

VARIABLY PLUMAGED ICELANDIC HERRING GULLS REFLECT FOUNDERS NOT HYBRIDS

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ABSTRACT.—During the 1920s, the breeding range of *Larus argentatus* (Herring Gulls) expanded to Iceland, which enabled secondary contact with *L. hyperboreus* (Glaucous Gulls). Variable patterns of primary feather melanism exhibited by *L. argentatus* in Iceland suggest subsequent interspecific hybridization with *L. hyperboreus*. However, plumage patterns of Icelandic *L. argentatus* are not significantly more variable than those of northern Norwegian conspecifics. The skeletal morphology of Icelandic *L. argentatus* populations is not significantly more variable than that of allopatric populations of *L. argentatus*, *L. cachinnans* (Yellow-legged Herring Gulls), or the significantly larger *L. hyperboreus*, as would be predicted in a population composed of variably introgressed hybrids. I hypothesize that intermediate plumage patterns in these Icelandic gulls represent the genetic legacy of light-winged *L. argentatus* founders, possibly dispersed from Scandinavia, where light-winged *L. argentatus* individuals are present, albeit in low frequency. Received 29 March 1990, accepted 16 October 1990.

HYBRIDIZATION between species of large white-headed larid gulls probably occurs frequently (for review, see Pierotti 1987). Earlier conclusions (Smith 1966a, 1969) on the efficiency of reproductive isolating mechanisms and thus frequency of hybridization appear unreliable. Those conclusions were based on a published set of experimental protocols (Smith 1966a, b, 1969) that, taken together, were logistically impossible (Snell 1989). Identification of apparently hybrid individuals is often based on a small set of external characters that summarize patterns of coloration or plumage patterning (e.g. Spear 1987). The associated hybrid indices are typically restricted to those same external characters (e.g. Ingolfsson 1970). This presents an epistemological problem. As Schueler and Rising (1976: 283) argued, "most studies of introgressive hybridization suffer from circularity: the hybrid zone is described in terms of the set of attributes that first suggested the phenetic intermediacy of the putative hybrids."

In situations of secondary contact, co-adapted polygenic complexes of the parental forms will be disrupted. As well, varying degrees of introgression among individuals will increase the relative variability of a hybrid population. Thus, in attempting to outline methodologies to distinguish hybridization from "hybridization-

like" phenomena (such as the spread throughout a species range of a character either newly evolved or previously present at low frequency in a restricted area), Mayr (1942) and Schueler and Rising (1976) predicted morphology of hybrid populations should not only be intermediate between parental forms that are allopatric, but also substantially more variable. None of the numerous putative hybrid zones in gulls have been tested for hybridization by examining relative variability.

I examined the phenetic affinities of apparent *Larus argentatus* (Herring Gull) × *L. hyperboreus* (Glaucous Gull) hybrids from eastern Iceland. These variably plumaged gulls are compared with allopatric populations of *L. argentatus*, *L. cachinnans* (Yellow-legged Herring Gulls; considered by some authors to be *L. argentatus michahellis*), and *L. hyperboreus*. I assess (1) statistical distributions of plumage melanism among different populations, (2) morphological relations among allopatric populations, (3) phenetic affinities of sympatric gulls from east Iceland, (4) possible association between plumage melanism and skeletal morphology, and (5) relative variability of east Icelandic gulls as compared with allopatric populations.

METHODS

I collected *argentatus* and possible *argentatus* × *hyperboreus* hybrids in two adjacent areas of secondary contact in east Iceland: Skruder (64°54'N, 13°37'W) and Karlsskali (65°01'N, 13°40'W). Though there is

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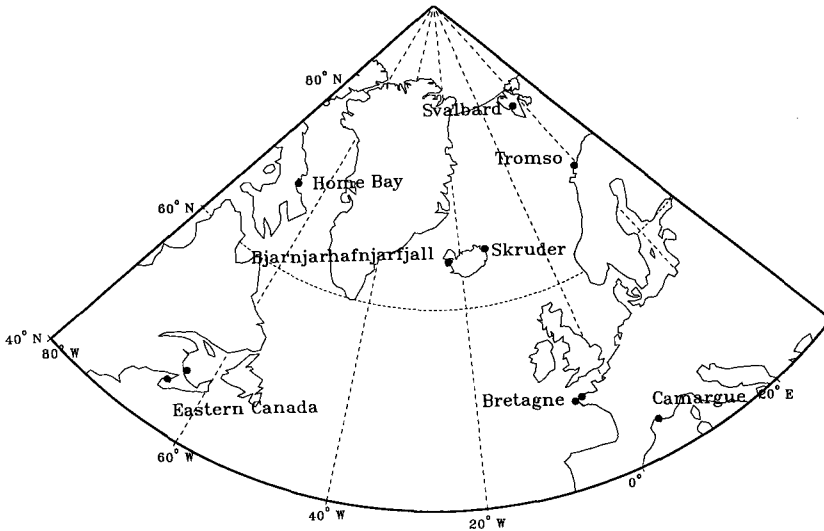


Fig. 1. Location of sampled gull populations. Birds were collected during the breeding seasons of 1985 through 1988.

likely little gene flow among gull colonies, even when close geographically (Ingolfsson 1987), birds from these two east Icelandic colonies, located ca. 6 km apart, were pooled to increase sample sizes. I refer to this pooled sample as Skruuder to facilitate comparisons with earlier studies by Ingolfsson (1970, 1987).

I collected allopatric reference samples (Fig. 1, Table 1) as follows: (1) *argentatus* from eastern Canada: Kent Island, Bay of Fundy, New Brunswick (44°35'N, 65°22'W), and Malpeque Bay, Prince Edward Island (46°30'N, 63°50'W); (2) *argentatus* from Bretagne, France (48°41'N, 3°54'W and 48°25'N, 4°59'W); (3) *argentatus* from near Tromsø, Norway (69°42'N, 19°00'E); (4) *cachinnans* from the region of Camargue, France (43°21'N, 4°40'E and 43°29'N, 4°37'E); (5) *hyperboreus* from colonies in Home Bay, Baffin Island (ca. 69°00'N, 68°00'W); (6) *hyperboreus* from Bjarnjarhafnjarfjall in western Iceland (65°00'N, 23°00'W); and (7) *hyperboreus* at or near Longyearbyen on the Svalbard archipelago (78°14'N, 15°39'E). Where possible, birds were collected at breeding colonies; otherwise, at nearby refuse dumps. Birds were collected during the breeding season by shooting, trapping, or drugging with either tribromoethanol or alpha-chloralose. Each gull was sexed by dissection. All birds in this study were prepared as skin/skeleton specimens, and all are housed in the Royal Ontario Museum in Toronto, the National Museum of Iceland in Reykjavik, or the University of Tromsø, Norway.

