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HYBRIDIZATION OF GLAUCOUS AND HERRING GULLS IN ICELAND

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ABSTRACT.—I report here some results from studies during the last two decades on the extensive hybridization between the Herring Gull, *Larus argentatus* and Glaucous Gull, *L. hyperboreus,* which resulted from a massive immigration of *argentatus* to Iceland commencing about 1925. Mate selection was found to be random with respect to primary pigmentation and body size, but site tenacity had an effect. *Argentatus*-like birds raise fewer young per nesting attempt than do *hyperboreus*-like ones, whereas birds of intermediate appearance have a higher incidence of non-breeding than do others. There are also indications that adult *hyperboreus*-like birds survive better than do others. The population is not becoming more *hyperboreus*-like, probably because of continuing low-level immigration of pure *argentatus* from Europe.

Extensive hybridization is taking place in Iceland between Herring Gulls (*Larus argentatus*) and Glaucous Gulls (*L. hyperboreus*). This hybridization is the result of a massive immigration of *L. argentatus* into Iceland which commenced about 1925–1930. The results of field studies of this hybridization up to 1966 are given in Ingolfsson (1970b).

The earlier studies indicated that, following the colonization by *argentatus,* rapid changes in phenotypic traits occurred in gull colonies in southern and eastern Iceland. However, in western Iceland *argentatus* did not make its presence felt to any degree. The aims of the present studies are to follow further developments of the hybridization by investigating selected colonies in western and southeastern Iceland, and to obtain further information on various population phenomena, such as mortality rates and mate selection.

These studies rely largely upon the pattern of pigmentation of the outermost primaries to indicate the degree of "hybridness" of the gulls. In addition, then, an effort was made to study the effectiveness of the "hybrid index," based on primary pattern, by investigating its relationship with other characters.

METHODS

Four gull colonies were studied, all of which had been studied previously. The colony at Bjarnahöfn (or Bjarnarhafnarfjall) is located in western Iceland, while those at Skrudur, Hromundarey and Horn are in southeastern Iceland (see map in Ingolfsson 1970b). At Bjarnarhöfn, samples of gulls were obtained in 1971, 1972, 1978 and 1986 by shooting or by killing the gulls by means of the drug Avertin (tribromoethanol). At other colonies I attempted to capture gulls alive by drugging them with an appropriate dose of Avertin; in this procedure the mortality rate was only about 20%. All adults were tagged with a numbered ring. Those from Hromundarey and Horn as well as a proportion of those caught at Skrudur, were also individually color-ringed. At Skrudur, adults were ringed in 1972, 1974 and 1978; in 1986 a sample of gulls was taken there by killing with Avertin. At Hromundarey gulls were ringed every summer from 1971–1975, and at Horn in the summers of 1971–1973. Additional visits were paid both to the Hromundarey colony for checking of color-ringed gulls in the springs of 1977, 1978 and 1979 and to Horn in 1977. At all of these colonies, chicks were frequently marked as well by use of wing tags and leg rings.

The hybrid index (HI) of all gulls handled was determined. The index, described in Ingolfsson (1970b), is based on the pattern and amount of pigmentation of the five outermost primaries and ranges from 0 (apparently pure *argentatus*) to 5 (apparently pure *hyperboreus*). Values are given to one decimal place. For dead birds the index was assessed in the laboratory and the wings stored for reference. For live birds the index was assessed in the field, and in addition both wings were photographed in color in an outstretched position. Standard body measurements (culmen length from base of feathers on top of bill, bill height at the gonial angle, tarsus length and weight) were taken on all adults handled. The state of primary moult was examined on all dead birds and a primary moult score (PMS), as described in Ingolfsson (1970a), was obtained. The PMS ranges from 0 (all primaries old) to 100 (all primaries new and fully grown). The score progresses rather steadily with time during the moult.

RESULTS

THE RELATIONSHIP OF PRIMARY-BASED HYBRID INDEX TO OTHER CHARACTERS

The effectiveness of the primary pattern as an indicator of hybridness is obviously dependent upon its constancy with age. Photographs were available of 50 gulls captured and photographed in two or more years (interval 1–6 years) in the eastern colonies. Three of these gulls were photographed in three years and so the number of comparisons between successive examinations is 53. The hybrid index had changed in 33 cases. In 28 cases the change was 0.2 HI units or less and the maximum change was 0.5 units (3 cases). There was little indication of correlation between age and HI value. In 20 instances the HI value had lowered with age, while in the remaining 13 cases the index had increased. Changes in pig-

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TABLE 1
CORRELATION COEFFICIENTS BETWEEN HYBRID INDICES AND BODY MEASUREMENTS OF GULLS AT THREE COLONIES IN EASTERN ICELAND

