The Arctic Skua *Stercorarius parasiticus* on the Faeroe Islands: abundance and plumage polymorphism

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Introduction

The Arctic Skua Stercorarius parasiticus is a common and widespread breeding bird on the Faeroe Islands (Joensen 1966a, Bloch & Sørensen 1984). Scattered, solitary or loosely aggregated pairs are found all over the islands and in some places small to relatively large colonies occur, especially near concentrations of breeding seabirds. In the 20th century the number of breeding Arctic Skuas on the Faeroes is thought to have fluctuated and in the last decades declined. On the basis of a census in 1981, covering all of the archipelago (Bloch 1981, Bengtson & Bloch 1983), the population was estimated at 1200-1500 pairs (Bloch & Sørensen 1984), which corresponds to about one pair per km². Since then several authors seem to be of the opinion that the population has decreased (Mardal 1988, Bloch et al. 1996), though others leave the question open (e.g. Asbirk et al. 1997). In Britain the species has increased during the same period, markedly so in recent years (Cramp & Simmons 1983, Furness 1987, 1997).

The latitudinal cline in plumage polymorphism (melanic and pale morphs) of the Arctic Skua was described a long time ago by Southern (1943). Although there have been some changes in the proportions of the morphs in some areas (see below) the general pattern of the cline remains unaltered. The frequency of the pale morph is in the order of 15-20% in the southern parts of the distributional range (Britain, the Faeroes and southern Iceland) and increases northwards to around 40% in northern Iceland and northern Norway, and to >99% in Svalbard (Southern 1943, Cramp et al. 1983, O'Donald 1983, Furness 1987). On the Eurasian

tundra east of the Kola Peninsula, and on the Canadian tundra, <3% of the Arctic Skuas belong to the melanic morph (Kjellén 1997, 2000). Thus, there are some marked changes in morph frequency over relatively short distances, e.g. on the Kola Peninsula and in Iceland (Bengtson & Owen 1973, O'Donald 1983, Kjellén 1997). The population breeding along the Baltic coast of Finland exhibits the highest frequency of melanic birds (96%) found in any region (Hildén 1971, Ulfvens et al. 1988).

Despite long-term detailed studies of the Arctic Skuas in Shetland (on Fair Isle and Foula) our understanding of the genetic basis of the plumage polymorphism, and the factors that maintains it, remains incomplete (Phillips 2001). The colour morphs seem to be determined by two alleles at a single locus, with the allele for dark plumage being semi-dominant, which explains the occurrence of individuals with intermediate plumage (O'Donald 1983). As to the maintenance of the polymorphism a number of hypotheses have been proposed, including some related to the feeding ecology of the species, especially the kleptoparasitic habits (aggressive camouflage and apostatic selection), and others related to timing of breeding and sexual selection (see Furness 1987, Caldow & Furness 1991 and references therein). A model, based on data on sexual selection from Fair Isle, predicts an increase in the melanic morph and an eventual elimination of the pale (O'Donald 1983). The melanic morph has, indeed, increased in frequency in Shetland, Iceland and in the Varanger area in northeastern Norway (O'Donald 1983, Furness 1987, Caldow & Furness 1991), though the pale morph is still present possibly owing to immigration from northern populations (O'Donald 1987). However, the general validity of the findings on Fair Isle with regard to selective pressures are questioned by recent data from Foula (Phillips 2001).

The plumage polymorphism of the Arctic Skua on the Faeroes has received limited attention in the past, though there are scattered published reports on morph frequencies based on actual counts from some colonies or areas ever since the 1930s, and many more "general impressions". During the population census in 1981 we obtained data on morph frequencies from many of the sub-areas and additional information was collected intermittently in the 1980s and 1990s. In 2000 and 2001 we made special efforts to cover all important skua areas known to us on the islands. These data from the past 20 years together with the historical data form the basis for describing and discussing the past and present status of the Arctic Skua population and the plumage polymorphism on the Faeroes. In particular we address the following questions: What is the size of the Arctic Skua population, and is there any evidence of temporal changes or trends? Is there any evidence of a geographic pattern or temporal changes in morph frequencies?