I took 16 skeletal measurements on each specimen with dial calipers to the nearest 0.1 mm. Measurements, which correspond (where indicated) to skeletal characters numbered, illustrated, and described

in Schnell (1970: figs. 3 and 4, and appendix I), are as follows: skull length (No. 11), os nasale-premaxillare length (No. 1), skull width (measured laterally across the fossa temporalis), skull depth (No. 10), mandible length (No. 12), coracoid length (No. 16), sternum length (No. 22), synsacrum length (No. 28), humerus length (No. 43), ulna length (No. 45), carpometacarpus length (No. 47), phalanx length (No. 49), pollex length (No. 51), femur length (No. 34), tibiotarsus length (No. 36), and tarsometatarsus length (No. 37).

Using Ingolfsson's (1970) hybrid-index (HI) criteria modified as noted below, I calculated a melanism score for each bird. I scored each of primaries 10–6 on both wings and calculated the average of these values (10 feathers where none were missing). Though Ingolfsson's index ranges from 0 to 5 (higher numbers represent more melanistic individuals), the distal-most primaries on some individuals were more heavily melanized than the examples provided of class 5 (Ingolfsson 1970: plate 4). Primaries 9 or 10 with "windows" partially or entirely filled in were assigned melanism scores of 5.5 or 6. Some primaries 9 and 10 were intermediate between Ingolfsson's classes, and these feathers were assigned intermediate values (0.5, 1.5, 2.5, 3.5, or 4.5). I could not reliably distinguish certain classes of melanism; consequently, primaries 6–8 that were assigned scores of 4 or 5 were all recoded with scores of 5; primaries 6 and 7 assigned scores of 2 or 3 were recoded with scores of 2.5. Primaries 6 or 7 with light melanism on the leading edge were assigned scores of 1.

Statistical analyses were done at the University of

TABLE 1. Results of MANOVAs comparing phenetics of male and female larid gulls over 16 skeletal characters at eight different localities. **** = $P \leq 0.0001$.

Locality	Species	Sample size		Wilk's lambda	Exact F	df
		Male	Female			
Home Bay	<i>hyperboreus</i>	26	22	0.0959	16.62****	17, 30
Svalbard	<i>hyperboreus</i>	25	23	0.0435	38.80****	17, 30
Bjarnjarhafnjarfjall	<i>hyperboreus</i>	26	27	0.0567	34.20****	17, 35
Skruder	<i>argentatus</i>	35	38	0.1496	18.39****	17, 55
Eastern Canada	<i>argentatus</i>	18	45	0.1633	13.57****	17, 45
Tromsø	<i>argentatus</i>	24	26	0.1156	14.40****	17, 32
Bretagne	<i>argentatus</i>	28	22	0.1412	11.45****	17, 32
Camargue	<i>cachinnans</i>	34	16	0.0943	18.07****	17, 32

Toronto Computing System, using SAS (SAS 1985a, b), SPSSX (SPSS 1986), and BMDP (Dixon 1983). Data were initially screened for errors using SAS-UNIVARIATE.

I tested for significant geographic variation, sexual dimorphism and any significant interaction effect in plumage melanism using two-way analysis of variance. I used histograms constructed with score intervals of 0.2 to assess visually the frequency distributions of melanism index scores for each population. I compared specific among-locality differences in mean melanism scores by one-way analysis of variance (ANOVA) followed by a posteriori comparisons (REGWF, SAS-GLM). I concur with Ingolfsson's (1970: 343) statement, "A bird would probably have to have a HI of between 1 and 4 to be recognized as a hybrid in the field." Therefore, I used Fisher's Exact Test to compare frequencies of light-winged and possible hybrids (scores <4) and apparently pure *argentatus* (scores ≥ 4) between gulls from Skruder and the variably plumaged *argentatus* population from Tromsø, Norway.

As with most morphometric studies, some skeletal characters on some specimens could not be measured as bones were broken. Of 6,960 skeletal measurements used (435 gulls \times 16 characters), 87 data points were missing (ca. 1.25% of the total). To estimate each missing skeletal datum, I used stepwise multiple regression limited to two predictor variables. Within each sex, I pooled localities. All skeletal data were log-transformed before all subsequent analyses.

To determine whether there was significant sexual dimorphism in skeletal characters, which would preclude pooling of sexes, I used MANOVA to compare males and females at each of the eight localities. The morphology of sexes differed significantly, so I performed subsequent morphometric analyses separately on males and females. For each sex, I used the among-skeletal-character correlation matrix to conduct principal component analysis (PCA) on all individuals. To evaluate the morphological distinctiveness of the allopatric populations, and to test the hypothesis of phenetic intermediacy of the Skruder

gulls, I compared among-locality differences on PC1 and PC2 using ANOVA followed by a posteriori comparison tests to determine statistically homogeneous subsets.

To separate maximally the seven allopatric gull populations from each other morphologically, I used stepwise discriminant analysis based on the 16 skeletal characters. Steps (and thus predictor variables) in the discriminant analysis were limited to five. I examined a posteriori classification probabilities for individuals from the seven allopatric populations. Following calculation of discriminant axes among allopatric populations, the phenetic affinities of each Skruder gull were evaluated by a posteriori classification. These relations were illustrated by superimposing predicted locations of all individuals on the first two discriminant axes.

I investigated a possible association between the character used to identify apparent hybrids (the melanism index) and a morphometric axis separating *hyperboreus* from *argentatus* and *cachinnans* (the first discriminant axis) using Spearman rank correlation. I evaluated the degree of this association for the two populations of gulls with the most variable melanism scores.

I compared variation in variability among the eight populations across each skeletal character by Levene's test (Levene 1960, Brown and Forsythe 1974). I calculated Levene's test from the absolute value of log-transformed deviates from the means of each sample. Log-transformation removes the effect of differential size on variability (Lewontin 1966 and Van Valen 1974), to allow direct comparison of relative variance. A posteriori comparisons (REGWF, SAS-GLM) defined statistically homogeneous subsets of populations (i.e. populations whose relative variability does not differ significantly).

RESULTS

Sexual dimorphism in plumage melanism.—Results of the two-way analysis of variance pro-

vide strong evidence of among-population differences in mean melanism ($F = 2303.62$; $df = 7, 419$; $P < 0.0001$). However, sexual dimorphism in melanism is not significant ($F = 0.02$; $df = 1, 419$; NS), nor is there a significant interaction effect between sexual dimorphism and differences among populations ($F = 0.42$; $df = 7, 419$; NS). Therefore, I pooled males and females in subsequent analyses of plumage melanism to increase sample sizes.

