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Phenotypic Variation among Thick-billed Murres from Colonies in Hudson Strait

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ABSTRACT. Thick-billed Murres (*Uria lomvia*) breeding in the Canadian Arctic are restricted to a small number of colonies, all comprising more than 10 000 pairs. Five of these colonies are scattered through Hudson Strait. We collected adult breeders at three of the colonies — Digges Island, Hantzsch Island, and Akpatok Island — and compared wing and bill measurements and body weights to look for inter-colony differences. Significant inter-colony differences were present for all measurements and a discriminant function analysis showed that some individuals fall completely outside the range of variation for the other colonies. Because of the presence of the Laurentide ice-sheet over Hudson Strait, the present colony sites could not have been occupied for more than 10 000 years. If the observed differences reflect differences in genotype then their evolution must have occurred over this period.

Key words: Thick-billed Murre, *Uria lomvia*, phenotypic variation, Hudson Strait, evolution

RÉSUMÉ. Les Marmettes de Brunnïch (*Uria lomvia*) nichent dans l'arctique canadien et sont réparties dans un petit nombre de colonies de 10 000 couples et plus. Cinq de ces colonies se retrouvent dans le détroit d'Hudson. Nous avons collectionné des adultes dans trois de ces colonies: îles Digges, Hantzsch et Akpatok. Nous avons comparé les mesures de la longueur de l'aile et du bec ainsi que les poids pour vérifier s'il y avait des différences entre les colonies. Nous avons observé des différences significatives entre les mesurations et les poids des trois colonies et l'analyse discriminante nous indique que quelques spécimens se situent en dehors des limites de variation des autres colonies. A cause de la présence du glacier Laurentien sur le détroit d'Hudson durant la dernière glaciation, l'occupation des sites actuels par la Marmette de Brunnïch daterait d'environ 10 000 ans. Si les différences observées traduisent des génotypes différents, leur évolution se serait produite à l'intérieur de cette période.

Mots clés: Marmettes de Brunnïch, *Uria lomvia*, variation des phénotypes, détroit d'Hudson, évolution

Traduit par les auteurs.

INTRODUCTION

The Thick-billed Murre (*Uria lomvia* L.) has a circumpolar distribution in arctic and subarctic waters (Voous, 1961). The species is divided into three, perhaps four races, exhibiting clinal variation with increasing wing and bill length eastwards across the Atlantic and northern Eurasia (Vaurie, 1965). Populations nesting in eastern Canada are the smallest and belong to the race *U. lomvia lomvia* (A.O.U., 1957).

Some variation within the Canadian population was detected by Storer (1952) who showed that birds from Baffin Bay were generally smaller than those from the small, peripheral colonies in the Gulf of St. Lawrence. He also showed that sexual dimorphism in the Thick-billed Murre was very slight, particularly in Atlantic populations, being most marked in bill depth.

Populations of Thick-billed Murres in arctic Canada are concentrated in a few very large colonies, all exceeding 10 000 pairs and ranging up to 300 000 pairs (Gaston, 1980). They are distributed in the Lancaster Sound-Jones Sound area (four colonies), east Baffin Island (one colony) and Hudson Strait (five colonies) (Brown *et al.*, 1975; Gaston, 1980). Measurements of samples from three Lancaster Sound colonies are similar, suggesting that the population is phenotypically fairly uniform within this area (Birkhead and Nettleship, 1981; Gaston and Nettleship, 1981). Recent field work by the Canadian Wildlife Service at three of the colonies in Hudson Strait — Digges Sound, Akpatok Island (south), and Hantzsch Island (Fig. 1) — has enabled us to examine inter-colony variation in measurements within this area and also differences between birds from these colonies and those from colonies on Lancaster Sound.

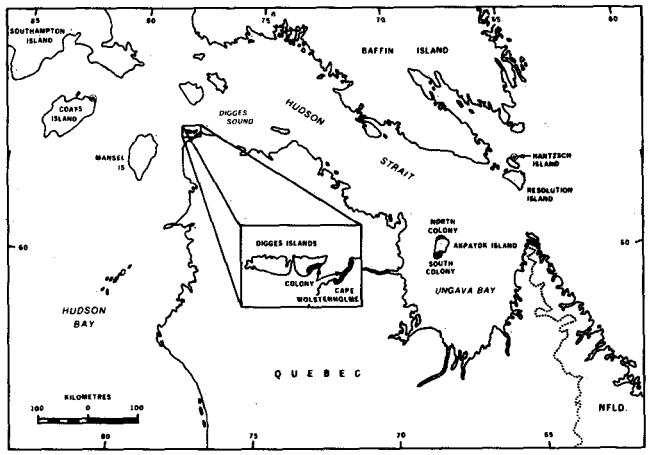

FIG. 1. Map of Hudson Strait showing the position of Thick-billed Murre colonies from which birds were collected.