Locality	Year	Sex	N	Correlation between HI and		
				Culmen	Bill depth	Tarsus
Horn	1965–1966	♂	16	−0.7099**	−0.8040**	−0.6031**
Horn	1965–1966	♀	19	−0.6052**	−0.2923	−0.7421**
Horn	1971–1973	♂	14	−0.3710	−0.2579	−0.3434
Horn	1971–1973	♀	23	−0.5855**	−0.3584	+0.0108
Hromundarey	1965–1966	♂	41	−0.3619*	−0.0302	−0.2843
Hromundarey	1965–1966	♀	30	−0.1014	−0.3191	−0.1365
Hromundarey	1971–1975	♂	88	+0.0500	−0.2223*	+0.1297
Hromundarey	1971–1975	♀	97	−0.1812	−0.1256	−0.1148
Skrudur	1965	♂	22	−0.1076	−0.1264	−0.1240
Skrudur	1965	♀	19	+0.3137	−0.3836	+0.4614*
Skrudur	1972–1978	♂	180	+0.1254	+0.0589	+0.1314
Skrudur	1972–1978	♀	172	−0.0194	+0.1502	+0.1546*
Skrudur	1986	♂	28	+0.0797	−0.2887	−0.2210
Skrudur	1986	♀	32	+0.1947	−0.1392	+0.3077

* $P < 0.05$.
** $P < 0.01$.

mentation pattern of at least one primary were noted in virtually all cases. Most gulls showed some change in the score of individual feathers, although this did not necessarily lead to a change in the overall hybrid index, since changes in individual primaries sometimes cancelled each other out. The scores for the 9th and 10th primaries tended to become lower with age (their pigmentation tended to decrease), while the reverse was true for the 6th, 7th and 8th; the difference between the two sets of feathers was highly significant ($\chi^2 = 8.28$, $P < 0.005$). Changes in HIs between years, although frequent, were clearly not of such a magnitude as to invalidate the use of the index.

L. argentatus and *L. hyperboreus* differ in body size, the former being smaller, although there is some overlap when birds of the same sex are compared (Ingolfsson 1970b). As body size is likely to be under the control of a greater number of genes than is the primary pattern, an investigation into body size of hybrid populations is of interest. Also, an investigation of the degree of correlation between hybrid index and body size can be expected to indicate the effectiveness of the index as a measure of hybridness.

An overall correlation between body size and primary pattern has been demonstrated using material from a large number of colonies (Ingolfsson 1970b). A closer examination of both old and new data shows, however, that the situation is complex (Table 1). In the Horn colony in 1965 and 1966, where both apparently pure *hyperboreus* and *argentatus* were found nesting, a strong negative correlation between body size and HI was generally found. During 1971–1973 this negative correlation was much less evident, and in some instances significant differences in correlation coefficients between the two periods are found. The HI distribution had at the same time changed markedly (see below). At Hromundarey where no pure *hyperboreus* have been found (probably indicating that hybridization has been taking place for a longer period), the situation is different. Here negative correlation is slight and is significant only for some measurements in males, both during 1965–1966 and 1971–1975. At Skrudur, the largest colony examined and the one where *argentatus* traits are most evident, there is little or no indication of negative correlation between body size and HI. However, there are some instances of significant positive correlations (Table 1). Although this is significant only in the case of females, a similar tendency is seen for the males during 1972–1978. No correlation appeared at Bjarnarhöfn, but the sample is very crowded in the low HI-range.

These results indicate a decrease in correlation between HI and body size as hybridization progresses. This is to be expected if genes for body size and primary pattern are not closely linked. No explanation can be offered for the curious reversal of correlation seen at Skrudur.

Birds from Horn scoring in the low range (HI 0–1.0) are significantly larger than birds scoring in this range from Hromundarey and Skrudur, but significantly smaller than such birds from Bjarnarhöfn. Even 0-scoring birds (i.e., apparently-pure *hyperboreus*) from Horn are small in comparison with Bjarnarhöfn gulls. This may indicate that 0-scoring birds from Horn contain some *argentatus* genes in spite of absence of primary pattern. Interpopulation differences between pure *hyperboreus* populations might provide an alternative although less likely explanation. The Horn *hyperboreus* population would have to contain by far the smallest individuals of any population in the North Atlantic for this explanation to hold (unpublished data). The few birds from Bjarnahöfn scoring above 1.0 are very large compared with eastern birds of similar appearance; some in fact are larger than any bird examined from the east coast.

It is difficult to compare the time of moult of *hyperboreus* and *argentatus*. There are indications of differences in timing among colonies, birds in colonies in southern Iceland moulting a little earlier than more northern ones. There are also differences between years. The gulls examined at Skrudur on June 8–10 1972 were significantly less advanced in primary moult than those examined there on June 8–10 1978 (Mann Whitney U on PMS, $P < 0.01$). In spite of these difficulties the indications are that *hyperboreus* moults its primaries somewhat earlier than does *argentatus* living under similar conditions. Thus at Horn, both in 1965 and in 1966, a significant negative correlation was found between PMS and HI (1965: $r = -0.6518$, $df = 20$, $P < 0.01$; 1966: $r = -0.6480$, $df = 11$, $P < 0.05$) (Fig. 1). No such correlation is found during these years at Hromundarey or at Skrudur. Data on moult for later years are rather scant, except for the Skrudur colony, and give no indication of a correlation between hybrid index and time of moult.

