Polymorphism in the Arctic Skua *Stercorarius parasiticus* in NE Norway

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In a breeding population of Arctic Skuas in Finnmark, NE Norway, the proportions of pale and intermediate/dark birds in 1976—78 were 43 and 57 %, respectively, and no geographical trend was evident in the morph ratio. The proportion of pale birds seems to have decreased in recent decades. No significant preferences were revealed by the matings between morphs. Solitary pairs did not differ from colonial pairs in morph proportions or mating preferences.

According to the hypothesis of apostatic predator selection (Paulson 1973), the rarer, pale morph might be a more efficient forager, but no significant difference in foraging success was found between the morphs.

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Introduction

The Arctic Skua provides an example of plumage polymorphism, three morphs being recognizable: pale, intermediate and dark (Williamson 1951, 1965). Pale birds are common in northern parts of the species' range, while dark birds predominate in the south.

Despite much work since Southern's (1943) review, the cause of the morph cline remains unknown. The genetics of the morphs was studied by O'Donald & Davis (1959). They concluded that the polymorphism is probably determined by two alleles at a single locus, the dark allele being semi-dominant. Heterozygotes range in colour from intermediate between the dark and light morph, to almost identical with the dark homozygote. Later, O'Donald and his coworkers analysed mating preferences and sexual selection among Arctic Skuas at Fair Isle (review in O'Donald 1980a, b). Dark males in new pairs nest earlier in the season and with greater success than pale males. On the other hand, pale birds are younger at first breeding, which more than compensates for this disadvantage. O'Donald & Davis (1975) therefore predicted that the pale morph will increase in proportion.

Plumage polymorphism is common among raptors (Falconiformes), skuas (Stercorariinae) and other avian vertebrate predators. Paulson (1973) suggested that it may be maintained by 'reversed' apostatic selection: "The rarer of two morphs of a predator should be less familiar to a potential prey individual and thus have a greater chance for successful capture of that individual. This slight advantage of the rarer

morph should lead to balanced polymorphism in the population" (Paulson 1973, p. 270).

Arnason (1978) tested this hypothesis on Arctic Skuas, which obtain most of their food by kleptoparasitizing seabirds. As predicted, he found higher hunting success in the rarer, pale morph at an Icelandic colony. However, Furness & Furness (1980) found no significant differences in success between the two morphs at another colony in Iceland, nor at three Shetland colonies, where the pale morph is even rarer.

In this paper we examine the occurrence of the different colour morphs of the Arctic Skua in Finnmark, NE Norway, and look for deviations from random mating between morphs. Apart from the report by Bengtson & Owen (1973), we know of no study of matings in northern populations with a relatively high proportion of the pale morph. Data on hunting times are used to test Paulson's (1973) hypothesis. As Arctic Skuas nest in both colonies and solitary pairs in Finnmark (Andersson & Götmark 1980), we also examine whether this affects morph frequencies and mating types.

Study area

The greater part of the study region in Finnmark (Fig. 1) is treeless. Small areas with birch *(Betula pubescens)* occur in the south, but mountain heath and barren boulder fields predominate, interspersed with small lakes, pools, streams and bogs.

The authors MA and FG studied breeding Arctic Skuas on the Varanger peninsula in 1977 and 1978 (Andersson & Götmark 1980). While studying Little Stints *Calidris minuta* in 1976—78, OH independently collected data on the colour morphs of skuas in a somewhat larger area in Finnmark. Two skua colonies were studied by MA and FG: one at Holmfjellet (70°07′N, 30°10′E; 13 pairs), 7 km NNE of the seabird colony at St. Ekkeröy in Varangerfjord, the other at Yttre Syltefjord (70°34′N, 30°10′E; 31 pairs), 2 km W of the fjord and its large seabird colony (Norderhaug et al. 1977). The area surveyed by OH in 1976 extends from Porsangerfjord in the west to the border of the Soviet Union in the east. In 1977—78, the studies were confined to the Varanger peninsula. Two additional colonies were found, one at Lille Tamsöya in Porsangerfjord (70° 46′N, 25°50′E; c. 15 pairs), the other near Hamningberg (70°32′N, 30°33′E; c. 60 pairs), 10 km SE of the seabird colony at Syltefjord. Solitary pairs were studied by MA and FG over 22 km² around Falkgården N of St. Ekkeröy, and counted by OH at various places along the coast.

