Size Variables in Puffins Fratercula arctica from Iceland, and Bill Features as Criteria of Age

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Size variables in Puffins *Fratercula arctica* (family Alcidae) from two Icelandic colonies, one in the North and one in the South, were examined. In general, male Puffins were larger than females. A marked size difference was shown between Puffins from the two colonies, birds from North Iceland being larger. A comparison of size was made between Faeroese Puffins (subspecies *grabae*) and Puffins from South Iceland (subspecies *arctica*). Differences between birds from these two populations were smaller than those found between Puffins from South and North Iceland. This contradicts the conventional thinking that all Icelandic Puffins belong to the same subspecies. Some discussion is devoted to nomenclature difficulties in *Fratercula arctica*. For the first time bill features have been proved to be indicative of age in Puffins. Descriptions are given of Puffins of the ages 2, 3, 4, 5, and 6 years and older, from the South Iceland colony.

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Introduction

Size seems to be the only morphological character which varies geographically in Puffins *Fratercula arctica* (L.) (Salomonsen 1944, Vaurie 1965). Body length, wing length, and bill size have all been found to increase towards higher latitudes, from Britain and France at the southernmost end of the species' breeding range to Spitsbergen at the northern extreme. Three subspecies have been generally accepted on the basis of differences in size: the high-arctic *naumanni*, which is the biggest subspecies; the intermediate, nominate *arctica*; and then *grabae*, the smallest and most southerly subspecies (Hartert 1921–22, Peters 1934, Witherby et al. 1941, Salomonsen 1944, Dement'ev & Gladkov 1951, Kozlova 1957, Vaurie 1965). Belopol'skii (1957), however, only accepted two subspecies viz. *naumanni* and *arctica*, the latter including *grabae*. For breeding distribution of the different subspecies, see Salomonsen (1944) and Vaurie (1965).

Salomonsen (1944) mentioned that some Puffin populations did not conform in size to birds from the type localities. Thus, Puffins from the Orkneys were intermediate between typical *grabae* and *arctica*. Similarly, Puffins from Jan Mayen and the Murman Coast were intermediate between typical *arctica* and *naumanni* (Salomonsen loc. cit.). This and the fact that size of Puffins increases towards north suggest a clinal, rather than a discontinuous variation. Therefore, it has been proposed (Myrberget 1963) that Puffins were best described as conforming to a cline. Pethon (1967) reached the same conclusion, and he recognized two clines from the British Isles, one to northwest and one to northeast.

Mayr (1969) stated that it was inadvisable to recognize subspecies in strongly clinal species, with the possible exception at the extremes of the species' breeding range. In the case of Puffins, even this would lead to various taxonomic difficulties as data become available from many different localities. The type locality of *Fratercula arctica* is now generally fixed as North Norway (Vesteraalen Islands by Hartert 1917). The type locality has been variously designated as Norway, Sweden, Faeroes, or British Isles (Salomonsen 1944), as a result of the vague description given by Linnaeus (1758).

In the present study, information on size of

Puffins from two Icelandic colonies is given. A steep north-south cline in size is shown to be present in Iceland. On the basis of rather few data, this was first suggested by Timmermann (1949).

Another aspect considered is how accurately the age of Puffins can be determined by the use of bill features. The Puffin is one of relatively few bird species in which age can be determined using morphological characters, besides such broad groups as 'immatures' and 'adults'. Puffins are also unusual among birds in shedding the horny sheaths of the bill annually (Bureau 1877, 1879). The ridges and furrows present on the bill of old Puffins are apparently produced at moult. These features, together with the overall shape and size of the bill, allow the age to be determined. Salomonsen (1944) seems to have been the first to draw attention to these bill features for determining age in Puffins. Later workers have used the same age categories as put forward by Salomonsen (loc. cit.): e.g. Lockley (1953), Myrberget (1962, 1963), and Nettleship (1972). Corkhill (1972) also dealt with age criteria in Puffins. However, as Myrberget and Corkhill pointed out, the crucial evidence from ringing, as to whether or not ridges and furrows do indicate age differences, has been lacking.