Among population differences in plumage melanism.—The a posteriori comparisons following ANOVA of melanism scores for each of the eight populations yielded three distinct, nonoverlapping subsets (Fig. 2). First, the three *hyperboreus* populations are composed of exceedingly light-winged birds, which do not differ significantly in mean melanism score, and which are significantly less melanistic than other populations. Though there is faint melanism on some *hyperboreus* from Svalbard and Bjarnjarhafnjarfjall, particularly on the distal edge of primary 10, these traces are not evident on birds observed in the field. Second, mean melanism scores do not differ significantly between the Skruder gulls and the *argentatus* from Tromsø, which contain fewer melanistic gulls (Fig. 2). Gulls from Tromsø and Skruder did not differ significantly in the frequencies of lighter-winged birds (scores < 4) or more melanistic birds (scores ≥ 4) (Fisher's Exact Test: $P = 0.78$, two-tailed). These results provide no evidence of relatively fewer light-winged birds among northern Norwegian than Icelandic *argentatus*. Third, the eastern Canadian *argentatus*, Bretagne *argentatus*, and Camargue *cachinnans* populations all have melanism scores not significantly different from each other, but significantly higher than the Tromsø and Skruder birds.

Sexual dimorphism in skeletal morphology.—Separate MANOVAs between males and females at each of the eight localities indicated significant differences between sexes (Table 1). Therefore, males and females were analyzed separately in all subsequent morphometric analyses.

Principal components analysis of skeletal morphology.—Separate PCAs of males and females yielded one eigenvector with an eigenvalue greater than one. The first eigenvectors explain almost all the variation in the two data matrices (Table 2). The associated character loadings are all high and positive, providing evidence that PC1 scores of both males and females are largely

a measure of size. The eigenvalue associated with the second eigenvector of each analysis is small (0.51 and 0.52), and little variance is explained (3.2% of the total, in each case). However, as loadings are quite similar between analyses of males and females (head and body characters load positively, and wing and leg characters, especially tarsometatarsus, with the joint exception of femur length, load negatively), and as the second eigenvectors explain more than twice the variation of the third ones, I investigated the relative position of Skruder birds on this axis.

ANOVAs of PCAs on different populations.—The ANOVAs of PC1 scores provided evidence of significant differences among locality means for both males ($F = 282.05$; $df = 7, 211$; $P \leq 0.0001$) and females ($F = 338.38$; $df = 7, 208$; $P \leq 0.0001$). Consistent patterning emerged from a posteriori comparisons (Table 3). For both males and females, *hyperboreus* from Home Bay and Svalbard were largest and did not differ significantly from each other in size. The *hyperboreus* from Bjarnjarhafnjarfjall are significantly smaller than Home Bay or Svalbard birds, and significantly larger than *argentatus* or *cachinnans*. The *argentatus* from Bretagne are significantly smaller than any other population. Gulls from Skruder are significantly larger than Bretagne birds, and significantly smaller than all other populations.

ANOVAs of PC2 scores also provided evidence of significant differences among locality means for both males ($F = 20.99$; $df = 7, 211$; $P \leq 0.0001$) and females ($F = 22.94$; $df = 7, 208$; $P \leq 0.0001$). The a posteriori comparisons were consistent (Table 3). Both male and female *cachinnans* from the Camargue had significantly larger PC2 scores than other populations. These Mediterranean gulls possess heads and bodies that are relatively larger and wings and legs that are relatively smaller. *Larus argentatus* from eastern Canada and Tromsø have PC2 scores that do not differ significantly, but that are both significantly smaller than *cachinnans* and significantly larger than the other populations.

Discriminant analysis.—There was no evidence that the variance-covariance matrices differed significantly among the seven allopatric groups of either males (Box's $M = 106.79$; approx. $F = 1.08$; $df = 90, 28721.4$; NS), or females (Box's $M = 119.61$; approx. $F = 1.21$; $df = 90, 33840.1$; NS). However, MANOVAs provided strong evidence of multivariate differences among group