One of the colonies (Lille Tamsöya) was on a low island covered with heath vegetation, the other three on open mountain heath with several small lakes and pools. Solitary Arctic Skuas also nested on mountain heath, often near bogs and lakes with richer vegetation (for details, see Andersson & Götmark 1980).

Methods

Our combined observation periods cover 27 June to 8 July 1976, 15 June to 30 July 1977 and 17 June to 20 July 1978. In their open habitat breeding skuas are easy to census. They were counted mainly in late June and early July, when most pairs had eggs or small chicks. Only breeding birds at their nest sites (and a few non-breeding, territorial pairs) were counted by MA and FG, whereas OH also included some skuas observed flying inland away from breeding grounds (c. 13 % of all his birds). Skuas observed at sea were omitted.

On the Varanger peninsula, some areas were surveyed in two or three consecutive years. Since the long-lived Arctic Skuas tend to return to the same breeding site, and often mate with the same partner (Berry & Davis 1970, Davis 1976), most birds recorded in the same breeding areas in successive years will be the same individuals. We have therefore included each subarea only once in the combined colour morph material (Table 1), using the highest number of birds counted. The same applies to our data on the frequency of mating between the different colour morphs. Only definite pairs (with nests or territories) were included in the analysis of mating frequencies.

MA and FG used the description of the morphs by O'Donald & Davis (1959) for identification. Pale birds were easily recognized, only differing in the occurrence and width of a dark band across the breast. The intermediate morph grades into the dark morph, which is almost uniformly dark brown. Intermediates