These analyses show that body size and time of moult are genetically influenced. Genes for these attributes are not closely linked with those influencing amount and pattern of pigment on primaries, and a correlation of HI with these features becomes indistinct or indistinguishable after hybridization has been taking place for some time. The HI is at present consequently a poor indicator of the hybridness of individual gulls. It seems, however, reasonable to assume that low-scoring birds have on the average a greater proportion of *hyperboreus* genes than do higher scoring ones. Changes in the HI distribution of a colony with time would thus probably reflect changes in the relative frequency of *argentatus* and *hyperboreus* genes in that colony. A similar argument can be applied to body size, while there are many problems in the use of PMS in this connection.

It is relevant to note that Patten (1980), who studied hybridizing populations of *L. argentatus* and *L. glaucescens* in southern Alaska, found a significant correlation between a hybrid index based on primary pattern (actually a modified form of the index here used) and two other attributes in which the parent populations differed.

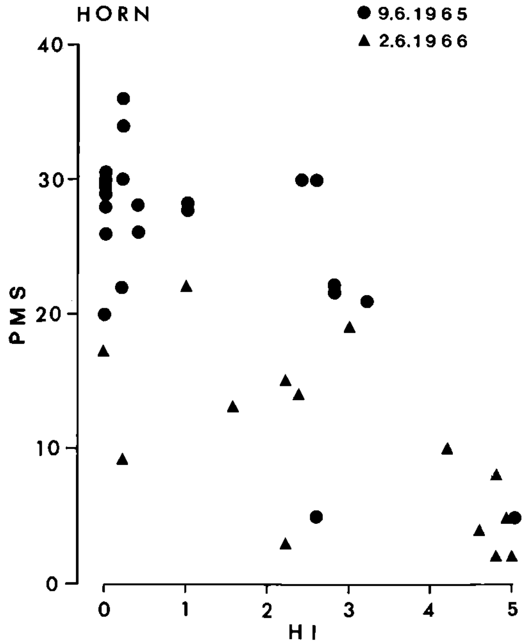

FIGURE 1. Primary moult score (PMS) and hybrid index (HI) of gulls collected on two dates in the Horn colony, southeastern Iceland. A negative correlation is significant for both dates (see text).

The HI Distribution of the Colonies since 1964

Earlier findings indicated a rapid change in average HI of colonies after the immigration of *argentatus* (Ingolfsson 1970b). For the colony at Krisuvík in southwestern Iceland an average increase of at least 0.12 HI units per year is indicated for the 35 years prior to 1965; and a similar value can be obtained for the Vestmannaeyjar colony, also in southwestern Iceland. Furthermore, between 1965 and 1966 a significant increase in mean HI occurred at Horn, and a similar although non-significant tendency was also seen at Hromundarey (excluding the nearby colony of Thvottareyjar from this analysis).

In further analyses of possible changes in the HI distribution birds have been grouped into 6 HI classes. The establishment of these classes has taken into consideration the changes with time in HIs of individual gulls, the overall HI distribution (especially in the eastern colonies), and the form of the relationship between HI and size. The classes are as follows:

class I	HI	0
class II	HI	0.1–1.7
class III	HI	1.8–2.6
class IV	HI	2.7–3.5
class V	HI	3.6–4.4
class VI	HI	4.5–5.0

TABLE 2
THE HI DISTRIBUTION OF GULLS FROM BJARNARHÖFN, WESTERN ICELAND, 1964–1986, SHOWN AS NUMBER AND PERCENTAGE OF GULLS BELONGING TO EACH HI CLASS

HI class	1964–1965 No.	1964–1965 %	1971–1972 No.	1971–1972 %	1978 No.	1978 %	1986 No.	1986 %
I	7	47	35	58	22	61	36	64
II	8	53	24	40	14	39	20	36
III								
IV								
V			1	2				
VI								
Total	15		60		36		56	

TABLE 3
THE HI DISTRIBUTION OF GULLS IN THE A AND B COLONIES AT HORN, SOUTHEASTERN ICELAND, 1965–1973, SHOWN AS THE NUMBER AND PERCENTAGE OF GULLS FALLING IN EACH HI CLASS

HI class	1965, A No.	1965, A %	1966, A No.	1966, A %	1971–1973, A No.	1971–1973, A %	1971–1973, B No.	1971–1973, B %
I	7	32	1	8	1	3		
II	8	36	3	23	3	10		
III	3	14	3	23	4	14		
IV	3	14	1	8	3	10	1	8
V			2	15	6	21	1	8
VI	1	5	3	23	12	41	10	83
Total	22		13		29		12	

On the basis of examination of a large number of museum skins of gulls from outside Iceland, I feel certain that no pure *hyperboreus* will score above 0, while pure *argentatus* may score as low as 4.5, and an occasional aberrant one even lower (see Ingolfsson 1970b for a fuller discussion of this). Results discussed above, however, indicate that classes I and VI may include birds of hybrid origin indistinguishable from pure birds.