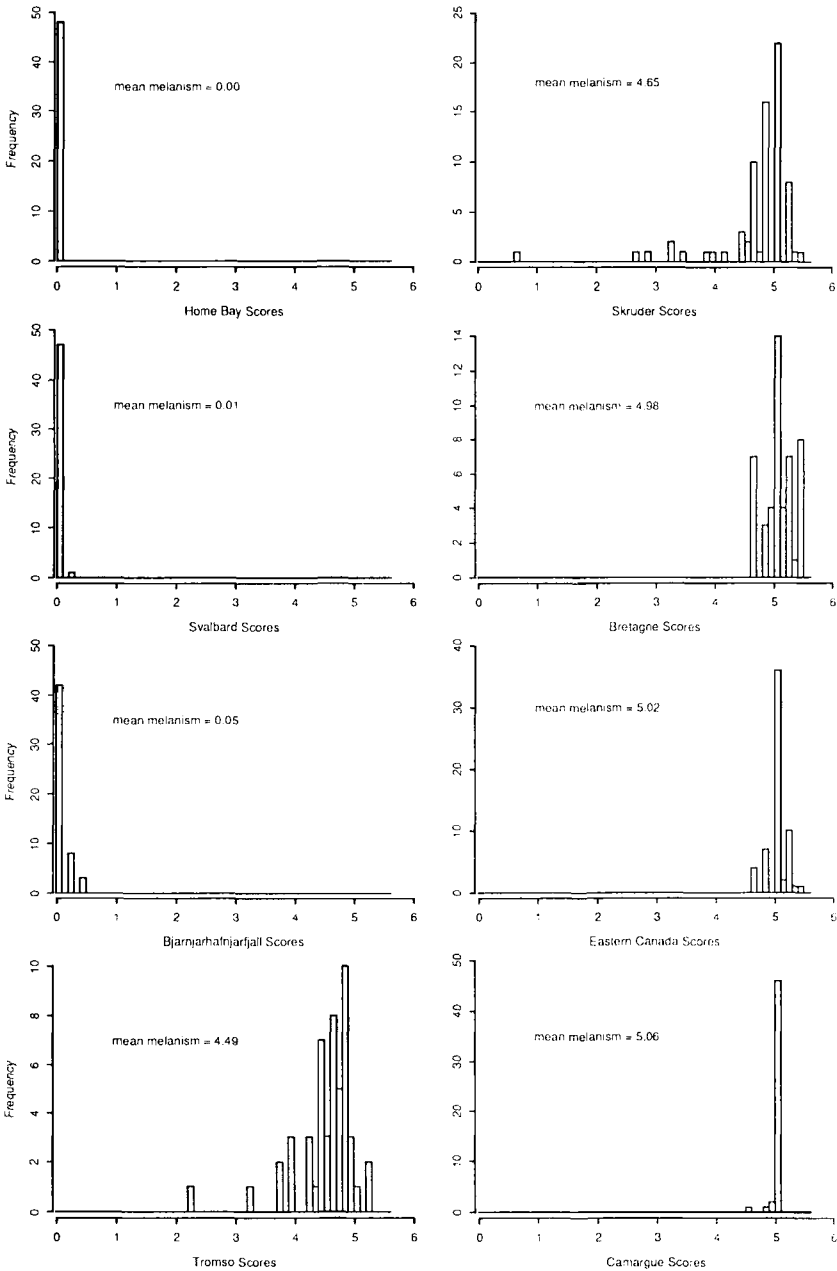


Fig. 2. Distribution of melanism scores from eight gull populations. Home Bay, Bjarnjarhafnarfall, and Svalbard are allopatric *hyperboreus*. Tromsö, Bretagne, and Eastern Canada are allopatric *argentatus*. Camargue gulls are allopatric *cachinnans*. Skruder birds include putative *argentatus* × *hyperboreus* hybrids, based on plumage patterns.

centroids of the allopatric populations for males (Wilk's lambda = 0.0009; approx. $F = 20.67$; $df = 119, 1281.4$; $P \leq 0.0001$), and females (Wilk's lambda = 0.0004; approx. $F = 24.97$; $df = 119,$

1261.85; $P \leq 0.0001$). Following the significant MANOVAs, I entered five variables in stepwise discriminant analysis.

In separate analyses of each sex, the first 3 of

TABLE 2. Character loadings on PC1 and PC2 for male and female gulls, separately. Each analysis was based on a correlation matrix of 16 skeletal characters. Characters are defined in text.

Character	Males		Females	
	PC1	PC2	PC1	PC2
Skull length	0.970	-0.117	0.970	-0.098
Os nasale-premaxillare	0.951	-0.099	0.951	-0.098
Skull width	0.913	-0.256	0.918	-0.173
Skull depth	0.891	-0.272	0.872	-0.269
Mandible	0.967	-0.078	0.965	-0.059
Coracoid	0.972	-0.049	0.968	-0.092
Sternum	0.949	-0.098	0.937	-0.146
Synsacrum	0.924	-0.153	0.937	-0.162
Humerus	0.980	0.074	0.977	0.092
Ulna	0.970	0.147	0.962	0.163
Carpometacarpus	0.966	0.198	0.969	0.181
Phalynx	0.928	0.247	0.936	0.185
Pollex	0.905	0.171	0.914	0.164
Femur	0.958	-0.107	0.955	-0.152
Tibiotarsus	0.958	0.037	0.956	0.059
Tarsometatarsus	0.871	0.363	0.851	0.424
Eigenvalue	14.21	0.51	14.16	0.52
% Variance explained	88.9	3.2	88.5	3.2

5 axes provided significant discrimination among groups ($P \leq 0.0001$). The first and second axes explained almost all the among-locality variance of males (90.5 and 8.3%, respectively) and females (86.3 and 12.1%, respectively). The third axes were likely unstable and were not considered further.

The first discriminant axes (DF1) separate the *argentatus* and *cachinnans* populations from the *hyperboreus* groups for males (Fig. 3) and females (Fig. 4). However, there is considerable overlap among the *hyperboreus* and also among the *argentatus* and *cachinnans* groups. Standardized character loadings (Table 4) of each analysis are markedly consistent, which indicates that both males and females with higher DF1 scores (more *hyperboreus*-like birds) tend to have longer skulls and femora, but shorter tarsometatarsi than gulls with lower DF1 scores (more *argentatus*- or *cachinnans*-like birds). In each analysis, the second discriminant axis (DF2) produced poor separation of *argentatus* from *cachinnans* populations, and did not distinguish among *hyperboreus* groups. Standardized character loadings indicate that individuals with higher DF2 scores tend to have longer ulnae (males) or humeri (females) and shorter femora.

Probability of a posteriori classification of any individual into any particular allopatric group was set equal to the relative sample size of that group. Errors in classification reflect the overlap

between some groups illustrated in Figures 3 and 4. Among male gulls, all *hyperboreus* birds ($n = 75$) were classified correctly, although there were errors in classifying birds (18 of 75) to specific *hyperboreus* populations. Of the *argentatus* or *cachinnans* individuals ($n = 109$), only one bird was misclassified as *hyperboreus*, despite errors in determining which specific *argentatus* or *cachinnans* population many birds (31 of 109) were from. The Bretagne *argentatus* population was distinct, as all 22 males were correctly identified. Among female gulls, phenetic affinities among populations were markedly similar to males. Of the *hyperboreus* gulls ($n = 74$), all but one were correctly classified to taxa, although there were errors in assigning many individuals (12 of 74) to a specific *hyperboreus* population. Similarly, in *argentatus* and *cachinnans* individuals ($n = 104$), all but two were identified correctly to taxa, though there were errors (22 of 102) in determining specifically the group association of individuals. Again, *argentatus* from Bretagne were distinct, as all 28 females were correctly identified.

Morphological affinities of Skruder gulls.—In a posteriori classification using the discriminant functions separating the seven allopatric populations, all Skruder males ($n = 35$) were classified into one of the *argentatus* populations. None were classified into any of the *hyperboreus* groups. Further, the probability of a posteriori

TABLE 3. Results of a posteriori comparisons following ANOVAs on PC scores for male and female gulls. Mean PC scores of localities with the same subset letter do not differ significantly.

Subset	Mean score	Sample size	Locality	Species
Male – PC1				
A	1.457	26	Home Bay	<i>hyperboreus</i>
A	1.362	23	Svalbard	<i>hyperboreus</i>
B	0.519	26	Bjarnjarhafnjarfjall	<i>hyperboreus</i>
C	0.036	16	Camargue	<i>cachinnans</i>
D	-0.228	45	Eastern Canada	<i>argentatus</i>
D	-0.212	26	Tromsö	<i>argentatus</i>
E	-0.877	35	Skruder	<i>argentatus</i>
F	-1.673	22	Bretagne	<i>argentatus</i>
Female – PC1				
A	1.454	25	Svalbard	<i>hyperboreus</i>
A	1.436	22	Home Bay	<i>hyperboreus</i>
B	0.564	27	Bjarnjarhafnjarfjall	<i>hyperboreus</i>
C	-0.074	24	Tromsö	<i>argentatus</i>
C	-0.095	34	Camargue	<i>cachinnans</i>
D	-0.308	18	Eastern Canada	<i>argentatus</i>
E	-0.786	38	Skruder	<i>argentatus</i>
F	-1.526	28	Bretagne	<i>argentatus</i>
Male – PC2				
A	1.562	16	Camargue	<i>cachinnans</i>
B	0.511	45	Eastern Canada	<i>argentatus</i>
B	0.501	26	Tromsö	<i>argentatus</i>
C	-0.222	35	Skruder	<i>argentatus</i>
C	-0.453	22	Bretagne	<i>argentatus</i>
C	-0.467	26	Home Bay	<i>hyperboreus</i>
C	-0.544	26	Bjarnjarhafnjarfjall	<i>hyperboreus</i>
C	-0.738	23	Svalbard	<i>hyperboreus</i>
Female – PC2				
A	1.282	34	Camargue	<i>cachinnans</i>
B	0.457	24	Tromsö	<i>argentatus</i>
B	0.382	18	Eastern Canada	<i>argentatus</i>
C	-0.340	27	Bjarnjarhafnjarfjall	<i>hyperboreus</i>
C	-0.350	38	Skruder	<i>argentatus</i>
C	-0.364	22	Home Bay	<i>hyperboreus</i>
C	-0.435	28	Bretagne	<i>argentatus</i>
C	-0.752	25	Svalbard	<i>hyperboreus</i>