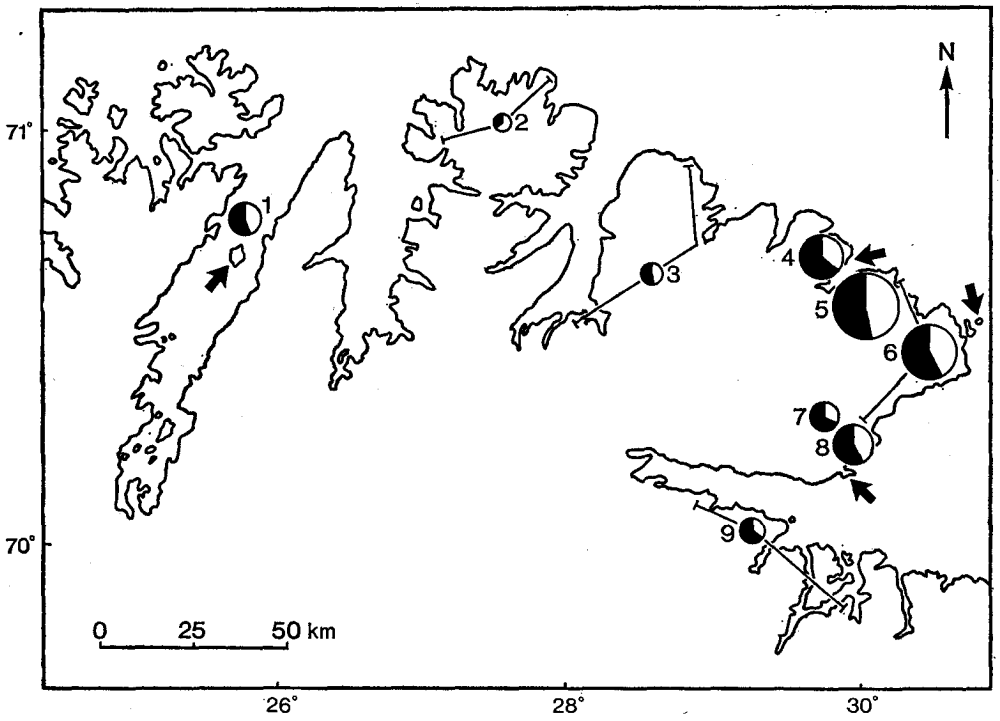

FIG. 1. The study area in Finnmark. The circles show the proportions of dark + intermediate and pale Arctic Skuas in the different parts of the area; the sizes of the circles correspond to the number of birds counted. The localities are numbered as in Table 1. Locations of large seabird colonies are indicated by arrows.

are usually recognized by the pale neck and cheeks, or pale cheeks alone, but it is sometimes difficult to decide whether a bird belongs to the dark or the intermediate morph. Therefore, OH did not separate intermediates from dark birds, and in our final analyses we pool these two morphs. Light intermediates (with yellowish cheeks and neck and with smoky, yellowish grey underpart, cf. Southern 1943), which are common in the Baltic (Hildén 1971), seem to be lacking in Finnmark. Of the 367 individuals noted by OH, only six were close to this type but with a darker underpart. No such skuas were seen by MA and FG.

In late June and July 1977, MA and FG studied altogether 8 colonial and 8 solitary pairs during 200 hours, recording the duration of foraging flights from the nest to remote feeding areas at sea (Andersson & Götmark 1980). These observations are used to compare hunting efficiency, estimated from time spent on foraging trips, between pale and dark skuas. In the statistical analysis χ^2 tests are used unless otherwise stated.

Results

Occurrence of colour morphs. The frequencies of the colour morphs in the different parts of the study area are given in Table 1 and Fig. 1. Overall, the proportion of pale skuas averaged 43.2 % and that of dark and intermediate birds 56.8 %. At localities 4, 7 and 8 (Fig. 1), where we distinguished between the two latter morphs, there were 30.1 % intermediates and 32.2 % dark birds (N = 146, using the highest number of pairs at each locality

TABLE 1. Frequencies of the two colour morphs among Arctic Skuas in different parts of Finnmark in 1976—78. Intermediate and dark skuas are lumped together under "dark".

Locality	Dark (*N*)	Pale (*N*)	Pale (%)
1. Porsangerfjord	21	16	43.2
2. Nordkinnhalvöya	4	7	63.6
3. W Varanger[1]	8	7	46.7
4. Syltefjord	44	25	36.2
5. Hamningberg	86	78	47.6
6. E. Varanger[2]	66	50	43.1
7. Falkgården	20	10	33.3
8. Holmfjellet	31	23	42.6
9. S coast of Var.fjord[3]	13	7	35.0
Total	293	223	43.2

[1] Outlet of the River Tana (9 ind.), Straumen — Berlevåg (6 ind.)
[2] Along Road 98 from Langsmedvatnet to Hamningberg
[3] Between Revholmen and Neidenfjord

in 1977—78). However, due to the difficulty of separating these morphs, the proportions are uncertain.

The morph proportions did not differ between westerly and easterly sites (1—3 and 4—9 in Fig. 1, respectively; $P>0.3$). However, there was a higher proportion of pale birds (45 %, N = 296) at northern localities (1—5) than at southern ones (7—9; 38 %, N = 104), although the difference was not significant ($P>0.2$). Additional data would be desirable from the northernmost locality (2, Nordkinnhalvöya), where more pale than dark birds were recorded.

There was no difference ($P>0.5$) in morph proportions between skuas breeding in solitary pairs (Falkgården) and in colonies (Lille Tamsöya, Y. Syltefjord, Holmfjellet). Nor could between-year differences be found in the two areas censused carefully in 1977 and 1978. In the colony of Holmfjellet, the same area held 44 % pale birds in 1977 (N = 34) and 39 % in 1978 (N = 36), at Falkgården the corresponding values were 33 % (N = 30) and 39 % (N = 28). This result conforms to expectations (see p. 50).

