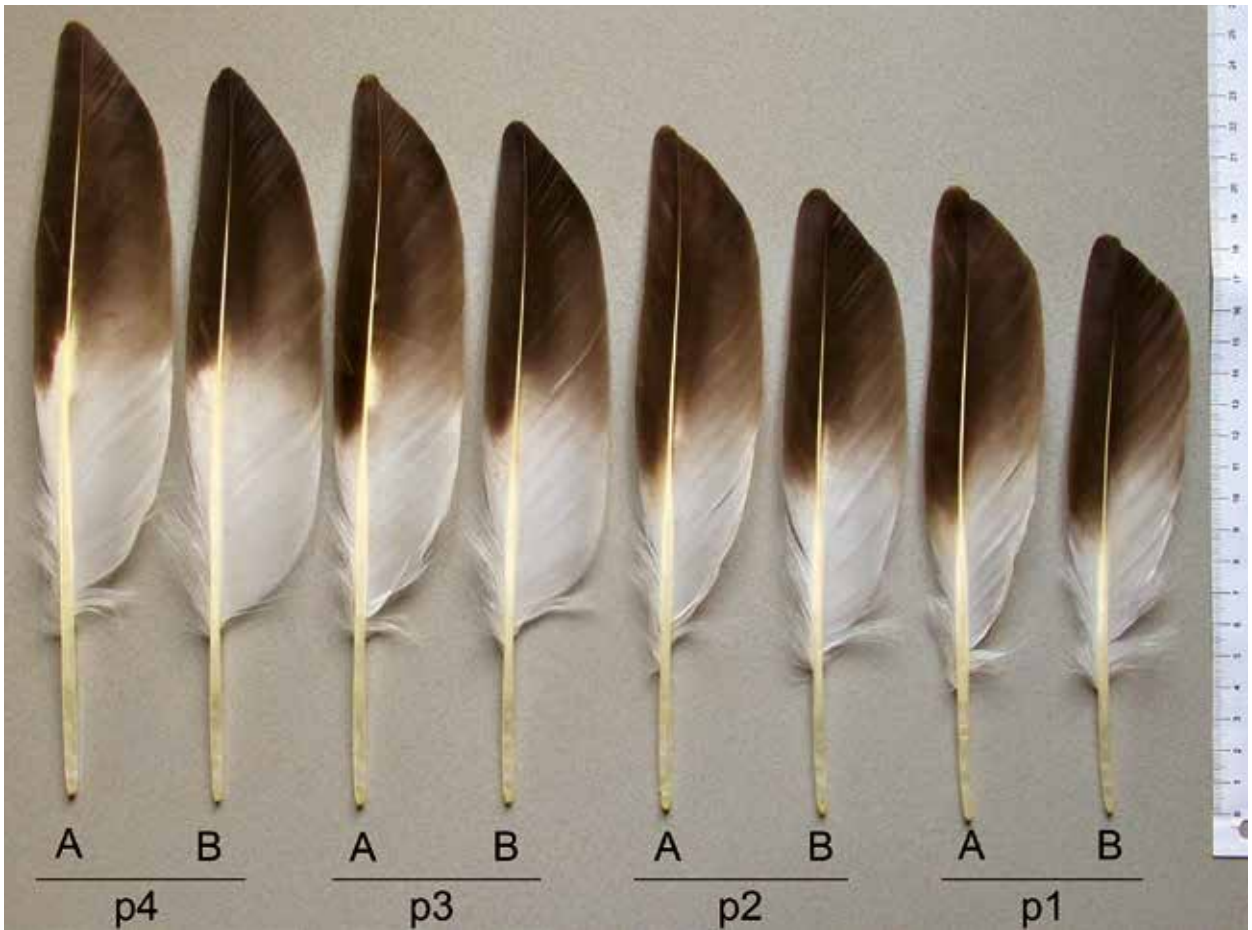

table 2. Repeatability of the identification method for moulted primaries, between two assignment rounds. The number of feathers is presented. The proportion of the first round that was assigned to the same type in the second round is given in the last column.

Determinatie van handpennen in twee rondes. Het aantal veren is gegeven. Het aandeel correct toegewezen handpennen staat in de laatste kolom.

first assignment *eerste ronde*	**second assignment** *tweede ronde*					**proportion similar** *aandeel gelijk*
	p1	**p2**	**p3**	**p4**	**unknown**	**(%)**
p1	147	-	-	-	-	100
p2	8	102	3	-	-	90.3
p3	-	5	33	-	-	86.8
p4	-	-	-	3	-	100
unknown	1	3	1	-	-	0
total	156	110	37	3	-	-

determined molecularly with blood taken from the leg vein (Hammer 2017).