Field data and methods

In 1981 (12 June – 3 July) a total of 37 experienced ornithologists surveyed all parts of the Faeroes (Fig. 1) in an attempt to estimate the abundances of breeding land-birds, excluding the Starling Sturnus vulgaris and House Sparrow Passer domesticus (Bloch 1981). Each two-man team covered all ground within an assigned area, which is why some of the census work was carried out during one-day-visits, whereas some sub-areas were visited a varying number of times. All observations were plotted on field-maps which, together with notes, are kept at the Museum of Natural History in Tórshavn. The field-work is described in more detail by Bengtson & Bloch (1983). In the 1980s and 1990s scattered counts at some Arctic Skua colonies were carried out as one-day-visits by one of the authors (SAB). The surveys in 2000 and 2001, when all the major areas with concentrations of skuas were visited, involved a number of observers and were mostly made over a period of time in each area. All counts were made at a time when the skuas were on their breeding grounds and the estimated numbers are based on territorial behaviour and in many cases nest

records. Because of the many observers involved the accuracy of the estimates is difficult to assess. Counts of Arctic Skua tend to under-estimate true numbers, as suggested by studies on Fair Isle (O'Donald 1983: 32, cf. Lloyd et al. 1991).

The colour morphs of skuas on their breeding grounds were scored whenever possible. In areas with aggregations of pairs the scores consisted of samples in order to avoid counting the same bird twice. Such a sample might be obtained by recording all skuas visible during an instantaneous scan of the area, or by recording pairs at located nests or territories. The latter also yielded samples of pairs where the colour morphs of the mates could be ascertained. Occasionally a sample included all birds in an area. Since intermediate morphs are sometimes difficult to distinguish from the dark morph, at least at some distance, and since many observers were involved, all melanic birds (i.e. dark and intermediates) have been pooled and are referred to as the melanic morph.

Numbers and changes

The Arctic Skua occurs all over the archipelago, but since about 80% of the pairs were found at an altitude below the 300 m level it was largely absent from the mountainous parts of Streymoy and Eysturoy as well as parts of the northern islands (Fig. 2). In 1981 the largest concentrations were found on northern Suðuroy, Skúvoy, Skúvoyarfjall on southern Sandoy, around Saksun on northwestern Streymoy, and on Mykines, Svínoy, and Fugloy; altogether 49% of the 1145 pairs (Table 1). Some of these strongholds have long been known as important areas for skuas, whereas some have not. The concentration on northern Suðuroy in 1981 is not historically documented and had apparently declined substantially already in the mid-1980s. On the other hand, at Akraberg on southernmost Suðurov, the number seems to have increased since 1981. In several areas the number of pairs have either fluctuated markedly (e.g. Skúvoyarfjall) or declined during the past 40-50 years (Table 1 and references therein). The once large aggregations in Svínaskóradalur near Saksun, at Fjallavatn, on Svínoy and on Skúvoy have all decreased more or less dramatically. On Fugloy and Mykines the numbers have fluctuated with moderate amplitudes since the first data in the 1950s, with the exception of a curiously high number on Mykines in 1957.

Prior to the census in 1981 scattered counts (or educated guesses) exist only for a few of the large



Fig. 1. The Faeroe Islands. The localities named in the paper are shown. *Færøerne med de i artiklen nævnte lokaliteter.*

aggregations. In 1961 Skúvoy, Svínoy and the Saksun area held a total of 580-750 pairs (Joensen 1966a), while about 20 years earlier the number had possibly been about 500 pairs. These figures are to be compared with 187 and 192 pairs in 1981 and 2001, respectively (Table 1). Thus, for these three areas the total number appears to have dropped markedly since the early 1960s, although they have remained relatively unchanged during the last two decades. However, if we compare counts in 1981 and 2001 and include Suðuroy, Skúvoyarfjall (Sandoy), Skúvoy, Fjallavatn (Vágar), Svínaskóradalur (Streymoy), Viðareiði (Viðoy), Svínoy, and Fugloy, there has been a 45% decline during the past 20 years. Much of this decline is caused by the drastic reduction in numbers of the exceptionally large concentration found on northern Suðuroy in 1981; disregarding this area the decrease stops at 22%.

Morph frequencies

Table 2 shows morph frequencies in samples from different areas and years. Actual counts are given in most cases, but for some estimates obtained during the 1930s and 1940s sample size or other de-

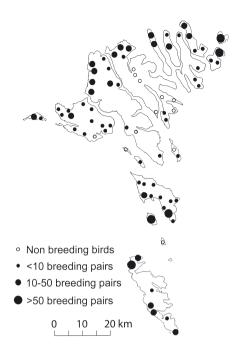


Fig. 2. Distribution of Arctic Skua on the Faeroe Islands in 1981. Black dots indicate altogether 1145 breeding pairs and open circles 26 presumably non-breeding birds. *Alm. Kjoves udbredelse på Færøerne i 1981. De udfyldte cirkler angiver i alt 1145 ynglepar og de åbne cirkler 26 tilsyneladende ikke-ynglende fugle.*

tails are missing (viz. Suðuroy, Skúvoy, Mykines (also for 1966), Fjallavatn, Svínaskóradalur, and Svínoy).