Results for the Bjarnarhöfn colony during 1964–1986 are shown in Table 2. At this colony there is no indication of change during the 22 years covered. The non-significant trend is towards lowering of the mean HI with time. Gulls at this colony rarely score above 0.6 and birds scoring 0 remain common.

The results for the Horn colony are shown in Table 3. In 1965 I killed the majority of the gulls, but the colony had regained its size the following year. The HI distribution in the Horn colony was now significantly different (classes I–IV vs. V–VI, Fisher's Exact Test, $P = 0.037$). The replacements were predominantly of classes V–VI, while birds of class I (apparently pure *hyperboreus*) were conspicuously lacking. In 1966 I again killed a large proportion of the gulls. The colony which contained about 20 pairs in 1965 was still of similar size in 1971, but decreased to about 10 pairs in 1973 and had almost disappeared in 1974, after which it has not been investigated. By 1971–1973, the difference from 1965 had become still more marked and the proportion of birds of class VI was now significantly higher than in 1966 (Fisher's Exact Test, $P = 0.014$). By 1971 a few pairs had established a loose colony among Lesser Black-backed Gulls, *L. fuscus,* about 2 km from the old one. The new colony (colony B) contained about 7–10 pairs during 1971–1973. These birds were almost all of class VI. The HI distribution of the two colonies, A and B, during 1971–1973 comes close to being statistically different at the 5% level when proportions of birds scoring above 3.0 are compared (Fisher's Exact Test, $P = 0.057$).

The Hromundarey colony was estimated to contain about 40 pairs in 1965 but in 1971–1979 the colony harbored between 100–150 pairs. Gulls have not been caught here since 1974. No significant changes have been noted at this colony since 1965 (Table 4) and there was no trend apparent during the 4 years 1971–1974.

The results for the Skrudur colony are shown in Table 5. This large colony of about 500 pairs has not shown a clear directional change in HI distribution during the 20-year period 1965–1986. The sample from 1972 is, however, aberrant in that the proportion of class VI birds is low. This sample differs significantly in this respect from the samples of 1974 ($\chi^2 = 5.57$, $P < 0.025$), 1978 ($\chi^2 = 4.56$, $P < 0.05$), and 1986 ($\chi^2 = 11.46$, $P < 0.005$) (recaptures in these years of birds ringed as adults in 1972 are omitted) but not from the smaller sample of 1965 ($\chi^2 = 1.45$, $P > 0.1$). There is no indication of a difference between the sample from 1965 and those from 1974 and 1978. The proportion of class VI birds in the 1986 sample is higher than in any other

TABLE 4
THE HI DISTRIBUTION OF GULLS AT HROMUNDAREY, SOUTHEASTERN ICELAND, 1965–1974, SHOWN AS NUMBER AND PERCENTAGE OF GULLS FALLING IN EACH HI CLASS

HI class	1965 No.	1965 %	1966 No.	1966 %	1971–1974 No.	1971–1974 %
I						
II	9	23	3	10	27	14
III	2	5	3	10	22	12
IV	8	20	4	13	28	15
V	13	33	12	39	53	28
VI	8	20	9	29	57	30
Total	40		31		187	

TABLE 5
THE HI DISTRIBUTION OF GULLS FROM SKRUDUR, EASTERN ICELAND, 1965–1986, SHOWN AS NUMBER AND PERCENTAGE OF GULLS BELONGING TO EACH HI CLASS*

	1965		1972		1974		1978		1986	
HI class	No.	%	No.	%	No.	%	No.	%	No.	%
I										
II	1	2	2	1	5	5	1	1	1	2
III	2	5	1	1			3	3		
IV			17	11	4 (1)	4	7	6	3	5
V	11	26	50	33	27 (8)	25	27 (3)	23	9	15
VI	27	66	81	54	74 (11)	67	82 (7)	68	47 (1)	78
Total	41		151		110 (20)		120 (10)		60 (1)	

* For 1974, 1978, and 1986 the number of gulls ringed in previous years as adults is shown in parentheses.

sample, but the difference is not statistically significant from any single sample, except that from 1972. In 1978 and 1986, 15 breeders were caught that had been banded as chicks previously at the colony (1971: 6, 1972: 4, 1973: 4, 1974: 1). The HI distribution of these birds does not differ significantly from that of any other Skrudur sample.