Materials and methods

This paper is based on data from 108 Puffins collected in Iceland during 1952–1970 and 5 Puffins collected in the Faeroes in 1959. All the birds were collected during the breeding season and were prepared as study skins.

The Icelandic material was divided into two groups: a) birds of known age (n = 91) and b) breeders of unknown age (n = 17). The Puffins of known age were all ringed as chicks in the Westmann Islands (approx. 63°26′ N; 20°16′ W) off the south coast of Iceland. They were collected 2–8 years later at the place of ringing. Since these Puffins were collected away from burrows, albeit in a colony, it is not known with absolute certainty whether these birds were breeding at the time of collection. On the other hand, the Puffins considered as breeders were taken in burrows or when carrying food. These birds were all unringed and thus their age was not known. There were 17 breeders, 13 from a colony off the north coast of Iceland near the farm Baer in Hrutafjordur (65°19′ N; 21°05′ W), but 4 came from the Westmann Islands. The colonies at Westmann Islands and at Baer are approx. 210 km apart.

The Faeroese birds were collected around the north end of Kunoy (approx. 62°20′ N; 06°40′ W), all at sea. These Puffins were selected from a bigger sample of Puffins from the Faeroes, of which only the five used here were birds of breeding age according to bill features (Petersen, unpubl.).

In subsequent analyses of size variables, birds collected in the Westmann Islands and known to be 5 years of age or older were treated together with the four known breeders from the same locality to give adequate sample sizes.

Measurements

Four different bill measurements were taken: culmen length, bill depth, width of upper mandible and gape length. Measurements were also taken of tarsus and wing. The dimensions used (except that for wing) are depicted in Fig. 1, which also gives the terminology used in describing bill features.

Culmen length was measured as the shortest distance from the tip of the upper mandible to the cere at the top of the bill. Since the cere itself was excluded, this dimension is different from that used by Myrberget (1963) and Pethon (1967) who included the cere and called the dimension 'Length'. In the present study the cere was excluded since it was found that in many dry skins a split had developed between the cere and the rhamphotheca.

Depth of bill was measured at the base of the bill between points furthest apart on the culmen and the gonys. The cere was also excluded here. This dimension is therefore the same as that used by Corkhill (1972), but differs from that used by Myrberget (1963) and Pethon (1967) who included the cere and called the dimension 'Height'.

Width of upper mandible was measured between the most distant points, or the dorsal edges of the gape at the base of the bill.

Gape length was measured in the same way as Corkhill (1972), from the front edge of the cere along the gape to tip of the upper mandible.

Tarsus length was measured as the distance from the intertarsal joint to the tarso-phalangial joint.

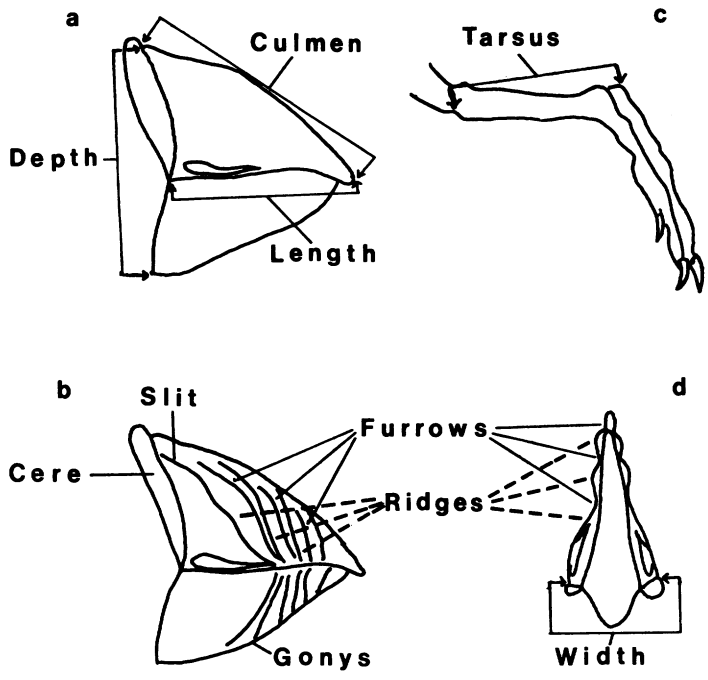

Fig. 1. Dimensions used (except that for wing) in determining size of Puffins collected in Iceland and the Faeroes. Bill terminology is also given. The figure shows: side-views of the bill (a and b), leg to show tarsus measurement (c), and bill viewed from underneath (d).