assignment of any male from east Iceland to either of the two most probable groups (for each male, these two groups were both *argentatus* populations) was $\geq 78.3\%$. Similarly, all Skruder females ($n = 38$) were classified as either *argentatus* or *cachinnans*. None were classified as *hyperboreus*. The probability of a posteriori assignment of any Skruder female to either of the two most probable groups (an *argentatus* or *cachinnans* population) was $\geq 68.7\%$. Placement of Skruder gulls on the discriminant axes (Figs. 3 and 4) illustrates the phenetic affinities of these birds. All Skruder gulls cluster among the *argentatus* from the eastern Canada, Tromsö, and *cachinnans* groups. None of these gulls mor-

phologically resembled *hyperboreus* or Bretagne *argentatus*.

Association between melanism and skeletal morphology.—Spearman rank correlations of DF1 scores within populations and wing melanism for Skruder and Tromsö gulls were inconsistent. Correlations were low ($r \leq |0.37|$), of inconsistent polarity, and not significant in all but one case. The significant (though barely so) negative correlation for males in east Iceland ($r = -0.37$, $n = 35$, $P \leq 0.05$) provides weak evidence that larger more *hyperboreus*-like males have slightly lower melanism scores. This pattern is not present among Skruder females ($r = 0.05$, $n = 38$, NS). Ingolfsson (1987: table 1) found

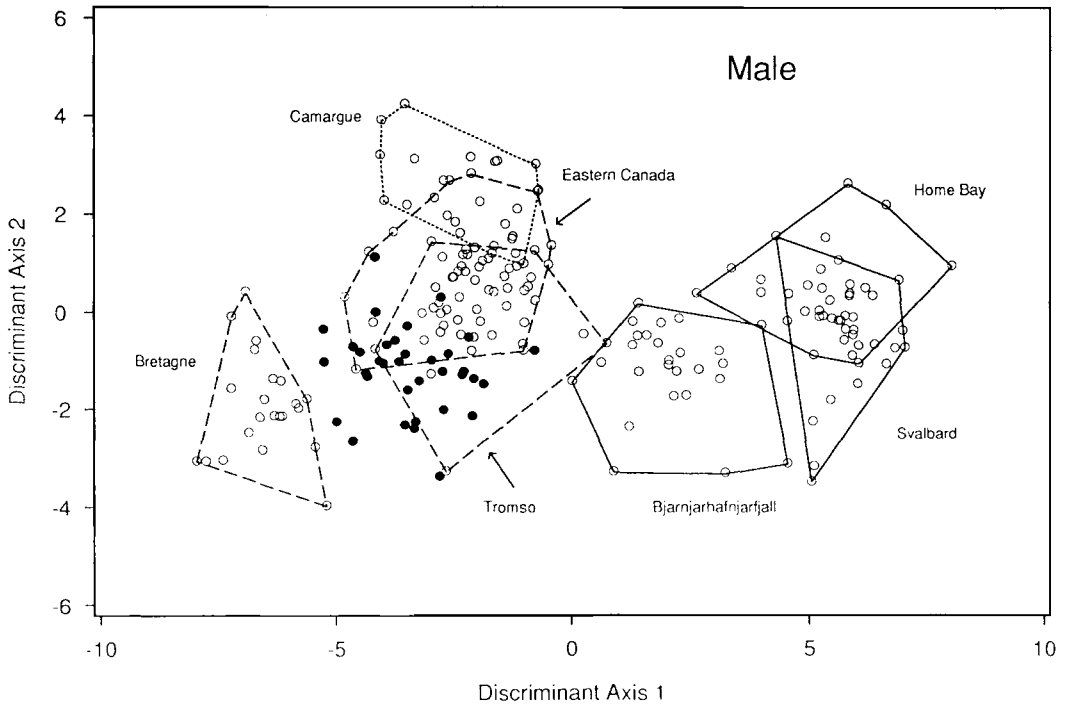


Fig. 3. Discriminant analysis of skeletal morphology of male gulls (open circles) from seven allopatric populations. Polygons are drawn about the outermost points of each locality (solid-edged are *hyperboreus*, dashed-edged are *argentatus*, and dotted-edged is *cachinnans*). Closed circles represent positions of individual Skruer gulls, including putative *argentatus* × *hyperboreus* hybrids (based on plumage patterns), in the discriminant space.

similarly inconsistent correlations of melanism with three external measurements, as well as inconsistencies among different sampling years. There is no consistent evidence for significant association between plumage melanism and morphology in these populations, and inconsistent correlations likely reflect sampling artifacts within a heterogeneously melanized population.

Variation in variability of skeletal characters.— For male gulls there are few significant differences in variability among populations (Levene's test, 16 characters). Only the variability of pollex length among *argentatus* from Bretagne and *cachinnans* from the Camargue differ significantly ($F = 2.13$; $df = 2, 211$; $P < 0.05$). There are no significant differences between any other locality pairs on any other skeletal vari-

TABLE 4. Standardized character loadings^a on discriminant axes separating seven allopatric gull populations. Male and female gulls were analyzed separately; characters are defined in text.

Character	Male		Female	
	DF1	DF2	DF1	DF2
Skull length	0.629	-0.174	0.435	0.572
Os nasale-premaxillare	—	—	0.237	-0.559
Skull depth	0.333	0.177	—	—
Humerus	—	—	0.147	1.179
Ulna	-0.036	1.114	—	—
Femur	0.732	-1.027	0.701	-1.245
Tarsometatarsus	-0.562	0.538	-0.538	0.404

^a Characters which did not meet stepwise entry criteria were not entered into stepwise analysis.