Observations in the four colonies show that the situation is now fairly stable with respect to HI distribution. There is no indication that pure *argentatus* is still immigrating on a large scale to preexisting colonies in Iceland. The Horn colony is aberrant in this respect. Birds killed here in 1965 and 1966 were obviously replaced by birds originating elsewhere and the replacements may have included immigrants from abroad. That immigrant Herring Gulls were involved in the formation of the new B colony at Horn is also likely, as the HI distribution there differs significantly from that of known neighboring colonies (except the A colony at Horn) in the high proportion of class VI birds (apparently pure *argentatus*). If this interpretation is correct, immigrant *argentatus* are still arriving in Iceland, but are usually unable to breed unless a vacuum is created by killing gulls in already existing colonies (see Ingolfsson 1978). The B colony at Horn is one of the very few new colonies known with certainty to have been established in Iceland in the last 15 years or so, which further indicates that Iceland as a whole may not have any additional carrying capacity for these gulls.

The observation that the Skrudur and Hromundarey colonies have maintained unchanged but significantly different HI distributions for close to 15 years, although the distance between them is only about 40 km (considerably less than one hour's flying time), shows gene exchange between neighboring colonies to be limited. This is further substantiated by color ringing. Although several hundred adults have been color-ringed in the three colonies in southeastern Iceland, there are only two instances of adults changing colonies, both gulls moving to Hromundarey, one from Skrudur, the other from Horn (55 km away). These are the two colonies closest to the Hromundarey colony.

MATE SELECTION

Previous studies did not indicate assortative matings with respect to HI (Ingolfsson 1970b). New data from the east coast on some 75 additional matings produce the same result: There is no hint of assortative matings with respect to primary pattern.

The data on matings have been analysed with respect to size. Bill height at the gonial angle was used as a measure of size, since sexual dimor-

TABLE 6
BILL HEIGHT AT GONIAL ANGLE IN KNOWN PAIRS FROM VARIOUS LOCALITIES IN SOUTHERN AND EASTERN ICELAND*

	Males			
Females	<20.0 mm	20.0–20.9 mm	>20.9 mm	Total
<18.0 mm	3 (4.28)	11 (8.32)	4 (7.39)	18
18.0–18.9 mm	10 (7.50)	20 (18.87)	19 (19.87)	49
>18.9 mm	3 (5.54)	17 (14.32)	16 (16.54)	36
Total	16	48	39	103

$\chi^2 = 5.42$ (df 4), $P > 0.1$.
* Figures in body of table show number of pairs with expected frequencies in parentheses. The expected frequencies were obtained for each colony separately and then totalled.

TABLE 7
THE HI OF FEMALES AND MALES THAT HAVE CHANGED MATES, AND THE HI OF THE MATES LISTED IN CHRONOLOGICAL ORDER

Mate changes of females		Mate changes of males	
Female	Mates	Male	Mates
2.0	4.1	0.2	0.6
	4.7		3.2
2.6	0.2	0.2	5.0
	3.5		2.6
2.8	4.8		0.1
	5.0	1.8	3.2
3.2	3.7		4.7
	2.3	2.3	4.0
3.6	3.9		3.2
	4.1	3.9	3.6
4.3	5.0		3.4
	0.6	4.1	2.0
4.8	2.0		3.6
	4.6	4.1	0.3
			4.6
		4.7	0.8
			2.4

phism is especially great in this dimension (Ingolfsson 1969). All available data have been used except those for the Horn and Hromundarey colonies, where only matings in the year with the maximum number of matings were used. This was 1972 for Horn and 1974 for Hromundarey. The results (Table 6) give no indications of assortative matings. Both Goethe (1961) and Harris and Jones (1969) claim that in *argentatus* the difference in bill size of members of pairs was considerably greater than expected by chance. However, as there was no statistical support for these conclusions, they cannot be properly evaluated. As the data are presented by Goethe, it seems in fact unlikely that statistical treatment would point to assortative matings with respect to size.

Harris (1970) has shown by cross-fostering experiments that imprinting of chicks on parents is of importance in mate selection of *L. fuscus* and *argentatus,* especially as far as females are concerned. I have no direct observations on the role of imprinting in the hybrid population of Iceland, but some information may be obtained by analysing mate changes (sometimes due to my killing a member of a pair). In all I have information on 7 females and 8 males that have changed from one known mate to another (Table 7). There is no indication that primary pattern has anything to do with selection of new mates and it is clear that both males and females frequently have successive mates differing widely in HI. It is therefore unlikely that imprinting on a primary pattern is of significance in mate selection.

Gulls show a high degree of site tenacity, pairs usually returning to the same territory to breed year after year. Gulls changing mates between years show almost the same degree of site tenacity as unchanged pairs. In a high proportion of cases members of newly formed pairs were known to be previous next-door neighbors. Site-tenacity was therefore clearly of importance in pair formation.

NESTING SUCCESS

An attempt was made to estimate the breeding success of birds, with known HI and body size, at Hromundarey. Culmen length was used as a measure of size as it is a less variable indication of body size than weight and was measured more accurately than bill height. The colony was visited frequently during the springs of 1973 and 1974 to check for eggs and chicks. The chicks were tagged as soon after hatching as possible. In 1973 the chicks were followed to a stage very close to fledging (about 4 weeks old), while in 1974 checking was discontinued when most chicks had reached an age of about one week to 10 days.