FEATHER COLLECTING

On Skúvoy, our search effort was highest. Feathers were collected on the whole island, but mainly in the Bergið colony and around the Vatndalsvatn club site. The colony was searched incidentally while conducting other fieldwork from late April to late July 2013 (see Schreven & Hammer 2019), and intensively on 4, 10, and 11 August 2013 and 30–31 May 2014. The club site around Vatndalsvatn was searched intensively (mostly in the main area on the shore, but sometimes also in additional areas) on 7, 17 and 30 June, 10 July, 8 and 11 August 2013, and on 31 May 2014. In Saksun, the club site was searched on 24 May and 9 June 2014, and the colony on 25 May 2014. On Svínoy, the colony was searched 10 and 11 June 2014. In 2012, one fresh feather was found incidentally on Skúvoy, date unknown. During our searches we found freshly shed feathers, but also feathers that were shed a longer time ago (figure 4). On fresh feathers, the brown part was darker and more glossy than on older feathers (*i.e.* feathers that we assume to have been shed in the previous year). Older feathers were also more abraded, had a less transparent quill, and the tip of their quill was often dirty. Old feathers that lay in a ditch had often become stiff, fragile and more abraded. Feathers that we assume to have been in the field for two years, consisted of only a quill, shaft, and some stiff barbs at the top. These two-year old feathers were left out of further analysis, because heavy wear made measurements and assignment to primary type unreliable.

ASSIGNING FEATHERS TO PRIMARY TYPES

To assign a found feather to a primary type (p1, p2, *et cetera*), we compared it with reference feathers of known primary type (figure 5). These came from five dead adults from the Faroes (found in May-June, 2012-2014, of which two were ringed in the Faroes as chick seven and ten years ago), one dead adult from Vlieland (found on 18-11-2013) and the shed marked feathers that we found in the field. In addition, a colleague sent us feather lengths of four dead adults (three from North-Germany, one from South-Iceland).

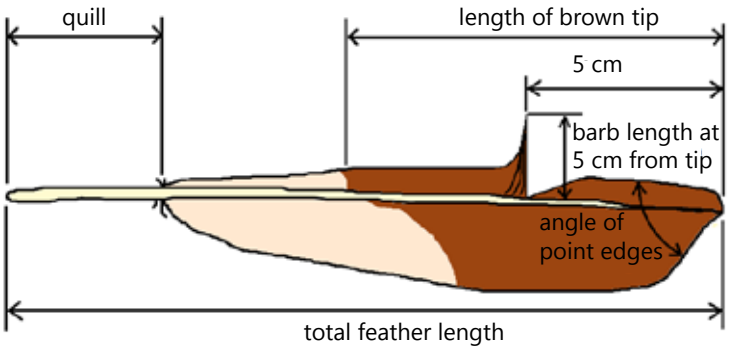

figure 6. Measurements taken from primaries to establish the primary type.

Maten voor het bepalen van het handpennummer (p1-p4).

The moulted primaries were assigned to the most likely primary type by visual comparison with the reference set by KS. Attention was paid to seven characteristics

of each feather (figure 6): the maximal total length (to the nearest mm, in stretched position), the length of the quill (mm, from the base of the feather till the sprouting of the barbs), the length of the brown distal part (mm, from the feather tip till the brown-white transition on the outer vane, measured along the shaft in a stretched feather), the length of barbs at 5 cm from the tip (mm, stretched out perpendicular to the shaft), the pointedness of the feather tip in natural position (to the nearest five degrees), the shape of the feather tip (more lobed in innermost primaries, more gradually pointed in further primaries) and the curvature of the rachis (more curved in innermost primaries, straighter in further outwards positioned primaries). The identification was done two times, by KS, with 3.5 years in between, to increase robustness. The proportion of feathers assigned to the same type in the first and second round was 95% (see table 2). We have highest confidence in the results of the final round and use these in further analysis. As a validity check, the first five above-mentioned characteristics were measured and compared between the reference set and the set of moulted feathers after they had been assigned to primary types (table 3). The moulted feathers were of similar shape and size as the reference feathers (table 3), but had clearly shorter brown tips (Linear model, β=6.3 mm, t=4.21, df=324, p<0.001) and tended to have shorter barbs (Linear model, β=0.42 mm, t=1.88, df=327, p=0.06), in statistical tests that corrected for primary type as a factor and

table 3a. Morphometry of p1-5 of reference samples. The average length and range (both in mm) of 5-13 individuals are presented, depending on the availability in our reference samples. The tip angle is given in degrees. For methodology of measuring see methods and figure 6.