Wing length was measured according to the maximum chord method, from the carpal joint to tip of the longest primary. The wing was pressed flat on the ruler and the longest primary stretched alongside it.

All the measurements, except that of wing, were taken to the nearest 0.1 mm using calipers with pointed jaws, calibrated to 0.1 mm. The wing was measured with a B.T.O. ruler (with a stopper) to the nearest 1 mm.

Culmen length and bill depth do not correspond to dimensions most commonly used in the literature. This is because, firstly, seasonal variation in bill size is particularly notable in Puffins and the above-mentioned artifact can develop in dry skins, rendering many published records of dubious value. Secondly, published materials have to be used with some caution in comparative studies because of personal errors in measuring.

Results

Size variables of Icelandic Puffins

The size variables of Puffins from the two Icelandic colonies are given in Table I. Male Puffins are generally larger than females. This is most noticeable in culmen length, bill depth, and bill width. In order to avoid heterogeneity related to sex, the sexes are treated separately.

As can be seen from Table I, Puffins from Baer (North Iceland) are larger than south coast birds. For a better comparison of differences, Student's t-test has been used. The size differences are statistically significant for most dimensions. The only dimension which is not significantly different, is gape length of males. Puffins still further north in Iceland, at Grimsey on the Arctic Circle (66° 30′ N), may be even larger than Puffins from Baer, as pointed out by Timmermann (1949). It is concluded from these results that Puffins show a strong clinal variation in size in Iceland, with considerable increases towards the north.

Five male Puffins from the Faeroes were also measured and compared with Puffins from the Westmann Islands (South Iceland). The differences in size are small (Table II), although the sample size for the Faeroese birds is small. Nevertheless, the material indicates that Faeroese and Westmann Islands Puffins differ less in size than Puffins from the two Icelandic colonies. This result raises questions

Table I. A comparison of size of Puffins from two different localities in Iceland. All birds were breeders or of breeding age (see text for further explanation). The statistical tests were made between sexes within each locality and between birds of the same sex from different localities. WI=Westmann Islands, B=Baer, SD=Standard deviation

	Westmann Islands (South Iceland)							Baer (North Iceland)					
	Bill measurements (mm)							Bill measurements (mm)					
	Culmen	Depth	Length	Width	Tarsus	Wing		Culmen	Depth	Length	Width	Tarsus	Wing
♀♀							♀♀						
n	12	11	12	12	12	12		8	8	8	8	8	8
Range	39.7–45.6	32.6–37.5	26.6–30.2	11.0–13.2	23.4–27.7	154–166		44.7–50.5	36.5–38.8	28.5–31.9	12.4–13.8	25.6–27.8	159–173
$\bar{x}$	43.1	35.3	28.1	12.3	25.6	161.6		47.5	37.5	30.6	13.2	26.8	166.5
SD	1.9	1.4	1.1	0.6	1.1	3.3		1.7	0.8	1.1	0.6	0.9	4.9
♂♂							♂♂						
n	9	9	9	9	9	9		5	5	5	5	5	5
Range	41.8–49.0	35.4–39.3	27.2–32.1	13.0–14.4	25.5–28.2	159–172		48.9–51.8	39.0–40.6	29.5–32.2	13.9–15.5	26.7–29.3	169–173
$\bar{x}$	45.7	37.7	29.8	13.7	26.5	163.7		50.3	40.6	31.0	14.6	28.3	171.2
SD	2.3	1.3	1.7	0.5	0.9	3.8		1.3	1.3	1.2	0.6	1.2	1.5
t	2.8	4.0	2.8	5.8	1.9	1.3		3.2	5.4	0.6	4.2	2.6	2.1
D.f.	19	18	19	19	19	19		11	11	11	11	11	11
P	<0.02	<0.001	<0.02	<0.001	>0.05	>0.05		<0.01	<0.001	>0.05	<0.01	<0.05	>0.05