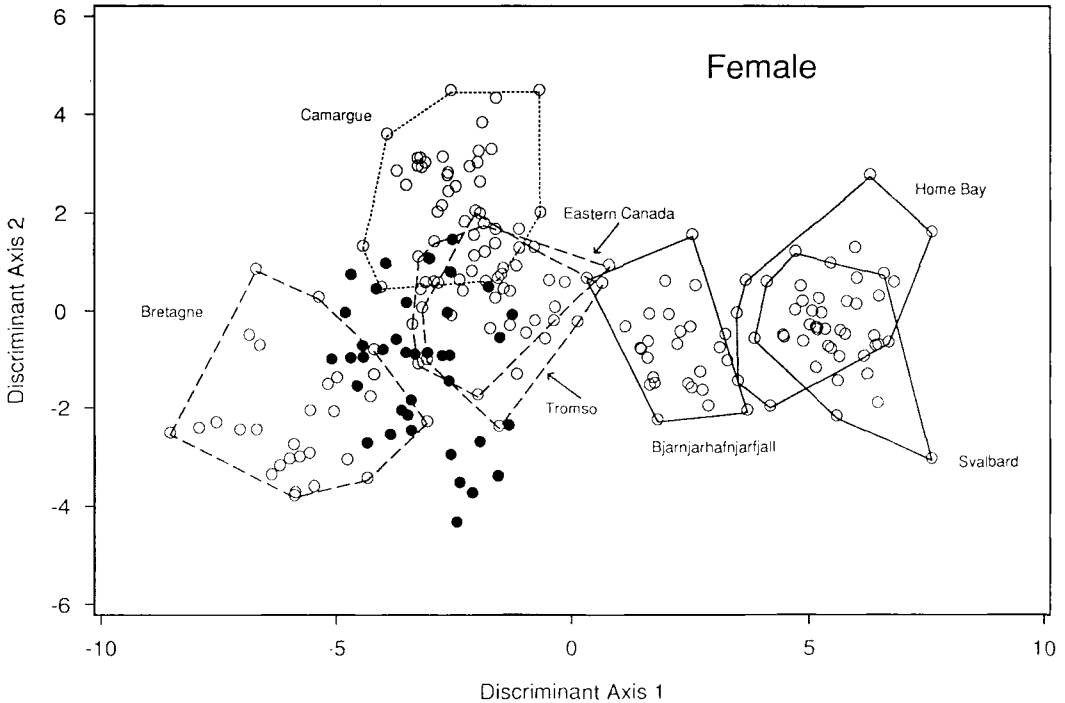


Fig. 4. Discriminant analysis of skeletal morphology of female gulls (open circles) from seven allopatric populations. Polygons and closed circles are defined as in Figure 3.

able. For female gulls, there are significant differences in variability in only 3 of 16 characters, and a posteriori comparisons indicate that populations that differ significantly are not consistent across characters (Table 5). Neither male nor female gulls from Skruder are significantly more variable than gulls of any allopatric population.

Though this composite Skruder locality is not identical to that sampled by Ingolfsson (1970, 1987), the pooling is statistically conservative. If Skruder and Karlsskali gulls were morphologically distinct, any artifact of pooling would increase variability in the combined sample. Because the combined Skruder sample is not significantly more variable than allopatric populations, there was no reason not to have pooled birds collected from the adjacent Skruder and Karlsskali colonies.

DISCUSSION

Historical origin of intermediate plumage.—Light-winged *argentatus* are present in low frequencies in Scandinavian populations (Goethe 1961,

Barth 1968, Ingolfsson 1970) and elsewhere. Lighter-winged birds (wing melanism scores >1 and <4) from northern Alaska through to the Mackenzie Delta area of the Northwest Territories, Canada, were previously considered *L. nelsoni* (Nelson's Gull) (Henshaw 1884, Dwight 1906). Subsequently such birds have often been considered *argentatus* \times *hyperboreus* hybrids (Dwight 1925, Jehl 1987, Spear 1987). However, these putative hybrids have been identified largely (e.g. Dwight 1925, Jehl 1987) or entirely (e.g. Spear 1987) on the basis of plumage pattern. Where morphology has been assessed, putative hybrids all lie within the range of morphometric extremes ascribed to *argentatus* (e.g. Jehl 1987: table 2). Dwight (1925: 249) noted, "The four or five known specimens of '*Larus nelsoni*' are chiefly in the plumage of *hyperboreus* with touches of grayish or dusky pattern on the outer primaries that might well be derived from the black of *L. argentatus vegae* reduced to the smudges that we find. Measurements do not throw much light on the question, for these specimens are so near the size of *hyperboreus*; but, on the other hand, they might very well

TABLE 5. Results of a posteriori comparisons following Levene's test on absolute deviates from means of log-transformed data. Only results for characters with significant among-locality differences are reported; characters are defined in text. Male and female gulls were analyzed separately. Statistically homogeneous subsets were identified (morphometric variability of localities with the same subset letter do not differ significantly).

Subset	Mean deviation	Sample size	Locality	Species
Male – Pollex				
A	0.044	22	Bretagne	<i>argentatus</i>
A B	0.039	26	Home Bay	<i>hyperboreus</i>
A B	0.039	45	Eastern Canada	<i>argentatus</i>
A B	0.033	23	Svalbard	<i>hyperboreus</i>
A B	0.031	26	Tromsø	<i>argentatus</i>
A B	0.027	35	Skruder	<i>argentatus</i>
A B	0.025	26	Bjarnjarhafnjarfjall	<i>hyperboreus</i>
B	0.020	16	Camargue	<i>cachinnans</i>
Female – Os nasale-premaxillare				
A	0.026	22	Home Bay	<i>hyperboreus</i>
A	0.026	34	Camargue	<i>cachinnans</i>
A B	0.025	28	Bretagne	<i>argentatus</i>
A B	0.024	38	Skruder	<i>argentatus</i>
A B	0.020	18	Eastern Canada	<i>argentatus</i>
A B	0.018	24	Tromsø	<i>argentatus</i>
A B	0.015	27	Bjarnjarhafnjarfjall	<i>hyperboreus</i>
B	0.014	25	Svalbard	<i>hyperboreus</i>
Female – Pollex				
A	0.049	28	Bretagne	<i>argentatus</i>
A B	0.033	24	Tromsø	<i>argentatus</i>
A B	0.032	22	Home Bay	<i>hyperboreus</i>
A B	0.032	38	Skruder	<i>argentatus</i>
A B	0.030	25	Svalbard	<i>hyperboreus</i>
A B	0.027	34	Camargue	<i>cachinnans</i>
B	0.026	27	Bjarnjarhafnjarfjall	<i>hyperboreus</i>
B	0.026	18	Eastern Canada	<i>argentatus</i>
Female – Tibiotarsus				
A	0.030	24	Tromsø	<i>argentatus</i>
A B	0.022	18	Eastern Canada	<i>argentatus</i>
A B	0.022	22	Home Bay	<i>hyperboreus</i>
A B	0.020	28	Bretagne	<i>cachinnans</i>
A B	0.018	38	Skruder	<i>argentatus</i>
B	0.017	34	Camargue	<i>cachinnans</i>
B	0.015	27	Bjarnjarhafnjarfjall	<i>hyperboreus</i>
B	0.015	25	Svalbard	<i>hyperboreus</i>

fit the dimensions of the larger specimens or of *argentatus vegae*."