Morfometrie van p1-p5 van referentiecollectie, gemiddelde lengtes en spreiding (in mm) van 5-13 individuen afhankelijk van de beschikbaarheid van de pennen. Zie ook figuur 6 voor het nemen van maten van de veerlengte en kleurpatronen.

primary type	**total length**	**quill length**	**brown tip length**	**barb length outer vane**	**angle of tip edges**
handpennr	***totale lengte***	***spoellengte***	***lengte bruine punt***	***baardlengte buitenvlag***	***hoek van veertop***
	n=11,13,12,9,10	n=7,9,8,5,6	n=7,9,8,5,6	n=7,9,8,5,6	n=7,9,8,5,6
p1	191.8 (174-203)	37.7 (36-41)	101.0 (90-114)	26.1 (25-27)	52.9 (50-55)
p2	207.3 (191-220)	42.7 (38-46)	103.6 (84-117)	24.5 (23-26)	45.6 (40-50)
p3	224.6 (206-236)	46.6 (44-50)	107.6 (93-124)	24.4 (22-25)	41.6 (40-45)
p4	241.8 (223-254)	50.3 (48-55)	111.8 (98-121)	23.6 (23-25)	40.0 (35-45)
p5	259.5 (241-276)	52.3 (50-55.5)	116.8 (98-147)	22.8 (22-23)	37.9 (35-40)

table 3b. Morphometry of moulted feathers, after being assigned to primary number p1-4 (in mm). The average and range is given for the primaries in which the measurement could be taken. See also table 3a.

Indeling en morfometrie van gevonden handpennen (p1-p4). Niet alle pennen konden worden gemeten. Zie ook tabel 3a.

primary type	**total length**	**quill length**	**brown tip length**	**barb length outer vane**	**angle of tip edges**
handpennr	***totale lengte***	***spoellengte***	***lengte bruine punt***	***baardlengte buitenvlag***	***hoek van veertop***
	n=153; 104; 36; 3	n=156; 110; 37; 3	n=152; 104; 36; 3	n=153; 105; 37; 3	n=149; 103; 34; 3
p1	191.8 (175-211)	37.7 (32-46)	94.6 (71-118)	25.3 (22-29)	50.7 (40-60)
p2	207.7 (194-222)	42.1 (36-52)	96.5 (80-114)	24.4 (20-27)	44.5 (40-60)
p3	224.6 (214-239)	46.1 (42-52)	99.3 (79-120)	23.8 (20-25)	41.3 (35-50)
p4	239.3 (234-243)	48.3 (48-49)	98.0 (94-100)	22.7 (22-23)	41.7 (40-45)

table 4. Extent of primary moult of great skuas on breeding grounds across the breeding range.

Handpenrui van grote jagers op verschillende broedlocaties.

latitude *breedte*	area *gebied*	site *locatie*	year *jaar*	extent of moult *handpenrui*	method *methode*	source *bron*
N 77°	Lurøya, Svalbard	breed + club	2018	p1-2	searching feathers (n=6), observing flying birds (August 8th)	Kees Schreven
N 74°	Bjørnøya, Norway	breed	2005-2013	yes (at least p1)	catching adults on nests (n=206), observing flying birds late in season	Hallvard Strøm
N 71°	Jan Mayen, Norway	breed	2014	p1	observing flying birds (August 17th)	Van Bemmelen *et al.* 2018
N 70°	Loppa island, Finnmark Norway	breed	2012, 2014, 2016	yes (at least p1-2)	catching adults (late June-early August, n=20)	Morten Helberg
N 66°	Fljótsdalshérað, Iceland	breed	2016	p1-3	searching fresh feathers (mid-August, n=6)	Halldór Walter Stefansson
N 62°	Skúvoy, Saksun, Svínoy, Faroe Islands	breed + club	2012-2013	p1-3 (and p4 after mid-August	searching fresh and old feathers (April - mid-August, n=306)	this study
N 60°	mainly Hermaness, Shetland	breed + club	1998-2003	p1-2(3?)	observing flying birds (late in breeding season)	Stephen Votier
N 60°	Foula, Shetland	breed + club	1971-2010	no	catching adults on nests (n=500) and immatures on club sites (n=100), observing flying birds, searching feathers. Only May-late July	Robert Furness

feather length.

All statistical tests were performed with R software (R Core Team 2017).

ESTIMATING THE NUMBER OF MOULTING SKUAS

By retrieving the marked feathers in the field, we estimated how many birds were involved in primary moult on Skúvoy. Because skuas moult their primaries descendantly (from the innermost outwards), and the left and right wing more or less simultaneously, we assume that if we find a specific primary, the bird must have shed the same feather of the other wing as well, plus the preceding primaries. We do not know if the bird has already shed more outer primaries, neither do we know if other birds have shed primaries that we did not find. Thus, we can only give a minimum estimate of shed feathers and a 'maximum' proportion found. We divided the total number of shed primaries found on Skúvoy by this proportion to get the (theoretical) minimum total number of shed primaries on Skúvoy. To know the number of individual skuas involved, we divided this number by two (because it included left and right primaries) and then multiplied this by the proportion of p1 in our found shed feathers. This gives a minimum estimate of the number of skuas that had started primary moult on Skúvoy. For this calculation, we assumed that p1–4 have the same encounter probability on land, which may not be completely realistic, because the time that skuas spend above land may decrease as their breeding season (and thus moult) progresses.