	Culmen	Depth	Length	Width	Tarsus	Wing
t ♀♀WI/♀♀B	5.3	4.1	4.9	3.5	2.5	2.7
d.f.	18	17	18	18	18	18
P	<0.001	<0.001	<0.001	<0.01	<0.05	<0.02
t ♂♂WI/♂♂B	4.2	4.1	1.4	3.2	3.1	4.2
d.f.	12	12	12	12	12	12
P	<0.01	<0.01	>0.05	<0.01	<0.01	<0.01

Table II. A comparison of size of male Puffins from the Westmann Islands (Iceland) and the Faeroes

		Bill measurements (mm)					
		Culmen	Depth	Length	Width	Tarsus	Wing
Westmann Islands	n	9	9	9	9	9	9
	Range	41.8–49.0	35.4–39.3	27.2–31.4	13.0–14.1	25.5–28.2	159–172
	$\bar{x}$	45.7	37.7	29.8	13.7	26.5	163.7
	SD	2.3	1.3	1.7	0.5	0.9	3.8
Faeroes	n	5	5	5	5	5	5
	Range	41.5–45.8	35.0–37.0	27.6–30.1	12.9–13.5	24.8–26.0	156–166
	$\bar{x}$	44.1	36.0	29.0	13.1	25.5	161.6
	SD	1.6	0.7	1.0	0.3	0.5	3.8
	t	1.3	2.7	1.0	2.5	2.2	1.0
	d.f.	12	12	12	12	12	12
	P	>0.05	<0.05	>0.05	<0.05	<0.05	>0.05

concerning the subspecific status of these populations (see Discussion).

Bill features as criteria of age

Immature Puffins have been thought to have a distinctly smaller and differently shaped bill than older Puffins. Moreover, it has been noticed that there may be differences in numbers of ridges and furrows on the bill, immature birds having fewer. However, not until the present study have ringing data been at hand to prove conclusively to what extent bill features are indicative of age.

According to my data, using Puffins of known age, the following bill features are characteristic of Westmann Islands Puffins of the ages 2, 3, 4, 5, and 6 years and older. The narrow slit on the Puffin's bill (see Fig. 1b) does not count as a furrow in the following descriptions. The numbers of birds examined are given in parentheses:

2-year olds (11): They have a distinctive triangular bill, easily distinguished from the deeper and more convex bill of older Puffins (cf. Fig. 2). Bill has one fully developed ridge on the upper mandible, and one partially developed ridge more anteriorly. There is one furrow, but always very shallow and broad. The most posterior part of the gonys is very soft and pliable, and shrivels to become deformed in some study skins.

3-year olds (27): Bill more convex than in 2-year olds but not so much as in older Puffins (cf. Fig. 2). There is one deep, narrow furrow on the upper mandible and one shallow furrow, rather broad.

4-year olds (36): Two deep, narrow furrows on the upper mandible, and usually ½–1 more. If so, this third furrow is always very shallow, broad, and with very little (if any) white, chalk-like substance in the furrow. In the sample of 36 birds, three Puffins (8 %) had 2 deep furrows only, 27 (75 %) had 2 ½, and six (17 %) had 3 furrows.

5-year olds (8): Two deep, narrow furrows on the upper mandible. Usually ½–1 more, and if so, deeper and narrower than in 4-year olds and always with this distinct white chalk-like substance in the last furrow (Fig. 2d). Two of the eight Puffins of this age had 2 deep furrows only, one had 2 ½, and five had 3 furrows.

6-year and older (9): Usually 3 deep and narrow furrows. If the third furrow is shallow, there is then a very distinct white substance in it (Fig. 2e, f). One bird out of nine had rather a shallow third furrow while eight had 3 deep, narrow furrows.