The frequency of the pale morph (Table 2) ranges from about 2 to 29%. However, much of this variation is accounted for by the extremely low figures for Fjallavatn in 1930 and Mykines in 1957. Most of the large samples fall in the range 11-17% pale morph, and there is no obvious geographic pattern in morph frequency within the Faeroes. Samples for eight islands in 1981 (Vágar represented by Fjallavatn; Table 2) do not show any statistically significant heterogeneity (P > (0.4); neither do pairwise comparisons between the samples. For seven islands in 2001 there is no significant heterogeneity (P = 0.14); however, pairwise comparisons show that the frequency of the pale morph on Skúvoy (20.0%) is significantly higher (P < 0.05) than on Suðuroy (10.8%) and nearly so (P = 0.06) when compared to Viðoy (7.5%). All 16 birds in the sample from the Sandvík area on Suðuroy were melanic (several were intermediates), and when excluding this small sub-sample the difference between Suðuroy and Skúvoy is no longer significant (P > 0.1). The Arctic Skua colony at Sandvík is known in recent years to have a markedly lower proportion of pale birds than colonies in other parts of Suðuroy (pers. obs. and Aksal Poulsen pers. comm.).

In a few places, notably at Fjallavatn on Vágar and on Mykines, there appears to have been a marked temporal fluctuation in morph frequency (Table 2). In 1930 at Fjallavatn only four pale individuals were recorded among about one hundred pairs (i.e. 2%); a most remarkable observation since the frequency of pale skuas was considerably higher in other parts of Vágar and on other islands in the same year (Salomonsen 1931). In the early 1940s the colony had about 23-26% pale birds (Williamson 1954), but already in 1948 the pale morph frequency was reported as 11.4%. Since 1964 the frequency of pale skuas at Fjallavatn has been uniform at 19-21%, the sample from 1981 being significantly different from that in 1948 (P < 0.05). For the entire island of Vágar the pale morph was significantly more frequent in 1964 than in 1981, 28.5% vs 16.9% (P < 0.02). Another example of temporal variation is found on Mykines where small samples (or "impressions") indicate that the frequency of the pale morph is in the range of 15-24% (Table 2), though in 1957 a large sample contained only 4% pale birds, significantly less than found in 1939 and 1981 (P < 0.001).

For other islands or areas no significant fluctuations in morph frequency have been detected. On Svínoy, Fugloy, and Skúvoy, where reasonably large samples have been obtained at intervals during the past 40-50 years, no marked fluctuations have occurred. For all years prior to 1981 the geographic coverage was too limited and sample sizes too small (heterogeneity prevents pooling) to make comparisons between years meaningful. In 1981 the overall frequency of the pale morph in the Faeroes was 16.5% (n = 1062; 887/175), and in 2001 14.5% (n = 653; 558/95) (P > 0.2). In 1987 Arctic Skuas were caught on their nests and ringed on Suðuroy, Sandoy, Skúvoy, Mykines, Vágar, Streymoy, Eysturoy, and the colour morphs of breeding pairs were noted on Fugloy; 10.6% of these birds were pale (n = 141; 126/15, see Mardal 1988), which was lower than in 1981, although the difference was not quite significant (P = 0.07).

Small samples of breeding pairs, where the colour morphs of both mates could be scored, were obtained on a few occasions (Table 3). Although the validity of the test may be questioned owing to low values of some expected cell frequencies, assortative mating was suggested on Fugloy in 2001,

but not in 1981, whereas on Svínoy, Skúvoy, and Viðareiði in 2001 and on Mykines in 1984 no deviations from randomness were found.

Discussion

Numbers and changes

The Arctic Skua breeds widely all over the Faeroes, and the only attempt so far to census the entire population was in 1981 with a total of 1145 pairs counted. Recognising that this almost certainly underestimates the true number the population was given as 1200-1500 pairs in Bloch & Sørensen (1984). In view of the difficulties in assessing the number of breeding pairs on the basis of one-day-visits, especially in densely populated areas, and problems associated with scattered counts made by different observers under varying circumstances, such information should be treated with caution (see O'Donald 1983). Nevertheless, we will discuss possible past and more recent changes in the number of the Arctic Skua in the Faeroes, using the census in 1981 as a baseline.