EXTENT OF PRIMARY MOULT IN OTHER BREEDING LOCATIONS

During 2013-2019 we asked 32 colleagues across the breeding range of great skuas whether they have

assessed (or want to assess in following years) the extent of primary moult on their study sites, either by catching adults late in the season, observing moult gaps of flying birds, or by searching shed primaries in the field. One person collected primaries and sent them to us for identification, which was done by KS following the method described above. In addition, KS had visited Svalbard on an expedition by NIOO-KNAW and Aarhus University, Denmark, (see Madsen *et al.* 2019) and collected feathers on the island of Lurøya.

RESULTS

PRIMARIES FOUND ON THE FAROES

In total 367 primaries were found, of which 302 on Skúvoy (55 from 2011, 141 from 2012, 106 from 2013), 58 in Saksun (6 from 2012, 52 from 2013) and 7 on Svínoy (all from 2013). The feathers from 2011 on Skúvoy and from 2012 in Saksun were found after two years and were left out of further analysis. The remaining 306 primaries were found in fresh condition during or after the breeding season (on Skuvoy 1 in 2012, 96 in 2013) or in the next spring and summer (on Skuvoy 151 moulted in 2012, 10 moulted in 2013; on Saksun and Svínoy all feathers, moulted in 2013).

We found more right (n=200) than left (n=167) primaries, but the deviation from parity was not significant (binomial generalized linear model with logit link-function, z=1.72, p=0.09).

SHED PRIMARY TYPES ON THE FAROES

All of the found shed primaries were the innermost four, p1 to p4. They were found in decreasing numbers, p1: n=156 (51%); p2: n=110 (36%); p3: n=37 (12%); p4: n=3 (1%). In 2013, the relative frequencies were not significantly different between Skúvoy, Saksun and Svínoy (figure 7, Fisher's Exact test, n=165, p=0.36). On Skúvoy, the extent of moult was not different between 2012 and 2013 (figure 7, Fisher's Exact Test, n=247, p=0.31). Only for Skúvoy (2012 and 2013 combined) we can make a comparison of moult between the breeding colony and club site, given the good search intensity and sample sizes. In the colony we found 77 primaries, on the club site 163 and on the rest of the island 7. The relative frequencies of p1-4 did not differ significantly between the breeding colony and the club site (colony: 49% p1, 39% p2, 12% p3; club site: 53% p1, 35% p2, 10% p3, 1% p4; Fisher's Exact Test, n=240, p=0.82).

Of the 190 marked feathers of breeding birds, we found 6 (one p1, three p2, two p3), of which four in the colony (p1, 2x p2, p3) and two on the club site (p2, p3). The primary number marks were readable, but the individual marks were very faded and difficult to read. Five out of six feathers could be assigned to individuals. The sixth could not be assigned with certainty, but was from a different individual than the other five. In the colony, one feather was found in the territory of the marked bird, one 250 m away, one 360 m away, and for one feather the location was unknown. The five feathers were from 2 males and 3 females of five clutches that were laid on average on 24 May 2013 (18 May – 5 June), whereas the clutches of the 13 individuals with marked feathers that we did not find back were laid on average on 30 May 2013 (16 May – 14 June). This difference was not significant (Kruskall-Wallis Rank sum test, Chi-square=1.53, df=1, n=18, p=0.22). Of these five clutches, four had hatched, whereas the fifth concerned a replacement clutch, which had hatched successfully.

THE TIMING OF MOULT ON SKÚVOY

Only on Skúvoy in 2013, our searches were frequent enough to allow an estimation of the timing of moult. The first freshly moulted feathers were found on 17 June (p3), 30 June (p1) and 10 July (p1). Following the calculations by Van Bemmelen *et al.* (2018), this suggested that the first individuals had started to moult between early June and early July. More individuals had started by early August (during 20 June – 8 August, fresh feathers were: 25 p1, 12 p2 and 3 p3), and fresh feathers on 10 – 11 August