From these descriptions it should be possible to determine the age of 2- and 3-year old Puffins from older Puffins with 100 % certainty. Furthermore, all 4-year old Puffins should be recognizable from 5-year olds and older, although there is an overlap in the number of furrows. An important determining factor here is the amount of chalk-like substance in the last furrow. This feature may, however, prove difficult to use in live birds. Most 6-year old Puffins (and older) would be confused with the

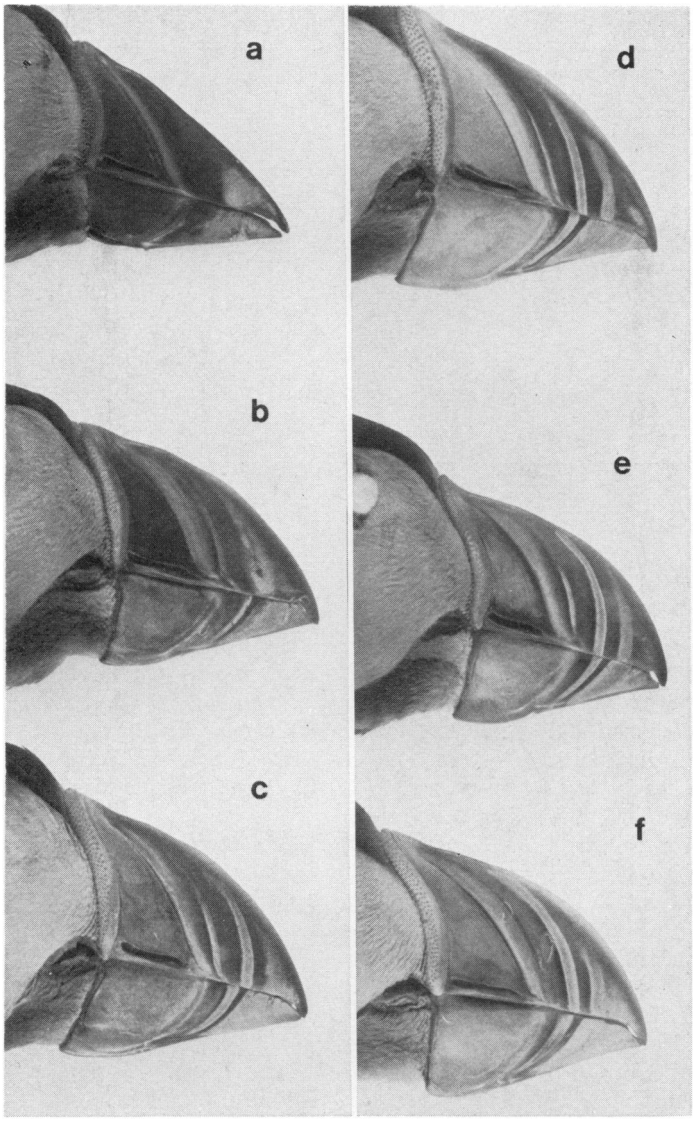

Fig. 2. Bills of Puffins of known age from the Westmann Islands, Iceland. Ages of the birds shown are as follows: a) 2-year old, b) 3-year old, c) 4-year old, d) 5-year old, e) 6-year old, and f) 7-year old.

5-year olds since the majority of both age groups have 3 furrows. However, it seems that proportionally fewer 5-year old birds have 3 fully developed furrows.

Unfortunately, no ringed yearling Puffins were available for study. This is primarily because Puffins do not normally return to the colonies in their first year (Petersen, unpubl.). Therefore, an obvious omission is how yearlings are distinguished from 2-year old birds in summer.

Discussion

Size variables of Icelandic Puffins

Icelandic Puffins as a whole have been generally regarded as belonging to the nominate subspecies *arctica* (e.g. Hartert 1921–22, Witherby et al. 1941, Vaurie 1965). Faeroese Puffins, on the other hand, have been considered to belong to the smaller subspecies *grabae* (Salomonsen 1944). This conventional division into subspecies cannot now be accepted in

view of the results set forth in the present paper, since South Iceland Puffins differ less from Faeroese Puffins than from North Iceland birds.