METHODS

Samples at Digges Sound were taken by AJG and DGN during June-August 1980-1982; those at Akpatok and Hantzsch islands were taken in August 1982 by GC and AJG, respectively. The majority of birds collected at Digges Sound were shot on the water 5-25 km from the colony, while those taken

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at the other two colonies were captured on the breeding cliffs. Only birds from Digges Sound with fully developed brood patches were included in these comparisons. A sample of birds taken on the cliffs at this colony did not differ significantly in any measurement from those obtained at sea, and both samples have therefore been combined for analysis. Because all the birds used in our analysis were breeding adults, they were likely to have been more than three years old [by analogy with Common Murres (*Uria aalge* L.) (Birkhead and Hudson, 1977)]. Hence, our comparisons are unlikely to be affected by age-related differences.

All birds at Digges Sound were weighed within 12 h of collection with a 3-beam balance reading to within 0.1 g; at the other two colonies we used "Pesola" spring balances calibrated to 20 g but estimated to within 10 g. One wing was measured to the nearest 1 mm from the carpus to the tip of the longest primary by flattening it along a ruler. Four bill measurements ("white line", "culmen", "nostril", and "depth") were taken using vernier calipers reading to 0.1 mm (Fig. 2). At Digges Sound and Akpatok Island all birds were killed and sexed by dissection, but at Hantzsch Island only 12 birds were sexed, the remainder being measured and released alive.

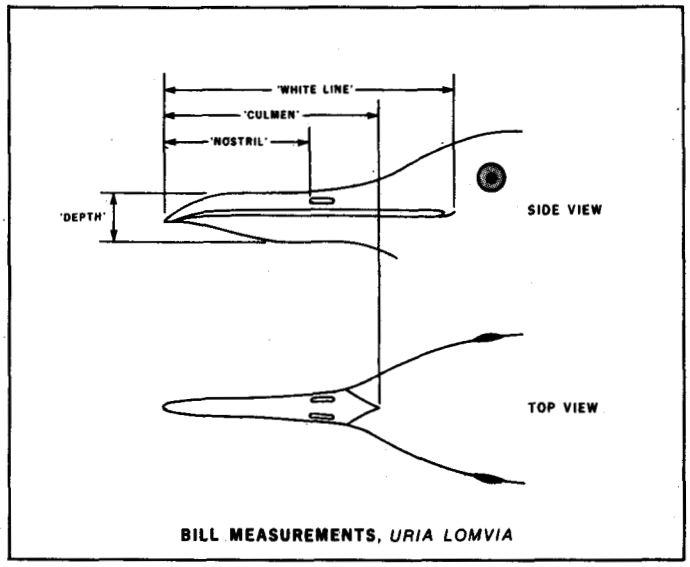

FIG. 2. Bill measurements used on Thick-billed Murres.

To test the comparability of our measurements, all three authors made replicate measurements on 40 birds collected at Digges Sound in 1982, using techniques identical to those adopted by us in the field. No significant differences were found between measurements made by AJG and DGN, but wing, depth, and nostril measurements carried out by GC were found to differ significantly from those made by the other two authors ($P<0.05$). All measurements made on birds at Akpatok Island for these three parameters have therefore been corrected by the mean difference between GC's and AJG's measurements. The correction factors used were: wing length, +4.0 mm; bill depth, +0.4 mm; nostril, +0.4 mm.

RESULTS

Sexual Dimorphism

The large sample of birds collected at Digges Sound showed significant differences between the sexes in all measurements except wing length. Females had slightly longer wings than males but males exceeded females in all other dimensions (Table 1). These results are in agreement with Storer (1952) who also found that males were larger than females in bill and tarsus measurements, but found no significant difference in wing length. Results for Akpatok Island were similar to those at Digges Sound, with all trends in the same direction, but differences were significant only for the white line. At Hantzsch Island females exceeded males in all measurements except bill depth, but none of these differences were significant. Sample sizes vary somewhat for different measurements because some birds were damaged in collection and because a proportion of birds collected at Digges Sound could not be weighed.

Inter-colony Comparisons

Comparing samples of known sex, we found significant differences among the three colonies in all measurements except the culmen (Table 1). Birds from Akpatok Island were smaller than those from the other two colonies in weight, wing length and bill depth, while females from Hantzsch Island were larger in white line and nostril measurements (Duncan multiple range test, $P<0.05$).