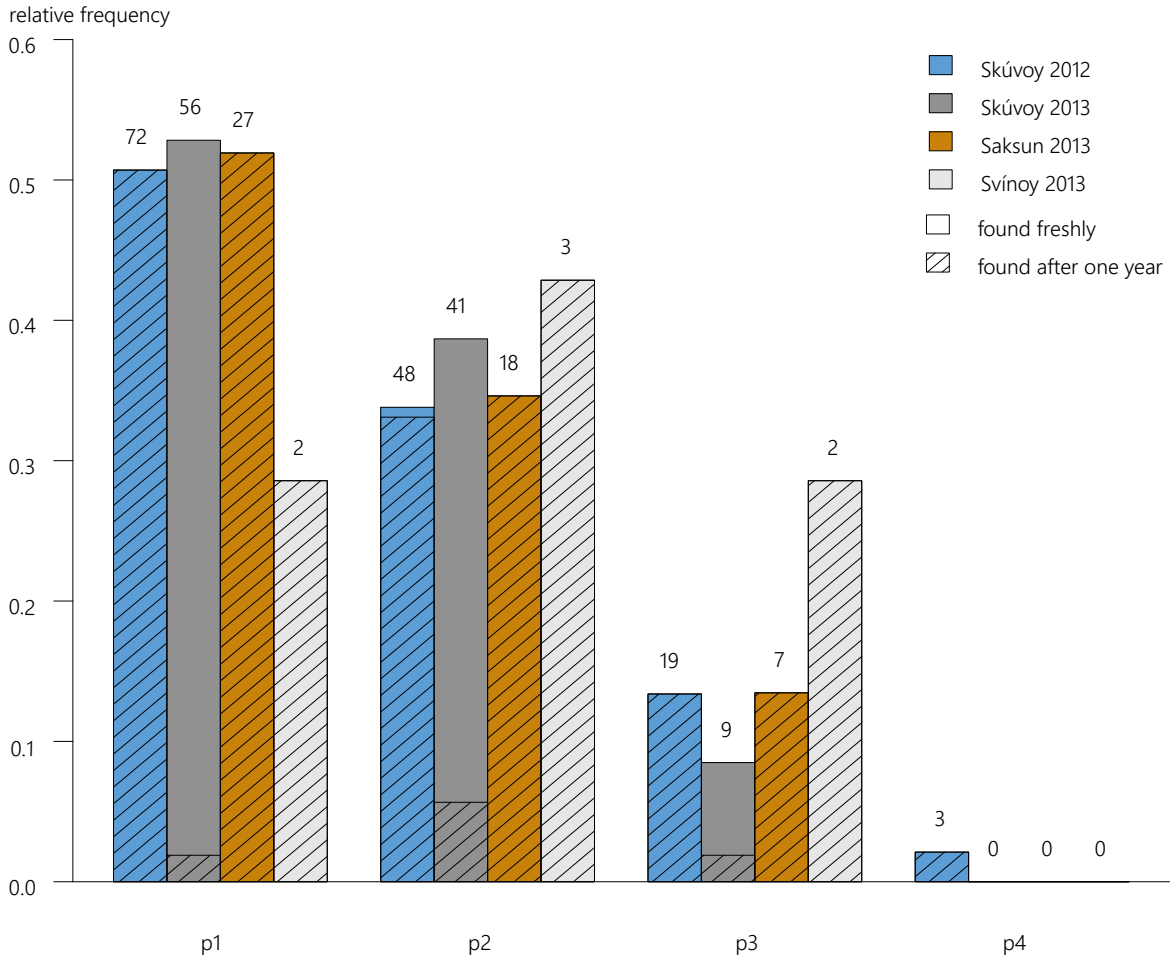

figure 7. Frequency distribution of moulted feathers on Skúvoy in 2012 and 2013, and on Saksun and Svínoy in from 2013, split up for years in which a feather was found (fresh or after one year). The numbers of feathers are indicated above each bar. The relative frequencies are calculated for each place within a particular year.
Relatieve frequenties van de geruide binnenste handpennen (p1-p4) die gevonden zijn op Skúvoy (in 2012 en 2013), en op Saksun en Svínoy (in 2013), onderverdeeld in verse veren en veren van een jaar oud. Het aantal veren is boven de staven gegeven.

showed that moult was progressing but also that other individuals started moulting (fresh feathers: 27 p1, 23 p2 and 3 p3).

NUMBER OF MOULTING SKUAS ON SKÚVOY

From the six marked marked primaries that we retrieved (all from different individuals) we surmise that these birds had moulted at least an additional 20 primaries that we had not found (namely, the more inner ones, and the ones from the other wing). Thus, we had only found 6 out of their 26 (23%) shed primaries. We may have missed more feathers, *i.e.* more outer-positioned and from other individuals, but this is unknown, and therefore this is a minimum estimate. The sample size was too small to allow calculation of primary-specific finding probabilities. Based on the 246 shed primaries that we found on Skúvoy from 2012 and 2013, the total number of moulted feathers would have been 1066 (*i.e.* 246/0.23). By dividing by two (because it included left and right feathers) and then taking 51% of this (which was the proportion of p1), it gives the number of moulting great skuas on Skúvoy: 272 in 2012 and 2013, so 136 per year. This is a minimum estimate, and would correspond to at least almost half (45%) of the approximately 300 skuas that are present on Skúvoy in the breeding season.