Furness (1987: 52-53) stated that the "numbers in the Faeroes have fluctuated ... but it is not clear if the population has declined as have been suggested by some authors." Furness (l.c.) quoted Joensen (1966a) for a total of about 1000 pairs in 1961, when in fact Joensen's (1966a: 121) figures for 1961 are 580-750 pairs for Skúvoy, northern Svínoy, and the area north of Saksun, and he also refers to previously published counts from Fjallavatn (100 pairs in 1930) and Mykines (150 pairs in 1957). Furthermore, Furness stated that in 1969 the total number had fallen to 250 pairs, which seems highly implausible; the actual source is unknown (given as "Bourne ... in Cramp & Simmons 1983"). A thorough survey by E. Mortensen (pers. comm. in Furness 1987) in 1977 located 1300 pairs and it was suggested that in 1960 there had probably been some 2000 to 3000 pairs in the Faeroes. Regrettably these figures can not be confirmed and should be regarded as no more than educated guesses (E. Mortensen pers. comm.). Similarly, in 1985-1987 Arctic Skuas were being ringed in various places in the Faeroes, and summarizing his observations Mardal (1988) suggested that the total number for the islands was between 800 and 1000 pairs, and that the population was declining. However, he admitted that there was a great deal of uncertainty and insufficient coverage in the counts, and only 286 pairs were actually counted. It has also been suggested that in

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Table 1. Numbers of breeding Arctic Skua pairs (p) or individuals (i) on the Faeroes in different areas and years. The estimates range from actual counts to rough estimates (see text and references).

Island	Locality	Year	Number	Source
Ø	Lokalitet	År	Antal	Kilde
Suðuroy	All	1981	314 p	Present study
, see a second	Akraberg	1981	31 p	Present study
	Akraberg	1985-87	>20 p	Mardal (1988)
	Akraberg	2001	>57 p	K. Janssen in litt.
Skúvoy	All	1939	101 p	Southern (1943)
2	All	1961	280-300 p	Joensen (1963)
	All	1981	102 p	Present study
	All	1987	c. 450 p	Mardal (1988)
	All	1991	c. 30 p	S. Sørensen in litt.
	All	1992	184 i	Højgaard (1995)
	All	2001	128 p	I. Olsen in litt.
Sandoy	All	1966	210-300 p	Gibbs & Mawby (1968)
-	All	1981	138 p	Present study
	All	1985-87	>40 p	Mardal (1988)
	Skúvoyarfjall	1966	90 p	Gibbs & Mawby (1968)
	Skúvoyarfjall	1972	10 p	Flensted-Jensen (1973)
	Skúvoyarfjall	1981	80 p	Present study
	Skúvoyarfjall	2001	>15 p	Present study
Hestur	All	1981	1 p	Present study
Vágar	All	1981	70 p	Present study
-	Fjallavatn	1930	c. 100 p	Salomonsen (1931)
	Fjallavatn	1941-45	c. 300 p	Williamson (1949)
	Fjallavatn	1948	281 i	Nørrevang (1950)
	Fjallavatn	1959	60-70 i	S-A. Bengtson (unpubl.)
	Fjallavatn	1964	67 i	J.L. Pedersen in litt.
	Fjallavatn	1970	25 p	Böhme & Reimer (1973)
	Fjallavatn	1972	c. 50 p	Flensted-Jensen (1973)
	Fjallavatn	1981	46 p	Present study
	Fjallavatn	1985-87	>20 p	Mardal (1988)
	Fjallavatn	1991	c. 10 p	S. Sørensen in litt.
	Fjallavatn	2001	>38 i	Present study
Mykines	All	1957	192 i	Nørrevang (1960)
	W part	1958	12-15 p	Mathiasson (1962)
	All	1959	c. 80 p	S-A. Bengtson (unpubl.)
	All	1966	50-100 i	Meltofte (1967)
	All	1970	21 p	Böhme & Reimer (1973)
	All	1981	46 p	Present study
	All	1985	<15 p	S. Sørensen in litt.
	All	1991	c. 45 p	S. Sørensen in litt.
	All	2001	> 38 i	P. Ketil in litt.
Nólsoy	All	1981	1 p	Present study
Streymoy	All	1981	163 p	Present study
	Svínaskóradalur	1930	c. 150 p	Salomonsen (1931)
	Svínaskóradalur	1942	"large colony"	Southern (1943)
	Svínaskóradalur	1961	150-250 p	Joensen (1966b)
	Svínaskóradalur	1970	30 p	Böhme & Reimer (1973)
	Svínaskóradalur	1972	c. 150 p	Flensted-Jensen (1973)
	Svínaskóradalur	1981	21 p	Present study
	Svínaskóradalur	2001	<10 p	Present study
Eysturoy	All	1981	54 p	Present study
Borðoy	All	1981	7 p	Present study
Kalsoy	All	1981	37 p	Present study
Kunoy	All	1981	20 p	Present study

Antal ynglende Par (p) eller individer (i) af Alm. Kjove på Færøerne på forskellige lokaliteter og år. Angivelserne omfatter både nøjagtige optællinger og grove vurderinger (se tekst og referenser).