The historical origin of light-wings in *argentatus* is unknown. The source of reduced melanism in *argentatus* may have been hybridization with *L. glaucooides* (Iceland Gulls) as suggested by Barth (1968: 43), or with *hyperboreus*. In either case, the reduced melanism was present before the colonization of Iceland by *argentatus*. Alternatively, dark-winged birds may simply represent the ancestral condition of *argentatus*, and the reduced melanism in primary feathers reflects subsequent (perhaps neutral)

mutation. Many or all of these light and variably plumaged gulls from Alaska through to the Mackenzie Delta, Scandinavia, and eastern Iceland may simply be examples of less melanistic *argentatus*.

Colonization of Iceland by Larus argentatus.—*Larus argentatus* commenced immigration to eastern Iceland in the early part of this century and came into secondary contact with *L. hyperboreus* during the 1920s (Ingolfsson 1970). Subsequent *argentatus* populations in east Iceland increased and then stabilized at approximately 2,500 individuals (Ingolfsson 1970, 1987). Few

hyperboreus breed on east Iceland, and most individuals and colonies are restricted to western and northern coastal areas (Ingolfsson 1970). As there would initially have been few *argentatus* founders, mate choice within both *argentatus* and *hyperboreus* would have been restricted, and hybridization was a possible outcome. Indeed, on the basis of patterns of plumage melanism intermediate between typically dark-winged *argentatus* and light-winged *hyperboreus*, many of these Icelandic gulls were considered variably introgressed hybrids (Ingolfsson 1970, 1987; Jehl 1987; Pierotti 1987; Snell 1989).

Whether the founders of Icelandic *argentatus* populations dispersed from the Baltics, Scandinavia, Faroe Islands, Britain, France, or elsewhere is unknown. However, as the Camargue *cachinnans* differ from Skruder birds on the second discriminant function and possess different foot/leg color, it is exceedingly unlikely that *cachinnans* individuals founded the Icelandic *argentatus* colonies.

Barth (1968: fig. 12) argued that Icelandic *argentatus* form a subspecific complex (*argentatus argenteus*) with birds from the Faroes, Britain, and France. However, even disregarding the issue of the utility of subspecific epithets, my results provide evidence that the skeletal morphology of Icelandic *argentatus* differs significantly from that of subspecific counterparts from northern France. The Icelandic *argentatus* are more like conspecifics from Tromsø (*argentatus argentatus*) or eastern Canada (*argentatus smithsonianus*), and broadly overlap these populations (Figs. 3 and 4).

Founders of the *argentatus* populations in Iceland may have been smaller Norwegian birds. Such speculation is complicated by possible size reduction through environmental induction. For example, significant reductions in size of Snow Geese (*Chen caerulescens*) near Churchill, Manitoba, have been associated with increasingly impoverished food supplies (F. Cooke and E. Cooch pers. comm.). The clinal variation in morphology among *argentatus* populations worldwide makes historical reconstruction of the origin of Icelandic *argentatus* dubious (at least when based on analyses of morphological characters).

Phenotypic intermediacy.—If east Icelandic gull populations consist at least partially of *argentatus* × *hyperboreus* hybrids, then some Skruder individuals—in particular the gulls with variable plumage—should be morphologically in-

termediate between allopatric populations of *argentatus* and *hyperboreus*. However, there is no evidence the Skruder birds are intermediate between Norwegian or Canadian samples of *argentatus* and any of the three samples of *hyperboreus*. In the discriminant analyses, the east Icelandic birds all classify among allopatric *argentatus*. These results provide no evidence to support the hybridization hypothesis.

Phenotypic distinctiveness.—If the differences between the parental taxa are large, the hybrid gulls may be morphologically distinct. For instance, in populations of *Anas platyrhynchos* (Mallard) and *Anas superciliosa* (Gray Duck) in New Zealand, where hybrids were initially identified by plumage, morphometric analyses showed that virtually all apparent hybrids are morphometrically distinct from both pure Mallard and pure Gray Duck (Gillespie 1985). My results provide no evidence of relative morphometric distinctiveness among variably plumaged Icelandic *argentatus*, and no evidence these birds are hybrids. However, if gulls hybridize in Iceland, this might be occurring in the *hyperboreus* colonies with light-winged *argentatus* founders or the descendants of such immigrants. Bjarnjarhafnjarfjall *hyperboreus* are intermediate in size between conspecifics from Home Bay or Svalbard and *argentatus* populations.

Increased phenotypic variability.—If Skruder gulls include *argentatus* × *hyperboreus* hybrids, this Icelandic population should be more variable morphologically than allopatric ones. The extent of phenotypic variation would be predicted to span the range of both parental forms. (Of course, were the entire population composed of F1 hybrids, all birds might be intermediate, but this seems most unlikely.) The comparisons of variance (Table 5) provide no evidence Icelandic gull populations are significantly more variable than other populations. These data provide no evidence in support of hybridization.

Founder effect hypothesis.—As an alternative to hybridization, I hypothesize that, among the original *argentatus* founders of the Icelandic population, there were a disproportionately large number of light-winged individuals, possibly dispersed from Scandinavia. Hybridization need not be invoked as a mechanism to account for plumage pattern variability in Icelandic *argentatus*.

Evaluating whether the observed primary

feather melanism patterns reflect an *argentatus* × *hyperboreus* hybrid zone or a composite of *argentatus* plumage polymorphisms is difficult, for at least four reasons. First, the genetic basis of the variability in wing melanism among individuals or among-species is not understood. Earlier studies of forced hybridization (Lönnberg 1919) between *hyperboreus* and Greater Black-backed Gulls (*L. marinus*) revealed only slight lightening in primary melanism in F1 individuals. If alleles that control presence and pattern of melanism are dominant in a presumably pleiotropic complex of loci, as suggested by Lönnberg's (1919) results, substantial introgression may precede the phenotypic expression of intermediate plumages. (Unfortunately these tantalizing studies have never been followed up, to my knowledge.) Second, data from the early years of *argentatus* colonization in Iceland are sparse. Third, there are as yet no genetic markers for different gull species. Allozyme analysis (Snell 1991) provides evidence these species are extremely similar genetically. Fourth, the relationships among the various gull taxa in east Iceland may have not yet stabilized.