Mating between morphs. In Table 2, the observed numbers of matings within and between morphs are compared with the numbers that could be expected if mating was random. At the localities censused by OH (1—3, 5, 6, 9) only a fraction of all the matings could be determined. We assumed that these pairs represented random samples of the breeding populations, and hence at each locality we included all birds recorded in the calculation of expected matings (Table 2). There is no significant deviation from the numbers for random mating in the combined material ($P>0.3$). The data from each single locality are too few for meaningful analysis. A comparison of the frequencies of the observed and expected mating types in the two census years at Holmfjellet and Falkgården shows no consistent trends. The frequency of mating types in solitary and colonial skuas did not differ significantly ($P>0.5$).

Foraging flights. Colonial skuas on foraging flights headed towards the nearby seabird cliffs at St. Ekkeröy and Syltefjord (Fig. 1). Observations from the seashore confirmed that the skuas took food from seabirds. At Ekkeröy, the skuas chased Kittiwakes *Rissa tridactyla*, the only common breeding species there. At Syltefjord they mainly kleptoparasitized alcids, especially Guillemots *Uria aalge* (Andersson & Götmark 1980). Foraging birds returned after about one hour (Table 3). The flight from the colony to the sea outside the seabird cliffs and back took less than 10 min at Holmfjellet (c. 12

TABLE 2. Frequency of matings within and between the two colour morphs in Arctic Skuas in different parts of Finnmark in 1976—78 (dark and intermediate birds are pooled in one group). The numbers expected for random mating, calculated as by Bengtson & Owen (1973), are given in parentheses.

Locality	Dark x dark	Dark x pale	Pale x pale
1. Lille Tamsöya	5 (3.5)	4 (5.4)	2 (2.1)
4. Syltefjord	13 (12.9)	14 (14.2)	4 (3.9)
5. Hamningberg	5 (5.8)	12 (10.5)	4 (4.8)
6. E Varanger	4 (3.9)	6 (5.9)	2 (2.2)
7. Falkgården	7 (6.7)	6 (6.6)	2 (1.7)
8. Holmfjället	8 (8.8)	15 (13.2)	4 (5.0)
Other localities	3	10	3
Total	45 (42.9)	67 (65.4)	21 (24.8)

km) and 15 min at Syltefjord (c. 16 km). (This may account for the longer duration of flights at Syltefjord, see Table 3.)

There is no reason to expect differences between colour morphs in the allocation of time to activities other than hunting on foraging trips. We therefore tested for differences in foraging efficiency between dark and pale birds by comparing the duration of their foraging flights (Table 3). Unfortunately, it was not possible to measure the amount of food that each individual brought to the chicks. In at least 34 out of 40 flights, the skuas returned with food, since they were observed feeding the chicks.

In the statistical analysis, we treated individual birds as sample units, and calculated the mean duration of foraging flights for each individual (if the flights of all the individuals had been pooled, the test might have been biased by one or two highly successful foragers that were often recorded). The average for each morph was then calculated from these individual means (Table 3). We could not separate all the birds because in three pairs the two skuas were of the same morph; in these cases we calculated one mean for the pair. The limited data do not show any significant difference in hunting efficiency between the morphs at either Holmfjellet ($P = 0.6$) or Syltefjord ($P = 0.8$, Mann-Whitney U-test). However, at both colonies, the mean duration of the flights was shorter for pale Arctic Skuas than for dark birds.

Discussion

There are a number of earlier reports from Varanger on the frequency of skua morphs. Venables (cited in Southern 1943) found 56 % pale birds in 1937 ($N = 127$), which differs significantly from our estimates of 41.9 %

TABLE 3. Duration (min) of foraging flights to remote feeding areas in dark[1] and pale Arctic Skuas.