HOW WIDESPREAD IS MOULT ON BREEDING GROUNDS?

In recent years, primary moult has been observed across the breeding distribution of great skuas (table 4). However, R.W. Furness (pers. comm.) had not observed primary moult on Foula, Shetland, in 1971–2010, but he had visited these breeding grounds only in May till late July, so possibly too early to observe birds in active moult. Neverthess, he had never found moulted primaries in the field, and he thinks that he could not have overlooked any moult occurring during his studies. Stephen Votier observed primary moult on Shetland in 1998–2003 but had mainly worked on Hermaness. Because in all locations, the moult was assessed in early or mid-August, we can compare the extent of moult over a latitudinal gradient. Primary moult seems to be most extensive on the Faroes with p1-3 (and p4 after mid-August), Iceland and Shetland (p1-3), but was also recorded in Norway, Jan Mayen, Bjørnøya and Svalbard, with (at least) p1-2. However, it must be noted that the intensity of the study was much higher in the Faroes than elsewhere.

DISCUSSION

Based on 306 moulted primaries found in three locations on breeding grounds in the Faroe Islands, we have shown that great skuas moult p1 up to p4 there, late in the breeding season. On Skúvoy, we estimated that at least 45% of the great skuas start moult on the breeding grounds, and that they start primary moult from June (July) onwards. Elsewhere in the breeding range, primary moult is common as well nowadays.

PRIMARY IDENTIFICATION METHOD

The identification of primary types seemed reliable, because the measurements of moulted feathers (after being assigned to primary types) were in line with those of reference specimens, and the repeatability of the assignments was high. Because the reference feathers were all fresh, the 6.3 mm difference in the length of the brown tip between found shed feathers and reference feathers could be largely explained by fading in the field. Indeed, shed feathers found after one year had on average a 4.6 mm shorter brown tip than freshly found shed feathers, in a statistical model that corrects for primary type as a factor and feather length (Linear model, $t=-5.50$, $df=289$, $p < 0.001$). Similarly, feathers found after one year had 0.33 mm shorter barbs (Linear model, $t=-2.36$, $df=290$, $p=0.01$) and a 3.1 degrees pointier tip (Linear model, $t=-6.91$, $df=282$, $p < 0.001$) than freshly found feathers. Both are also likely to be caused by wear in the field after moult.

WHICH BIRDS HAVE MOULTED THESE FEATHERS?

Great skuas only come to land on the breeding grounds during the breeding season (Del Hoyo *et al.* 1996, Magnusdóttir *et al.* 2012) and also on Skúvoy, great skuas are only seen between late April and late September. Because foraging trips are maximum several tens of kilometres (for Shetland: Votier *et al.* 2004), the birds moulting on the Faroes are probably only Faroese skuas.

The fact that we found primaries on all three visited locations shows that moult is widespread on Faroese breeding grounds, and we estimated that at least 136 great skuas are involved on Skúvoy annually. Strictly, we do not know which birds exactly moult there. At least, our marked feathers showed that some local breeders are involved. To what extent the remaining fraction consists of immatures, non-breeders and breeders is not known. The primaries that we found on the Faroes were moulted from early June (July) onwards. Such early onset would correspond to early moulting adults and possibly some immatures. We found feathers both in breeding colonies and club sites. However, this does not translate directly into breeders versus non-breeders and immatures, because breeders visit club sites regularly (Furness 1987, and pers. obs.), and non-breeders and immatures from club sites may also visit the breeding colony.

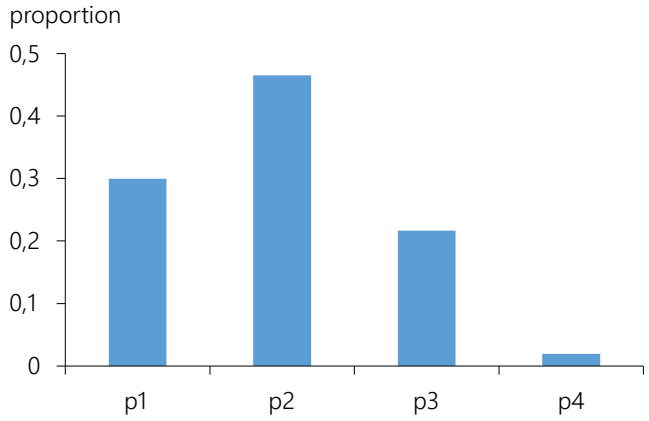

figure 8. Distribution of the last shed primary before departure of moulting great skuas in the Faroe Islands. This was calculated based on figure 7, using the total number of found feathers for each primary. See text for calculation.
Laatst geruide handpen voor vertrek uit de broedgebieden van ruiende grote jagers op de Faeröer, gebaseerd op de gegevens in figuur 7.