Viðoy	All	1981	63 p	Present study
Svínoy	All	1949	>200 p	Petersen (1950)
	All	1953	250-300 p	Williamson (1954)
	All	1961	150-200 p	Joensen (1966b)
	All	1981	64 p	Present study
	All	1983	c. 60 p	L.C. Lund Hansen in litt.
	All	1985-87	c. 30 p	Mardal (1988)
	All	2001	54 p	P. Simonsen in litt.
Fugloy	All	1953	85 i	Williamson (1954)
	All	1981	65 p	Present study
	All	1986	98 i	Present study
	All	2001	42 p	J. Lydersen in litt.

the early 1990s the number was 500-1000 breeding pairs (S. Sørensen in Phillips 2001). These limited counts and "impressions" have lead other authors to put the total population size at 900 pairs (Bloch et al. 1996, Asbirk et al. 1997).

The mostly unknown degree of accuracy associated with the counts, the lack of time series, and the restricted geographic coverage greatly limit the possibility to provide evidence for population changes and trends. The historical data show that prior to 1981 several large aggregations of breeding skuas existed in places where present numbers are considerably lower. At Fjallavatn up to 300 pairs bred in the 1940s (Williamson 1949) but more than 50 pairs have never been reported since then. Similarly, the colony in Svínaskoradalur seems to have contained >100 pairs until at least 1972, but thereafter only about a tenth of that number has been found. On Skúvoy and Svínoy the numbers have been several times higher than they are today, at least until 1961. The drastic reductions in the sizes of the large concentrations of breeding skuas referred to above must inevitably mean a decline of the total Faeroese population, unless some new concentrations were established elsewhere or the number of small aggregations or solitary pairs increased markedly. There is no firm evidence of such displacements or shifts in the distribution of breeding skuas, although numbers may vary a great deal between years and colonies (W. Mardal pers.comm.); e.g. the appearance and subsequent drastical decline of the concentration around Sandvík and Hvalba on northern Suðuroy in 1981 (Fig. 2).

Although Arctic Skuas tend to be faithful to their natal colony, considerable inter-colony movements are known from Shetland and also between Shetland and Orkney (Phillips 2001). Adult skuas, however, rarely change breeding grounds, as shown by a large number of breeding-season recoveries of ringed skuas in the Faeroes, which were invariably found at or near the ringing site (W. Mardal pers.comm.). Assuming that the four concentrations mentioned above (Fjallavatn, Svínaskoradalur, Svínoy, Skúvoy) together held 700-800 pairs in the mid-1940s, as indicated by the published records (Table 1), the total Faeroese population most likely was larger then than in 1981. For three of the colonies (Svínaskoradalur, Svínoy, Skúvoy) the marked decline did not occur until some time between 1961 and 1981. The downward trend seems to have continued since 1981, albeit at a slower rate, and for several areas it may be a question of short-term fluctuations rather than a steady decline in numbers.

Possible causes of decline

Among the more obvious factors that may conceivably affect the numbers of Arctic Skuas on the Faeroes are changes in food resources, competition with the Great Skua *Stercorarius skua*, and human persecution. Since the Arctic Skua is longlived with an annual survival rate close to 90% (Phillips 2001) the taking of eggs or chicks would have a limited impact on the population relative to the killing of breeding birds. In contrast to the Great Skua, however, there are no reports that the Arctic Skua has ever been persecuted in the Faeroes.

Studies in Shetland have shown that the Great Skua, through competition for space and predation, influences the distribution and breeding success of the Arctic Skuas (O'Donald 1983, Furness 1987, Phillips 2001). Similarly, it has been suggested that the increase in numbers of the Great Skua has been detrimental to the Arctic Skua in the Faeroes (e.g. Joensen 1966a). Following a long period of heavy human persecution the Great Skua was on the verge to extinction on the islands (4 pairs in 1897) and was therefore given legislative

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Table 2. Frequency of the pale colour morph in Arctic Skuas on the Faeroes, mostly based on samples of birds scored but in a few cases on estimates (see text and references).

Hyppigheden af den lyse fase hos Alm. Kjove på Færøerne, i hovedsagen baseret på talte fugle, men i nogle tilfælde på skøn (se tekst og referenser).