Ingolfsson's (1970: 342) suggestion that the number of light-winged Norwegian *argentatus* "is so low as to be of little importance in analysing hybrid situations such as that found in Iceland," does not appear to apply to samples collected from Skruder. However, Ingolfsson was writing in the context of studies of the colonies done in the early 1960s. The colony at Skruder is large. It comprised several hundred pairs both in 1965 (Ingolfsson 1970) and in 1986 (Ingolfsson 1987). Mean melanism at Skruder has changed little from the mid-1960s (melanism score = 4.41; Ingolfsson 1970: fig. 4) and 1986 (melanism score = 4.65; this study: Fig. 2). The apparent stability of the Skruder population, and the similarity of Skruder and Tromsø gulls with respect to both patterns of melanism and morphology may reflect initial colonization by large numbers of *argentatus* from Norway. It seems less likely that the large and stable population at Skruder reflects intrinsic increase from a few *argentatus* founders hybridizing at low frequency with *hyperboreus*.

Small Icelandic gull colonies have undergone fluctuations in size, melanism scores, or both (Ingolfsson 1987). Some small sites, such as the Horn colony (Ingolfsson 1970: fig. 3), may have been abandoned. Melanism scores at some oth-

er colonies (such as Hromundarey) have increased slowly (Ingolfsson 1987: table 4), as the proportion of light-winged birds decreased. A small gull colony on Hellisey of ca. 30% *hyperboreus*-like birds in 1944 had changed by 1966 such that only approximately 5% of the gulls possessed so little melanism (Ingolfsson 1970). Perhaps the colonies with low mean melanism scores were established by primarily light-winged *argentatus* founders. These colonies were small, <100 and as few as 30 individuals. Despite the longer lifespan and greater reproductive success of lighter-winged birds (Ingolfsson 1987), subsequent and continued immigration of more melanistic individuals may have elevated the mean melanism levels of those colonies.

Although phenetic intermediacy and increased variability can be viewed as strong evidence in support of hybridization, failure to find such patterns is weak evidence against this hypothesis (Schueler and Rising 1976). I do not know whether *argentatus* and *hyperboreus* are currently hybridizing, nor whether they have ever done so either before or since secondary contact in Iceland in the 1920s. My results, however, provide evidence consistent with an alternative to hybridization. It is likely that the variable plumage in the Icelandic populations of *argentatus* simply represents heretofore unrecognized intraspecific variation.

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LITERATURE CITED

- BARTH, E. K. 1968. The circumpolar systematics of *Larus argentatus* and *Larus fuscus* with special reference to the Norwegian populations. *Nytt Magasin for Zoologi* 15(suppl. 1): 1-50.
- BROWN, M. B., & A. B. FORSYTHE. 1974. Robust tests for the equality of variances. *J. Am. Statist. Assoc.* 69: 364-367.
- DIXON, W. J. (Ed.). 1983. *BMDP Statistical Software*. Berkeley, Univ. California Press.
- DWIGHT, J. 1906. Status and plumages of the white-winged gulls of the genus *Larus*. *Auk* 23: 26-43.
- . 1925. The gulls (Laridae) of the world: their plumages, moults, variation, relationships and distribution. *Bull. Am. Mus. Nat. Hist.*: 63-401.
- GILLESPIE, G. D. 1985. Hybridization, introgression, and morphometric differentiation between Mallard *Anas platyrhynchos* and Grey Duck *Anas superciliosa* in Otago, New Zealand. *Auk* 102: 459-467.
- GOETHE, F. 1961. Zur taxonomie der Silbermöwe (*Larus argentatus*) im südlichen deutschen Nordseegebiet. *Vogelwarte* 21: 1-24.
- HENSHAW, H. E. 1884. On a new gull from Alaska. *Auk* 1: 250-252.
- INGOLFSSON, A. 1970. Hybridization of Glaucous Gulls *Larus hyperboreus* and Herring Gulls *Larus argentatus* in Iceland. *Ibis* 112: 340-362.
- . 1987. Hybridization of Glaucous and Herring gulls in Iceland. *Stud. Avian Biol.* 10: 131-140.
- JEHL, J. R., JR. 1987. A review of "Nelson's Gull *Larus nelsoni*." *Bull. B.O.C.* 107: 86-91.
- LEVENE, H. 1960. Robust tests for equality of variances. Pp. 278-292 in *Contributions to probability and statistics* (I. Olkin, Ed.). Stanford, Stanford Univ. Press.
- LEWONTIN, R. C. 1966. On the measurement of relative variability. *Syst. Zool.* 15: 141-142.
- LÖNNBERG, E. 1919. Hybrid gulls. *Arkiv for Zoologi* 12: 1-22.
- MAYR, E. 1942. *Systematics and the origin of species*. New York, Columbia Univ. Press.
- PIEROTTI, R. 1987. Isolating mechanisms in seabirds. *Evolution* 41: 559-570.
- SAS. 1985a. *SAS user's guide: basics*, version 5 ed. Cary, North Carolina, SAS Inst. Inc.
- . 1985b. *SAS user's guide: statistics*, version 5 ed. Cary, North Carolina, SAS Inst. Inc.
- SCHNELL, G. D. 1970. A phenetic study of the sub-order Lari (Aves) I. Methods and results of principal components analyses. *Syst. Zool.* 19: 35-57.
- SCHUELER, F. W., & J. D. RISING. 1976. Phenetic evidence of natural hybridization. *Syst. Zool.* 25: 283-289.
- SMITH, N. G. 1966a. Evolution of some arctic gulls (*Larus*): an experimental study of isolating mechanisms. *Ornithol. Monogr.* 4.
- . 1966b. Adaptations to cliff-nesting in some arctic gulls (*Larus*). *Ibis* 108: 68-83.
- . 1969. Polymorphism in Ringed Plovers. *Ibis* 111: 177-188.
- SNELL, R. R. 1989. Status of *Larus* gulls at Home Bay, Baffin Island. *Colon. Waterbirds* 12: 12-23.
- . 1991. Interspecific allozyme differentiation among North Atlantic white-headed larid gulls. *Auk* 108: 319-328.
- SPEAR, L. B. 1987. Hybridization of Glaucous and Herring gulls at the Mackenzie Delta, Canada. *Auk* 104: 123-125.
- SPSS. 1986. *SPSSX user's guide*, 2nd ed. Chicago, SPSS Inc.
- VAN VALEN, L. 1974. Multivariate structural statistics in natural history. *J. Theor. Biol.* 45: 235-247.