Because the sample of birds of known sex from Hantzsch Island was rather small, we also combined our data for both sexes for all three colonies to examine inter-colony variation. When this was done all measurements considered showed significant inter-colony variation (Table 2). Birds from Akpatok Island were lighter and had shorter wings than those from the other two colonies. Those from Hantzsch Island had significantly longer bills, the difference being most striking for the line and nostril measurements. The only measurement for which all paired comparisons were significant was bill depth, with birds from Digges Sound having the deepest and those from Akpatok Island the shallowest bills.

We carried out a discriminant function analysis (Nie *et al.*, 1975), based only on linear measurements, to assess the ability of these measurements to identify the colony affiliations of individual birds. All measurements were included in stepwise fashion except "line" which was excluded because the residual "F" value did not reach the exclusion level (1.0). The plot of the first two canonical discriminant functions (Fig. 3) shows that the first discriminant function separates birds from Digges Sound from the other two colonies, while the second separates principally those from Hantzsch Island from those from Akpatok Island. Relatively few birds can be assigned to a particular colony with 95% confidence. However, 85% of birds from Akpatok Island were correctly assigned when classified according to the nearest group, compared with only 67% of those from Hantzsch Island and 64% from Digges Sound. Unstandardized canonical discriminant function coefficients are given in Table 3.

TABLE 1. Sexual dimorphism among Thick-billed Murres at three colonies in Hudson Strait

	Male			Female			*P*
	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	
Digges Sound							
Weight (g)	972.53	91.89	94	939.04	98.99	53	0.046
Wing length (mm)	217.24	5.72	122	216.60	6.04	83	N.S.
Bill; line (mm)	55.98	2.11	127	54.42	2.20	84	<0.001
depth (mm)	14.84	0.75	124	14.51	0.96	78	0.007
culmen (mm)	34.85	1.91	127	33.82	1.97	84	<0.001
nostril (mm)	28.42	1.47	127	27.59	1.51	84	<0.001
Akpatok Island							
Weight (g)	842.40*	56.54	10	821.70*	56.87	12	N.S.
Wing length (mm)	207.30*	6.95	10	208.80*	5.00	13	N.S.
Bill; line (mm)	56.26	2.62	10	53.85	2.36	11	<0.01
depth (mm)	14.02*	0.9	10	13.59*	0.72	11	N.S.
culmen (mm)	35.19	1.72	10	34.63	2.01	11	N.S.
nostril (mm)	28.03	2.27	10	27.90	1.49	11	N.S.
Hantzsch Island							
Weight (g)	934.00	38.47	5	968.57	100.40	7	N.S.
Wing length (mm)	218.80	7.33	5	220.00	6.19	7	N.S.
Bill; line (mm)	55.94	1.45	5	57.63*	2.83	7	N.S.
depth (mm)	14.56	0.36	5	14.37	0.60	7	N.S.
culmen (mm)	35.48	1.31	5	35.71	2.94	7	N.S.
nostril (mm)	28.86	0.97	5	29.53*	2.28	7	N.S.

* Differs significantly from the other two colonies ($P<0.05$, Duncan multiple range test)

TABLE 2. Measurements of adult Thick-billed Murres at three colonies in Hudson Strait (sexes combined)

Measurement	Digges Sound			Akpatok Island			Hantzsch Island			F	*P*
	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N		
Weight (g)	961.67	96.36	148	831.09*	56.36	22	958.05	62.34	95	24.59	<0.001
Wing length (mm)	216.96	5.75	215	208.17*	5.83	23	217.04	5.58	69	25.23	<0.001
Bill; line (mm)	55.37	2.28	211	55.00	2.72	21	56.89*	2.15	95	16.07	<0.001
depth (mm)	14.67*	0.85	211	13.80*	0.85	21	14.40*	0.55	95	14.22	<0.001
culmen (mm)	34.44	1.99	220	34.76	1.88	21	35.77	1.89	95	15.35	<0.001
nostril (mm)	28.04	1.54	219	27.96	1.85	21	29.43*	1.59	95	26.71	<0.001

* Population differs significantly from both the other colonies in this measurement (Duncan multiple range test, $P<0.01$)