Island	Locality	Year	% pale	Sample (dark/pale)	Source
Ø	Lokalitet	År	% lyse	Antal (mørke/lyse)	Kilde
Suðuroy	All	1946	c. 16	20-25 i (4 pale)	Ferdinand (1947)
-	All	1978	9.4	29/3	Present study
	All	1981	11.7	136/18	Present study
	All	1984	12.5	21/3	Present study
	All	2001	10.8	107/13	Present study
	Akraberg	1981	21.0	49/13	Present study
	Akraberg	2001	12.5	91/13	K. Janssen in litt.
Skúvoy	All	1939	20	101 p	Southern (1943)
·	All	1961	16.0	304/58	Joensen (1963)
	All	1981	14.9	131/23	Present study
	All	2001	20.0	148/37	I. Olsen in litt.
Sandoy	All	1966	15.7	145/27	Gibbs & Mawby (1968)
5	All	1981	17.6	42/9	Present study
	All	2001	10.4	43/5	Present study
Vágar	All	1964	28.5	93/37	J.L. Pedersen in litt.
	All	1981	16.9	128/26	Present study
	Fjallavatn	1930	c. 2	c. 100 p (4 pale i)	Salomonsen (1931)
	Fjallavatn	1942	26.1	"large colony"	Williamson (1954)
	Fjallavatn	1944	23	unknown	Williamson (1954)
	Fjallavatn	1948	11.4	249/32	Nørrevang (1950)
	Fjallavatn	1959	19.1	38/9	S-A. Bengtson (unpubl.)
	Fjallavatn	1964	19.4	54/13	J.L. Pedersen in litt.
	Fjallavatn	1981	21.2	52/14	Present study
	Fjallavatn	2001	21.4	33/9	Present study
Mykines	All	1939	c. 24	37 i	Southern (1943)
2	All	1957	4.2	184/8	Nørrevang (1960)
	W part	1958	c. 10	c. 25-30 i	Mathiasson (1962)
	All	1959	18.4	40/9	S-A. Bengtson (unpubl.)
	All	1966	c. 15	c. 50-100 i	Meltofte (1967)
	All	1981	21.4	33/9	Present study
	All	1984	14.7	29/5	Present study
Streymoy	All	1981	14.8	156/27	Present study
5 5	Svínaskoradalur	1930	15-20	c. 150 p	Salomonsen (1931)
	Svínaskoradalur	1942	c. 15	"fairly considerable col."	Southern (1943)
	Svínaskoradalur	1981	21.5	31/9	Present study
	Svínaskoradalur	2001	16.7	10/2	Present study
Eysturoy	All	1981	15.5	87/16	Present study
Viðoy	All	2001	7.5	37/3	Present study
Svínoy	All	1949	c. 20	>200 p	Petersen (1950)
	All	1953	16.4	249/49	Williamson (1954)
	All	2001	13.0	94/14	P. Simonsen in litt.
Fugloy	All	1953	16.5	71/14	Williamson (1954)
	All	1981	14.6	111/19	Present study
	All	1986	16.3	82/16	Present study
	All	2001	14.6	70/12	J. Lydersen in litt.

p pairs, i individuals

Table 3. Mati	ings be	tween	n melan	ic (D)	and pal	le (P) i	individua	als of	Arctic Sk	tua on th	e Faer	oe I	slands,	base	d on sar	nples
of pairs from	differe	ent are	eas and	years.												

ŀ	Parsammensætning aj	f mørke (D)) og lyse (F	?) individer af Al	n. Kjove på Færøerne	(data fra forskellig	e lokaliteter og år).
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Island/loc. Ø/lokalitet	Year År	Mating Kombination	Observed Observeret	Expected Forventet	χ^2 test (df=1)
Fugloy	1981	D×D	49	47.4	
0 9		$D \times P$	13	16.2	2.57
		$P \times P$	3	1.4	P = 0.11
Fugloy	2001	$D \times D$	31	28.5	
0.		$D \times P$	3	7.9	14.25
		$P \times P$	3	0.5	P = 0.0002
Svínoy	2001	$D \times D$	40	40.9	
•		$D \times P$	14	12.2	1.20
		$P \times P$	0	0.9	P = 0.27
Viðareiði	2001	$D \times D$	18	18.1	
		$D \times P$	2	1.9	0.06
		$P \times P$	0	0.1	P = 0.81
Mykines	1984	$D \times D$	13	13.5	
		$D \times P$	6	5.1	0.67
		$P \times P$	0	0.5	P = 0.41
Skúvoy	2001	$D \times D$	37	35.5	
-		$D \times P$	16	19.0	1.38
		$P \times P$	4	2.5	P = 0.24

protection. The recovery was remarkable and the total population numbered about 70 pairs in 1930, some 200 in 1946, and about 530 pairs in 1961 (Bayes et al. 1964). Thereafter numbers decreased to about 250 pairs in 1981, only to increase to 325-350 in 1990 and 450 a few years later (Bengtson & Bloch 1983, Bloch & Sørensen 1984, Fritze & Jensen 1991, Bloch et al. 1996). Thus, looking at the available information there appears to be a negative correlation between numbers of Arctic Skuas and Great Skuas on the Faeroes. However, this suggested relationship needs to be looked at more closely as there are several inconsistencies in the data. For instance, why did the suggested decline of the Arctic Skua on Svínoy not begin much earlier, when Great Skuas were abundant, and why did the large colony at Fjallavatn decline in the 1940s although there were - and still are - few Great Skuas in the area (Nørrevang 1950, 1955, pers. obs.). Clearly the relationship between the two skua species on the Faeroes deserves to be studied in more detail.