Some results with respect to HI are given in Table 8. There is little indication of differential breeding success, with one exception: in 1973 a significantly lower proportion of eggs laid by class VI females (apparently pure *argentatus*) resulted in chicks which reached 4 weeks of age than was the case for other females combined ($\chi^2 = 5.31$, $P < 0.025$). A similar tendency is seen among males, although non-significant ($\chi^2 = 2.04$, $P > 0.1$). However, a significantly lower proportion of chicks of class VI males reached the age of four weeks than was the case for chicks of all other class males combined ($\chi^2 = 4.08$, $P < 0.05$). In 1974 the results for females were similar, with close to significantly lower proportion of eggs laid by class VI females resulting in chicks about one week old ($\chi^2 = 3.34$, $P > 0.05$). No such tendency is seen among the males. It should be noted that of the four females of class VI that were investigated in 1974, one also figured in the 1973 sample.

To analyse nesting success in relation to body size, gulls of each sex were grouped into three size classes on the basis of culmen length. The size classes are delimited as follows; an equal number of gulls falls in each class on the average.

	females	males
large	>53.7 mm	>59.7 mm
medium	52.0–53.7 mm	57.5–59.7 mm
small	<52.0 mm	<57.5 mm

TABLE 8
NESTING SUCCESS OF GULLS OF DIFFERENT HI CLASSES AT HROMUNDAREY IN 1973 AND 1974*

		1973				1974			
Sex	HI class	No. nests	Eggs laid	No. chicks tagged	No. 4-week-old chicks	No. nests	Eggs laid	No. chicks tagged	No. 1-week-old chicks
M	II	8	24	14	6	5	15	9	6
	III	4	10	9	4	1	3	2	2
	IV	4	12	8	3	1	3	2	0
	V	4	11	9	4	5	15	9	5
	VI	7	19	15	2	5	14	11	7
	Total	27	76	55	19	17	50	33	20
F	II	4	12	7	4	5	15	12	8
	III	4	9	8	2	3	8	4	6
	IV	5	14	11	5	5	15	11	6
	V	5	13	7	2	5	15	8	4
	VI	6	16	8	0	4	12	8	2
	Total	24	64	41	13	22	65	43	26

* Chicks were usually tagged within 24 hours of hatching.

The results are given in Table 9. In 1973 a significantly smaller proportion of eggs fathered by small males resulted in four-week old young than was the case for eggs fathered by larger males ($\chi^2 = 7.69$, $P < 0.01$). A tendency for the females in the same direction is non-significant ($\chi^2 = 1.82$, $P > 0.1$). The proportion of eggs, laid by small females, that resulted in tagged chicks comes closer to being significantly smaller than for larger females ($\chi^2 = 2.44$, $P > 0.1$). In 1974 the results for males were similar, eggs fathered by small males producing relatively few chicks one week of age ($\chi^2 = 5.61$, $P < 0.025$). Among females no trend was discernible. It should be noted that of the 4 small males studied in 1974, two were also in the 1973 sample of small males.

In conclusion, the above analyses indicate that the breeding success of gulls with high HIs or small body size is lower than that of other gulls. Both features are *argentatus* attributes. At Hromundarey the negative correlation between body size and HI is slight (Table 1), and the HI distribution of the 20 gulls classified as small appears similar to that of the total sample. Only 6 of the small gulls (30%) belong to HI class VI, the percentage being similar for the total Hromundarey sample (30.5%).

SURVIVAL OF ADULTS AND NON-BREEDING BIRDS

Studies on adult survival and non-breeding birds were done at Hromundarey. The method consisted of a check for the presence of color-ringed birds in years subsequent to ringing. It is felt that scrutiny of the colony was so thorough that virtually all ringed breeding adults were seen. It was, however, clear that all living adults were not necessarily seen in a particular year, since missing gulls would often reappear in later years. During their years of absence these gulls were not breeding, had left after an unsuccessful nesting attempt, or were breeding elsewhere. As re-

TABLE 9
NESTING SUCCESS OF GULLS OF DIFFERENT SIZE CLASSES AT HROMUNDAREY IN 1973 AND 1974

		1973				1974			
Sex	Size class	No. nests	Eggs laid	No. chicks tagged	No. 4-week-old chicks	No. nests	Eggs laid	No. chicks tagged	No. 1-week-old chicks
M	Large	8	22	13	7	7	21	14	9
	Medium	11	27	24	8	6	18	14	10
	Small	7	20	15	0	4	11	6	1
	Total	26	69	52	15	17	50	34	20
F	Large	8	19	18	5	7	21	14	11
	Medium	10	26	16	7	8	24	15	6
	Small	6	18	9	2	7	21	16	9
	Total	24	63	43	14	22	66	45	26

* See text for size-class limits. Chicks were usually tagged within 24 hours of hatching.