It is easy to imagine how this inconsistency has come about. The reason appears to have been lack of material from the whole of Iceland. Relatively few Puffins from Iceland have been examined, while most of those that have were birds collected in North Iceland (Hantzsch 1905, Hartert 1921–22, Witherby et al. 1941, Salomonsen 1944, Timmermann 1949, Vaurie 1965). In these studies, all Icelandic Puffins available for examination have been lumped into one sample with the result that mean figures have been grossly biassed towards North Iceland birds. And average measurements for Puffins from North Iceland do indeed fall within the size ranges of the nominate *arctica*. All Icelandic Puffins have then, by extrapolation, been considered to belong to that subspecies. Thus, the steep size gradient within Iceland was not apparent, nor was the fact that South Iceland Puffins would be more appropriately regarded as belonging to subspecies *grabae*, if the subspecies concept is used at all.

A north-south cline in size is well-known in *Fratercula arctica* as a whole (e.g. Myrberget 1963, Pethon 1967) and three subspecies have been generally recognized on differences in size, as mentioned in the Introduction. However, the continuity of the size variation appears to be such that any division into subspecies is completely arbitrary. In fact Pethon (1967) stated that no subspecies could be recognized in *Fratercula arctica* by using standard methods for describing subspecies. This was also noticed by Myrberget (1963), who then proposed that the Puffin as a species would be best described as *Fratercula arctica* cl. *grabae/naumanni* in accordance with the proposal of the B.O.U. Taxonomic Sub-Committee (1956) on clinal species. In a biological sense this is more appropriate than the division into subspecies, although taxonomically this is perhaps not so, since cline is not a taxonomic category.

It may be argued that subspecies names of Puffins should be kept for the sake of convenience. This is perhaps convenient when discussing variation in size over the breeding range of the species as a whole. However, as soon as discussion is centred at the local level, e.g. within Iceland only, collecting localities become more suitable for reference. In the case of Icelandic Puffins we may argue that South Iceland birds belonged to the subspecies *grabae* but North Iceland ones to *arctica*. In so doing, difficulties would arise regarding Puffins from the west and east coasts which presumably are intermediate in size, although no data exist from these areas. The best solution is probably to describe size gradients in terms of isophenes (see Mayr 1969).

Bill features as criteria of age

Salomonsen (1944) proposed an age-determination scheme by which Puffins were divided into three age categories; 1-year old birds, 2-year olds, and 3-year old birds and older. Yearlings were supposed to have a bill which was more sloped and not so arched as older birds, and without any furrows. Two-year old Puffins were said to have a slightly smaller bill than still older birds, and only one furrow. All Puffins without the above features were apparently considered as being 3 years of age or more. Salomonsen's Figure 24 (p. 125) is said to depict these three age categories. Using my data for Puffins of known age, it appears that Salomonsen's Figure 24 shows a 2-year old bird, a 3-year old, and a bird 6 years or older. Salomonsen, who did not have birds of known age, seems therefore to have misjudged the age of the Puffins by one year. It was not known at that time (1944) that Puffins do not normally visit the breeding colonies as yearlings.

Following Salomonsen and apparently making the same mistake, Myrberget (1962, 1963) recorded yearlings as common on Lovunden (North Norway) during the breeding season. Yearlings were thought to be birds which had a single indistinct furrow on the upper mandible, or none at all, but 2-year old birds one well developed furrow and often one indistinct in addition. It is most likely in view of present data that Myrberget was really dealing with 2- and 3-year old Puffins, respectively.

The present study has shown, for the first time, using ringed birds, that bill features can be used to determine the age of Puffins. As such, this knowledge may be of importance in ecological studies on Puffins. However, the age descriptions may only apply without correction to Westmann Islands Puffins and other populations with bills of about the same size.

Salomonsen (1944) pointed out for the Razorbill *Alca torda* that different subspecies had a different number of furrows on the bill. The Razorbill is possibly another species in which bill features may be used for age determination. It is interesting that R. E. Ashcroft (pers. comm.) recorded a less clear-cut division into age classes for Puffins on Skomer Island (Wales) than that found for Puffins from the Westmann Islands. British Puffins have smaller bills than Icelandic birds and the size of the bill as such may be important since the numbers of ridges and furrows may depend not only on age but on size of the bill as well. If so, one would expect even more clear-cut differences between age classes in the large-billed Spitsbergen Puffins. The rate of furrow development on the bill is another possible variation factor between Puffins from different localities.

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