The same holds true also for the relationship between the Arctic Skua and its food resources. Mostly the food is obtained by steeling it from Arctic Terns *Sterna paradisaea*, Kittiwakes *Rissa tridactyla* and to a lesser extent Puffins *Fratercula arctica*. In Shetland the Arctic Skuas responded to a reduced food availability by exhibiting a lower territorial attendance, chick growth rate, and reproductive success and by switching from kleptoparasitising Arctic Terns to Puffins and other seabirds in years with a poor recruitment of sandeel Ammodytes marinus (Phillips et al. 1996a, 1996b), an important prey for several species of seabirds also on the Faeroes. Whether the availability of food is involved in the suggested decline in Arctic Skua numbers on the Faeroes during the past two decades is open to discussion. As in Shetland the recruitment of sandeel was low in most years from 1984 until 1993 when the situation started to improve (Gaard et al. 2002). Several species of seabirds, including the Arctic Skua, showed a poor reproductive success during this period, and the Arctic Tern population decreased from 9000-12000 pairs in 1981 to about 2000 pairs in 1993 - a decline that seems to have continued (Bloch & Sørensen 1984, Bloch et al. 1996, pers. obs.). Our counts of Arctic Skuas are too few and scattered in time to disclose any relationship between skua numbers and the availability of food. In Britain the Arctic Skua increased in the early 1970s but since the 1980s the population has been stable or slowly declining, whereas in southwestern Norway and on the west coast of Sweden numbers have declined since the 1960s or 1970s (Lloyd et al. 1991, Vader 1994, Åhlund 1996).

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Plumage polymorphism

The ratio of melanic to pale Arctic Skuas on the Faeroes is consistent with the gross geographic pattern where the frequency of the pale plumage morph increases with latitude, albeit with some irregularities (Southern 1943, and others). In Shetland (approx. 60°-61° N) the average frequency of pale birds was 26.5% in 1943-1979, and 21.6% and 22.5% in 1986 and 1992, respectively (Phillips & Furness 1998), which is to be compared with 16.5% in 1981 and 14.6% in 2001 on the Faeroes (approx. 61°20'-62°20' N). In southern Iceland (63°25' N) 9.7% of the birds were pale in 1971 and 13% in 1986 (Bengtson & Owen 1973, Schütt 1989) which is significantly lower than on the Faeroes (P < 0.01). Within Iceland the frequency of the pale morph is markedly higher in the northern parts (Bengtson & Owen 1973, Schütt 1989). Along the southwestern coasts of Scandinavia the Arctic Skua breeds in low numbers and the sample sizes are small. North of Gothenburg in Sweden (approx. 58° N) 30.8% (n = 96) of the breeding birds in 1966 were pale (Pehrsson 1967). For Norway, 5% pale birds have been reported from Jæren (approx. 59° N) and 30% further north on Smøla and Andøya at approx. 63° and 69° N, respectively (Haftorn 1971).

How the plumage polymorphism of the Arctic Skua is maintained is subject to debate and several different explanations have been proposed (see Introduction). An implication of the latitudinal change of the morph ratio is that the alleles associated with the melanic morph are at an overall selective advantage in the southern regions of the range and vice versa for the alleles of the pale morph. In fact, O'Donald's (1983, 1987) model, based on data from Fair Isle and involving demographic correlates and sexual selection, predicts the elimination of the pale morph. Although a slight but statistically significant decline in the frequency of the pale morph has occurred in Shetland, O'Donald (1983) postulates a gene-flow between colonies and an immigration from more northern populations which reduces the effects of the selection and prevents the elimination of the pale allelomorph. Since prior to the 1970s the pale morph has also declined in Orkney, Iceland, and northern Norway (see O'Donald 1983, Furness 1987, Janssen 1998, Phillips 2001). For Iceland no decline since the early 1970s is discernible (Schütt 1989, pers. obs.).