MOMENT OF DEPARTURE DURING MOULT CYCLE

We can get an impression of the moment in the moult cycle at which great skuas leave the Faroes, by regarding the difference in the numbers of subsequent primary types. If we take the total number of found feathers of a particular primary from figure 7 minus the total number of the following primary, and divided by the total number of p1, we get the proportion of moulting skuas that left the Faroes after moulting that certain primary. This shows that most moulting birds leave the Faroes after shedding p2 (figure 8). For this calculation, we assumed again that p1–4 have the same probability on land after being shed.

GEOGRAPHICAL VARIATION IN PRIMARY MOULT ON BREEDING GROUNDS

We cannot evaluate whether the discrepancy among earlier publications concerns variation among subpopulations, variation over time, or variation in methodology. Information from elsewhere shows that at present primary moult occurs across the entire breeding range (table 4). The extent of primary moult appears to be showing a possible latitudinal pattern: towards the north, primary moult seems less extensive on breeding grounds than in the south. Although differences in methodology, effort and precision of the assessments make it difficult to draw conclusions about geographical variation, we will explore several explanations for such a latitudinal pattern.

First, the timing of start of the breeding season. In northern breeding areas, this is later than in the southern areas (Bourgeon *et al.* 2012, Bourgeon *et al.* 2014, Schreven & Hammer 2019). If the overlap of breeding and moult is the same in all colonies, skuas breeding in the north would have a shorter time window for moult before mid-August, *i.e.* the time at which the moult was assessed by the various researchers in 1998-2018. That shorter time window could explain why moult is less progressed in the north by mid-August. However, Leat *et al.* (2013) describe that also the autumn departure date of breeders in the north is later than in the south. Therefore, as primary moult progresses after mid-August, the latitudinal pattern that we have described above may actually change or disappear.

Second, the breeding success. Failed breeders moult earlier than successful breeders. Is the breeding success lower in the south than in the north? This does not seem the case, as shown by Bourgeon *et al.* (2014) and in general, breeding success can vary greatly between years (Bustnes *et al.* 2015). Recently, the breeding success in the big colony of Foula has dropped dramatically due to food shortage (R.W. Furness pers. comm.), but primary moult was not seen on Foula in 1971-2010. On the other hand, primary moult was seen on Hermaness in 1998-2003. The methodology in both areas differed, but these contrasting results also raise other questions: do failed and non-breeders leave the breeding grounds earlier in a big colony (*e.g.* Foula, ca. 2000 pairs, Votier *et al.* 2007) than in a smaller colony (*e.g.* Hermaness, 700 pairs,

Votier *et al.* 2007), possibly to avoid competition, and therefore moult elsewhere?

Third, the age composition. Immatures and non-breeders moult earlier than adult breeders. Are there more immatures and non-breeders in the southern areas? Based on the age of the different sub-populations, one would expect the opposite. The northern breeding areas have been colonized more recently (Furness 1987, Del Hoyo *et al.* 1996), and the local skuas are therefore expected to be younger than skuas in the southern breeding areas. On the other hand, the presence of young skuas also depends on the local reproduction rate.

CONCLUSION

We confirmed that great skuas start moulting their primaries (maximally the innermost four, p1-4) on the breeding grounds. Whereas some literature sources state that primary moult only starts during migration, it is currently observed throughout the breeding range, with potentially a larger extent on southern than on northern breeding grounds, by the time of mid-August. The most likely explanation for this potential latitudinal pattern may be the later start of the breeding season in the north, resulting in a shorter time window for primary moult before mid-August. Such variation between sub-populations could partly explain on the one hand the discrepancies between literature sources and on the other hand the wide range in reported start dates of primary moult.

ACKNOWLEDGEMENTS

figure 9. Pair of great skuas in territory on Skúvoy, Faroe Islands, 24 May 2013. The male was (colour-)ringed in 2012. Photo: Kees Schreven

Paartje grote jagers in broedterritorium, Skúvoy, Faeröer, 24 mei 2013. Het mannetje is in 2012 gekleurringd.