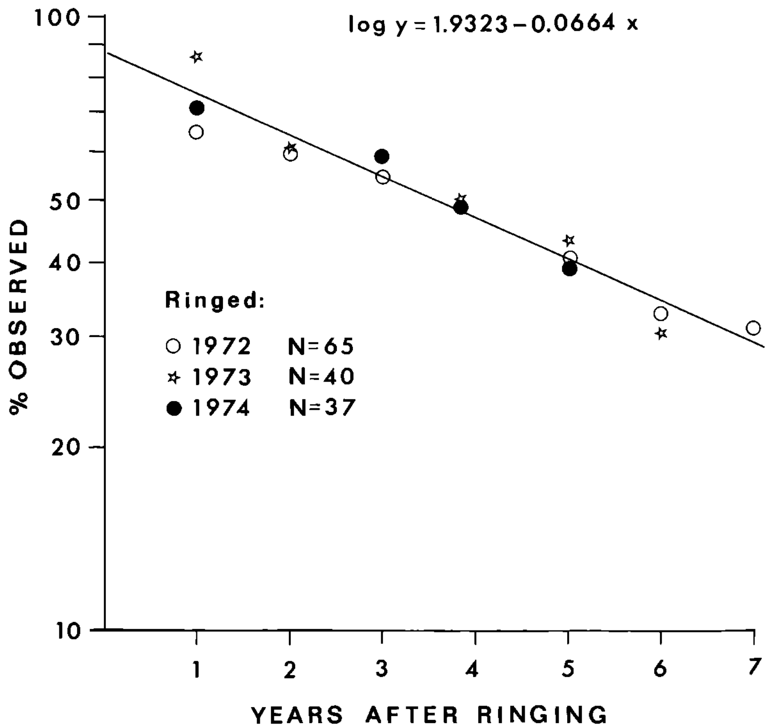

FIGURE 2. Percentage of gulls ringed as adult nesters observed in years subsequent to ringing at the Hromundarey colony, southeastern Iceland. The slope of the line indicates a mortality rate of 14.2% per annum, while the intersection of the line with the percentage axis indicates that 85.6% of surviving gulls are present in the colony in an average year.

corded instances of changing breeding colonies were extremely few and gulls usually relay after a nesting failure, it is probable that non-breeding was the prevalent cause of gull absence. Non-breeding in gulls is recorded frequently by other authors (e.g., Drost et al. 1961).

If it can be assumed that a similar fraction of surviving gulls is absent each year, which seems reasonable, the decline with time of the percentage of ringed gulls observed should be the result of mortality only. The slope of the decline (Fig. 2) indicates a mortality rate of 14.2% per annum (95% confidence limits 12.1–16.2). The intersection of the line with the percentage axis is at 85.6% (antilog 1.9323) (95% confidence limits being 81.7–89.6). This intersection indicates the percentage of surviving gulls present in the colony in an average year.

An adult mortality rate may also be assessed by using all available information to calculate the percentage of gulls known to be alive one year after ringing. This obviously gives a maximum rate, the true rate being possibly somewhat lower because of continuous non-breeding or of movement to other colonies. The maximum mortality rate calculated for 146 gulls ringed in 1972–1975 is 12.3%, a value in reasonable agreement with the values obtained above.

The adult mortality rate estimated at Hromundarey is somewhat higher than that recorded for *argentatus* in several recent studies, in which the rate has been found to be less than 10% per annum (Chabrzyk and Coulson 1976).

When the mortality rate of gulls of various HI classes is compared there is no indication of a differential mortality rate, except where class II gulls are concerned. These *hyperboreus*-like birds (there are no class I birds at Hromundarey) seem to survive better as adults than do other gulls, although the difference does not quite reach significant proportions (Fisher's Exact Test, $P = 0.08$).

There is, however, a difference in the degree of non-breeding (strictly absence from the colony). Table 10 indicates that the incidence of non-breeding is higher in birds of HI classes III–V than in birds closer to *argentatus* or *hyperboreus* in appearance. This tendency is statistically significant for data up to 1978; however, if data for 1979 are incorporated the difference is no longer significant, probably as a result of a smaller sample size (due to mortality).

There is little or no indication of differential adult survival or incidence of non-breeding with respect to body size.

DISCUSSION

The studies reported here from Hromundarey are insufficient to show the relative role of adult survival, non-breeding and nesting success in overall fitness of the gulls. It is possible that the higher degree of non-breeding shown by gulls of HI classes III–V is matched by the lower nesting success of gulls of HI class VI, so the overall selective fitness of these gulls may be similar. But the data indicate that *hyperboreus*-like gulls of HI class II show a selective advantage over other gulls. Furthermore, with respect to size, the data indicate a selective disadvantage of *argentatus*-like birds compared with other gulls. On the average, therefore, fitness of gulls at Hromundarey seems to be inversely related to proportion of *argentatus* traits.