As to the Faeroes the frequency of pale birds varies in time and space (Table 2) but much of the variation may simply be sampling effects, and no distinct geographical pattern is discernible. In some areas the frequency of pale birds seems to have fluctuated markedly in time (e.g. at Fiallavatn and on Mykines) but less so in others (e.g. on Suðuroy, Skúvoy, Svínoy, and Fugloy). For the anomalous records of about 2% pale birds at Fjallavatn in 1930 (Salomonsen 1931) and 4.2% on Mykines in 1957 (Nørrevang 1960) we can think of no plausible explanation. On Vágar there was a significant difference in the frequency of pale birds in 1964 (28.5%) and 1981 (16.9%) but this, and a few other instances where the changes in morph frequency approach statistical significance (Table 2), do not provide evidence of a general trend in support of the suggested directional selection, but rather fluctuations (or effects of small samples) in the prevalence of the morphs. However, as pointed out by O'Donald (1983), it may take in the order of ten generations for evolutionary changes to occur.

Old records that give any kind of precise information are exceptionally rare. However, observations on breeding Arctic Skuas made by the German ornithologist Graba during a visit to Sandoy in 1828 read like this: "... hier sassen sie paarweise auf etwas erhöhten Plätzen des Moores. Meistentheils war ein weiss- und ein braunbäuchiger gepaart. Ihrer 15 wurden erlegt, und wunderbar genug waren die acht weissbäuchigen sämmtlich Männchen, und sechs braunbäuchige Weibchen mit grossen Eiern" (Graba 1830: 189). Does this short passage indicate that the pale morph was more frequent then than today, that mating was non-random (melanic × pale), and that males were mostly pale and females melanic? First, the sample is small and conceivably Graba's collecting was biased. Secondly, non-random mating has been found in some colonies in some years (for references see Phillips 2001); mostly assortatively (i.e. between birds of the same morph) and only once disassortatively (Bengtson & Owen 1973). In our study, among six small samples of breeding pairs (Table 3), we found significantly non-random (assortative) mating on Fugloy in 2001 but not in 1981, nor in any of the other colonies. Such inconsistency between years is known from Shetland (Phillips & Furness 1998). Thirdly, the plumage colour is generally not considered to be related to sex (Furness 1987), though on Fair Isle and on Varanger in northeastern Norway a tendency for a higher frequency of the pale allelomorph in the females than in the males has been found (Berry & Davies 1970, Janssen 1998). Furthermore, among Arctic Skua skins from Iceland (n =



24) three quarters of the melanic ones were males and three quarters of the pale ones were females (Cramp & Simmons 1983: 675). In contrast to this, Graba's observations suggest a statistically significant tendency for males to be pale and females to be melanic (Fisher's exact test, P = 0.003). However, an examination of Faeroese skua skins in the collection of the Zoological Museum in Copenhagen did not indicate any such difference; among males (n = 15) 11 were melanic and among females (n = 11) 8 were melanic (J. Fjeldså in litt.).

Resumé

Den Almindelige Kjove Stercorarius parasiticus på Færøerne: Forekomst og farvefaser

Den Almindelige Kjove på Færøerne blev talt op i 1981, og ud fra tællingens resultat på 1145 par blev total-bestanden estimeret til 1200-1500 par. 80% ynglede mindre end 300 m over havniveau. I tidsrummet 1999-2001 er bestanden igen optalt, ligesom der foreligger spredte oplysninger fra 1980erne og 1990erne. Gennem de sidste 40-50 år har yngleantallet varieret kraftigt i flere af de største kolonier, og en sammenligning mellem optællingerne i 1981 og 2001 af de gammelkendte, store kolonier viser sammenlagt en tilbagegang på 22%. Nedgangen kommer op på 45%, hvis man medtager Suðuroy's nordlige del, hvor kjoven ynglede talrigt i 1981, men hvor der hverken før eller siden har været særlig mange. Der er opstået nye mindre kolonier andre steder, og flere steder er der kommet spredt beliggende isolerede par. I Svínaskoradalur og på Svínoy og Skúvoy skete den kraftigste nedgang i perioden 1961-1981, mens tilbagegangen siden har været langsommere. Mulige årsager til tilbagegangen er diskuteret: svigtende fødetilgang, konkurrence med Storkjove S. skua og forfølgelse; der er ingen evidens for den sidstnævnte mulighed, mens de to andre evt. kan have haft en vis betydning, om end formodningen mest bygger på undersøgelser uden for Færøerne.

Forholdet mellem antallet af lyse og mørke kjover falder fra Shetland via Færøerne til Sydisland. For Færøerne som helhed var 16,5% (1981) henholdsvis 14,6% (2001) lyse. Variationen i de store kolonier har været 11-17% lyse, men for visse andre kolonier har variationen været større. Der er ikke nogen statistisk signifikant geografisk tendens på Færøerne hvad angår forholdet mellem farvefaserne, og andelen af lyse kjover er heller ikke faldet, sådan som det er sket på Shetland og Island. I perioden 1930-1981 har en og samme koloni udvist en variation på op til 2-21% lyse, men kun i to kolonier er variationen signifikant.

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