We thank Harry Jensen for permission to work on his land. We thank Líggjas á Váli Smith, Rune Skjold Tjørnløv, Martin Berg, Martin Sirkovsky, Jónheðin Tróndheim, Marius Stokke Sønnedal, Rakul Mortensen and Katrin Hoydal for their help in the field seasons 2012 and 2013, and Stijn Schreven for helping to collect primaries in 2013. We thank Harry Jensen, Jens-Kjeld Jensen and Bergur Olsen for additional information about skuas on the Faroes. We thank Erwin Tyll for additional reference feather lengths, Kees Camphuysen for supplying an additional skua found dead by Carl Zuhorn, and Halldór Walter Stefánsson for sending feathers from Iceland. Further we thank all people that responded to our inquiry about moult in other locations: Rob van Bemmelen, David Boertmann, Kees Camphuysen, Miles Drake, Robert W. Furness, Maria Gavrilo, Lucy Gilbert, Peter Glazov, Jannik Hanssen, Svein Are Hanssen, Gunnar Thor Halgrimsson, Morten Helberg, Jens-Kjeld Jensen, Ko de Korte, Yuri Krasnov, Maarten Loonen, Elisabeth Masden, Ellen Magnúsdóttir, Mikhail V. Melnikov, Ivan Mizin, Børge Moe, Gerard Müskens, Bergur Olsen, Iryna Pokrovskaya, Jeroen Reneerkens, Hans Schekkerman, Vitaly Spitsyn, Halldór Walter Stefánsson, Hallvard Strøm, Tom Versluijs, Andrey Volkov and Stephen Votier. We were supported by a grant to SH from the Faroese Research Council (Granskingarráðið) and Statoil Faroes.

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SAMENVATTING - HANDPENRUI VAN GROTE JAGERS IN DE BROEDGEBIEDEN, MET SPECIALE AANDACHT VOOR DE FAERÖER

Handpenrui kost energie en vermindert het vliegvermogen. Daarom overlapt het bij veel vogelsoorten niet met het broedseizoen of met de trek, maar grote jagers beginnen de handpenrui al laat in het broedseizoen en gaan ermee door tijdens de trek. Echter, zestien publicaties tussen 1921-2018 geven verschillende informatie over de timing en locatie van de start van de handpenrui, en het is onduidelijk of dit geografische of temporele variatie weerspiegelt. Een kwantificering van de handpenrui in de broedgebieden ontbreekt. Wij onderzochten de rui van grote jagers op de Faeröer en vonden dat ze de binnenste vier handpennen (p1-4) al in het broedgebied kunnen ruien. We verzamelden 306 geruide handpennen in drie gebieden: Skúvoy (2012 en 2013), Saksun (2013) en Svínoy (2013). We bepaalden het handpentype (p1-4) van deze veren aan de hand van maten en vergelijking met

een referentiecollectie, en vonden 51% p1, 36% p2, 12% p3 and 1% p4. Deze frequenties verschilden niet significant tussen de drie gebieden, en ook niet op Skúvoy tussen 2012 and 2013. Opmerkelijk genoeg verschilden ze evenmin tussen een broedkolonie en een soos, terwijl we dit wel hadden verwacht, omdat een soos ook wordt bezocht door onvolwassen vogels, waarvan bekend is dat ze eerder in het seizoen ruien dan broedvogels. Op Skúvoy vingen we 19 adulten op het nest, merkten de binnenste vijf handpennen (p1-5) van beide vleugels (190 individuele veren), en vonden hiervan 6 (3,2%) gemerkte veren terug in het veld. Gebaseerd op deze gemerkte veren schatten we dat ten minste 45% van de 300 broedende grote jagers op Skúvoy ten minste hun binnenste handpen (p1) daar ruien. Navraag bij collega's wees uit dat in het gehele broedareaal grote jagers tegenwoordig enige handpennen kunnen ruien, maar rond half augustus schijnbaar vaker in het zuiden (IJsland, Faeröer, Shetland) dan in het noorden (Noorwegen, Jan Mayen, Bereneiland, Spitsbergen). We bespreken verschillende verklaringen voor dit patroon: variatie in de timing van het broedseizoen, het aandeel mislukte en niet-broeders, en voedselaanbod. Zulke variatie kan enerzijds de discrepanties in de literatuur verklaren, en anderzijds de grote spreiding in startdatum van de handpenrui.

Kees H.T. Schreven, Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands. kees_schreven@hotmail.com
Sjúrður Hammer, Institute of Biodiversity, Animal Health & Comparative Medicine, University of Glasgow, United Kingdom. Current address: Environment Agency, FO-165, Argir, Faroe Islands, sjurdur@hammer.fo

[verschenen 18 december 2019; herziene versie 27 januari 2020]

Displaying pair of great skuas in their territory. Note that the bird on the left is not yet moulting its primaries. Skúvoy, Faroer Islands, 30 May 2013. Photo: Kees Schreven
Baltsende grote jagers in hun territorium. De vogel links is nog niet aan de handpenrui begonnen. Skúvoy, Faeröer, 30 mei 2013.