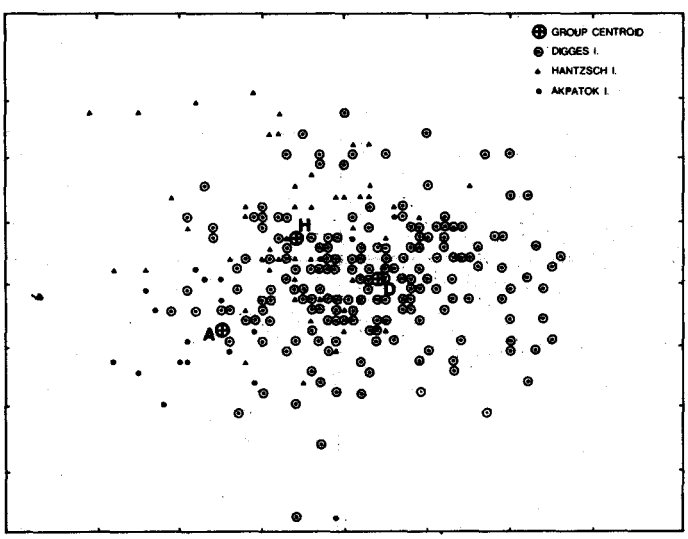

FIG. 3. Scattergram of first and second canonical discriminant functions showing the position of group centroids for the three populations compared: A — Akpatok Island; D — Digges Sound; H — Hantzsch Island.

DISCUSSION

The principal components analysis demonstrates clearly that measurements recorded for some birds at both Hantzsch and Akpatok islands fall completely outside the range of variation for the large sample from Digges Sound. This seems to exclude the possibility that observed differences are the result of biased sex ratios or age composition among the three samples.

In comparison with the differences recorded in the present study, those between colonies in the Lancaster Sound/Jones Sound area seem to be smaller. Birkhead and Nettleship (1981), comparing measurements for breeding birds at Cape Hay, Bylot Island, and Coburg Island, found a small difference in culmen length, but no significant difference in culmen depth or body weight. There was no significant difference in culmen length between these colonies and birds from Prince Leopold Island (Gaston and Nettleship, 1981). Body weights and culmen measurements at the Lancaster Sound/Jones Sound colonies were closest to those recorded at

TABLE 3. Formulae used in calculating unstandardized canonical discriminant functions (CDF)

CDF 1 = 0.0930 Wing + 1.0147 Depth − 0.1177 Culmen − 0.3630 Nostril
CDF 2 = 0.1076 Wing − 0.1716 Depth − 0.3545 Culmen + 0.5027 Nostril

Akpatok Island, although weights were slightly heavier, but the possibility of systematic differences in measuring techniques used by different people make such comparisons unreliable.

Assuming that the observed differences in phenotype represent colony-specific characteristics, the question arises of whether they are the result of environmental differences operating during the period of growth, or of differences in genotype resulting from selection or random gene fixation. The first alternative seems unlikely because, although chicks do grow at colony-specific rates (Gaston *et al.*, in prep.), they leave the colony at only about 20% of adult weight (Gaston and Nettleship, 1981). In addition, the lightest chicks at departure from the colony are those from Digges Sound, where adult weights are heaviest. Chicks undergo most of their development at sea and during this period chicks from all three colonies are probably intermingled as they make their way from Hudson Strait to their common wintering area off Newfoundland (Gaston, 1982; Orr and Ward, 1982). Chicks probably reach fully adult dimensions some time in their second year (Storer, 1952). Adult wing length is probably attained during the first annual moult which takes place in the fall of the second year (Storer, 1952), again while birds from the three colonies are intermingled on migration.

Without evidence on actual gene frequencies, the presence of genotypic differences between birds from the three colonies remains hypothetical. However, if there are significant differences in genotype, this would indicate that the three populations have probably been separated for a considerable period of time. The presence of the Laurentide ice-sheet over Hudson Bay and Hudson Strait during the last glacial period excludes the possibility that the Hudson Strait colonies could have been founded more than about 10 000 years ago (Bird, 1967; Flint, 1971), and a more likely date for Digges Sound appears to be about 8000 years B.P. (Andrews and Falconer, 1969; Andrews *et al.*, 1983). The other two colonies were presumably founded slightly earlier, as Hudson Strait opened up from east to west.

It would be useful if we could use observed differences in measurements to calculate approximate rates of evolution among the colonies. However, we have no way to judge the importance of the "founder principle" (Mayr, 1948, 1963) in determining initial differences among founder populations. These may have consisted of very few individuals and hence contained only a small portion of the genetic variation within the populations from which they originated. Random differences among these founder gene pools may have established variation right from the initial establishment of the colonies. What we can deduce, however, is that gene flow between the colonies at present is restricted and that they probably represent separate demes. This has implications for conservation in suggesting that a severe population decline at one colony is unlikely to be compensated by appreciable immigration from elsewhere. It also supports the contention by Gaston and Nettleship (1981) that arctic Thick-billed Murre colonies probably have been endogamous for a long time.

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