One would therefore expect a gradual change in HI distribution of colonies with time towards a more *hyperboreus*-like condition, but this has not in fact occurred. The situation at the colony at Horn strongly indicates that immigration of *argentatus* from abroad still occurs to a limited degree, based on changing HI distributions. This immigration may be sufficient roughly to balance the selective advantage of *hyperboreus*-like gulls, thus creating a relatively stable situation. The carrying capacity of Iceland for large intertidally feeding gulls seems to have been reached some decades ago; a future invasion by *argentatus* on a scale similar to that of 1925–1930 is therefore not to be expected, unless for some reason the situation in Iceland changes drastically in favor of *argentatus*-like birds. On the other hand, a decrease in the present "immigration pressure" caused by a change in the situation abroad (first and foremost in the British Isles) could be expected to lead to a decrease in the proportion of *argentatus* genes in the gull population of Iceland. It is probable that conditions are different in various parts of Iceland. In particular, future events in the northwest, the stronghold of *hyperboreus,* may well be different from those in the rest of the country. It is planned to continue intermittent observations of the four colonies that have been under study in the past to monitor developments.

The hybrid situation in Iceland is quite different from that reported by Hoffman et al. (1978) involving *Larus glaucescens* and *L. occidentalis* in the Pacific northwest of America. Although hybridization is extensive and possibly of long standing, mating patterns at the colony studied are assortative, individuals tending to pair with mates similar to themselves. Furthermore, pairs consisting of pure conspecifics hatched significantly fewer chicks than pairs containing at least one hybrid individual. Computer simulations indicate that the situation may remain stable if there is a regular but small influx of pure types.

TABLE 10
NUMBER OF GULLS IN DIFFERENT HI CLASSES AT HROMUNDAREY EVERY OBSERVATION YEAR FOLLOWING RINGING (A) COMPARED WITH THE NUMBER OF GULLS MISSING IN ONE OR MORE BREEDING SEASONS BUT REAPPEARING LATER (B)

HI class	Data up to 1978 A	Data up to 1978 B	Data up to 1979 A	Data up to 1979 B
II	9	2	7	3
III	2	1	2	1
IV	7	7	4	7
V	6	11	5	12
VI	16	8	10	11
Total	40	29	28	34

HI classes II + VI vs. III + IV + V: For data up to 1978 (3–5 observation years): $\chi^2 = 5.26$, $P < 0.025$. For data up to 1979 (4–6 observation years): $\chi^2 = 2.34$, $P > 0.1$.

Still different is the hybridization occurring in southern Alaska between *Larus glaucescens* and *L. argentatus* investigated by Patten (1980). A narrow hybrid zone exists here, with extensive hybridization. Mating patterns are significantly assortative as in the situation noted above including intergrades selecting like types as mating partners, but no difference in breeding success was noted between pure pairs and mixed pairs. It is thought that the situation is maintained both by continuous immigration of parental types into hybridization areas and through changed environmental conditions due to activities of man. Such differences between hybrid situations are of course expected. Each hybrid situation will show its own characteristics depending on a whole range of interacting factors such as age of contact, genetic similarity, selective pressures on populations while allopatric, habitat diversity of contact area, and dispersal patterns.

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LITERATURE CITED

CHABRZYK, G., AND COULSON, J. C. 1976. Survival and recruitment in the Herring Gull *Larus argentatus.* J. Anim. Ecol. 45:187–203.

DROST, R., FOCKE, E., AND FREYTAG, G. 1961. Entwicklung und Aufbau einer Population der Silbermöwe, *Larus argentatus.* J. Orn. 102:404–429.

GOETHE, F. 1961. Zur Taxonomie der Silbermöwe (*Larus argentatus*) im südlichen deutschen Nordseegebiet. Vogelwarte 21:1–24.

HARRIS, M. P. 1970. Abnormal migration and hybridization of *Larus argentatus* and *L. fuscus* after interspecific fostering experiments. Ibis 112:488–498.

HARRIS, M. P., AND JONES, P. H. 1969. Sexual differences in measurements of Herring and Lesser Black-backed Gulls. Br. Birds 62:129–133.

HOFFMAN, W., WIENS, J. A., AND SCOTT, J. M. 1978. Hybridization between gulls (*Larus glaucescens* and *L. occidentalis*) in the Pacific Northwest. Auk 95: 441–458.

INGOLFSSON, A. 1969. Sexual dimorphism of large gulls (*Larus* spp.). Auk 86:732–737.

INGOLFSSON, A. 1970a. The moult of remiges and rectrices in Great Black-backed Gulls *Larus marinus* and Glaucous Gulls *Larus hyperboreus* in Iceland. Ibis 112:83–92.

INGOLFSSON, A. 1970b. Hybridization of Glaucous Gulls *Larus hyperboreus* and Herring Gulls *L. argentatus* in Iceland. Ibis 112:340–362.

INGOLFSSON, A. 1978. Population phenomena associated with the colonization of Iceland by Herring Gulls. Ibis 120:126.

PATTEN, S. M., JR. 1980. Interbreeding and evolution in the *Larus glaucescens*-*Larus argentatus* complex on the south coast of Alaska. Ph.D. thesis, The Johns Hopkins University, Baltimore, Md.