Locality and morph	Duration Mean ±*SE*	No. of flights	No. of skuas
Holmfjellet			
dark	72±31	18	5
pale	60± 2.2	15	4
Y. Syltefjord			
dark	76±14	3	2
pale	68± 3.0	4	4

[1] 'Dark' includes the intermediate morph.

pale birds at Varanger ($P<0.005$; areas 3—9, $N = 461$). Southern (1943) listed three other references from 1900—41, all estimating the proportion of pale birds at about 50 %, but with little or no quantitative data. Watson (1957) reported 54 % pale skuas in 1952 ($N = 37$), but this does not differ significantly from our estimate ($P>0.1$). More recently, Bengtson & Owen (1973) found 33 % pale skuas in 1972 ($N = 51$).

We censused breeding skuas, whereas other workers presumably mainly counted birds along the coast of Varanger and so may have included some non-breeders (and may have counted some individuals twice). But even if allowance is made for this possibility, the decrease in frequency of the light morph appears large enough to be real.

From a demographic analysis of Arctic Skuas at Fair Isle, O'Donald & Davis (1975) predicted that the pale morph will increase in proportion there. No such increase seems to have occurred at Varanger; on the contrary, the proportion of the pale morph appears to have declined. Nor does the pale morph seem to have increased in proportion on the Swedish west coast. In 1931, Hasselblad (1931) found 13 % pale Arctic Skuas ($N = 54$) in a breeding population at Mollösund (58°04'N, 11°28'E). In 1972, one of us (MA) censused the same islands and found 16 % pale birds ($N = 31$). The population had declined, but the morph proportions were similar.

There was no evidence for deviations from random mating between colour morphs at Varanger. This seems to hold for most populations studied. O'Donald (1960) and Berry & Davis (1970) analysed data from six Shetland colonies in 1935—63. Assortative mating in pale and other morphs (dark and intermediate birds were lumped) was significant in three cases out of twelve. Later, O'Donald et al. (1974) and Davis & O'Donald (1976) studied matings in all three morphs at Fair Isle and Foula and found two cases of significant assortative mating (among intermediates at Fair Isle and among pale birds at Foula). No mating preferences were noted in Finland (Hildén 1971), while Bengtson & Owen (1973) found significant disassortative mating on Iceland.

Our limited data provided no significant evidence of the reversed apostatic predator selection suggested by Paulson (1973). However, the proportions of the pale and dark morphs are rather similar at Varanger. It is not clear at exactly which proportion the rare morph may begin to be favoured, because other factors than morph frequencies may influence foraging success in the different morphs. Earlier results both support (Arnason 1978) and contradict (Furness & Furness 1980) Paulson's hypothesis. Further tests are needed, especially those proposed by Furness & Furness (1980), in the far north where the dark morph is rare.

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Selostus: **Merikihun värimuodoista Ruijassa**

Merikihu esiintyy kolmena värimuotona: vaalea, välimuoto ja tumma. Ruijassa vv. 1976—78 kootun aineiston ($N = 526$) linnuista 43 % oli vaaleita ja 57 % välimuotoja/tummia (tyypit yhdistetty niiden hankalan erottamisen vuoksi). Merkitseviä eroja värimuotojen lukusuhteissa alueen eri osien välillä ei todettu (kuva 1, taul. 1). Vanhempiin tietoihin verrattuna vaalean muodon osuus näyttää pienentyneen

viime vuosikymmeninä. Värimuotojen pariutuminen keskenään ei poikennut sattumanvaraisen otannan perusteella odotetusta jakaumasta (taul. 2). Yksinäisten parien ja yhdyskuntien välillä ei ollut eroa värimuotojen eikä pariutumistyyppien lukusuhteissa.

Apostaattisen valinnan periaatteen mukaan (Paulsen 1973) harvinaisemman, vaalean värimuodon pitäisi olla tehokkaampi saalistaja. Tätä tutkittiin kahdella alueella tarkkailemalla saalistuslentojen kestoa pesimäpaikoilta merelle ja takaisin. Molemmilla alueilla vaaleiden kihujen saalistusmatkat tosiaan kestivät keskimäärin lyhyemmän ajan, mutta ero ei ollut tilastollisesti merkitsevä (taul. 3).

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