



MORPHOLOGICAL AND GENETIC PATTERNS OF HYBRIDIZATION OF HERRING GULLS (*LARUS ARGENTATUS*) AND GLAUCOUS GULLS (*L. HYPERBOREUS*) IN ICELAND

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ABSTRACT.—Recent hybridization has been reported between the Herring Gull (*Larus argentatus*) and Glaucous Gull (*Larus hyperboreus*; the larger of the species) in Iceland, after the arrival of Herring Gulls around 1925. We used samples of both species from various locations in Iceland and from three periods spanning >40 years. To analyze the nature of hybridization and the extent of introgression between the species, we compared morphological variation using genetic information based on microsatellite and mtDNA data. Both comparisons of single traits and multivariate analysis pointed to hybridization and introgression. Variation in genetic markers and morphological traits revealed two distinct groups, connected by a number of intermediates. A discrepancy in classification based on genetic or morphological information revealed introgression. Variation within each species reflected the effect of hybridization; for example, individuals with less pigmentation (i.e., more *hyperboreus*-like) tend to be larger. The differences we observed among samples and periods reflect changes in the overlap of the populations' distributions. *Received 5 May 2008, accepted 12 December 2008.*

Key words: genetics, Glaucous Gull, Herring Gull, hybridization, Iceland, introgression, *Larus argentatus*, *L. hyperboreus*, morphometrics.

Patrones Morfológicos y Genéticos de Hibridación entre *Larus argentatus* y *L. hyperboreus* en Islandia

RESUMEN.—Se ha documentado hibridación reciente entre *Larus argentatus* y *L. hyperboreus* (una especie de mayor tamaño) en Islandia, después del arribo de *L. argentatus* alrededor de 1925. Usamos muestras de ambas especies provenientes de varias localidades de Islandia y de tres períodos cubriendo más de 40 años. Para analizar la naturaleza de la hibridación y el grado de introgresión entre las especies, comparamos la variación morfológica usando información genética con base en datos de microsatélites y ADNmt. Tanto las comparaciones de rasgos individuales como los análisis multivariados apuntaron a la existencia de hibridación e introgresión. La variación en los marcadores genéticos y en rasgos morfológicos sugirió que existen dos grupos diferenciados que están conectados por algunos intermedios. Una discrepancia entre la clasificación basada en información genética con una basada en morfología reveló la existencia de introgresión. La variación presente dentro de cada especie reflejó el efecto de la hibridación; por ejemplo, los individuos con menos pigmentación (i.e., aquellos más similares a *hyperboreus*) tendieron a ser más grandes. Las diferencias que observamos entre muestras y entre períodos reflejan los cambios en la superposición entre las distribuciones de las poblaciones.

SECONDARY CONTACT ZONES between taxa re-expanding from separate glacial refugia during the Holocene have been found in diverse kinds of organisms, representing all stages of the genetic divergence process (Hewitt 2000). Incomplete reproductive isolation, with or without gene flow, is common in birds and has been documented in >9% of all bird species (Grant and Grant 1992), possibly because of the relatively slow evolution of postmating barriers in those species (Fitzpatrick 2004). Recently, several examples of incomplete reproductive isolation have been documented, for

example between Greater Spotted Eagle (*Aquila clanga*) and Lesser Spotted Eagle (*A. pomarina*) (Helbig et al. 2005), among the hierofalcon species (Nittinger et al. 2007), between Golden-winged Warbler (*Vermivora chrysoptera*) and Blue-winged Warbler (*V. pinus*) (Vallender et al. 2007), and among several taxa of the large white-headed gulls (*Larus*) (overview in McCarthy 2006).

“Hybrids” were broadly defined by Harrison (1990) as the offspring of individuals from populations that differ by one or more heritable characters. Hybridization can lead to introgression,

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where genes of one species recombine into the genetic background of a second species (Barton and Hewitt 1985). Genes or gene regions that are not associated with reduced hybrid fitness are expected to introgress readily. Young hybrid zones are of particular interest, because they provide a valuable opportunity to follow the initial stages of hybridization, but most zones are ancient (Barton and Hewitt 1985, Goodman et al. 1999).

The large white-headed gulls provide an excellent system for studying hybridization and introgression between species of recent origin. Liebers et al. (2004) suggested that extant taxa of large white-headed gulls in the northern hemisphere are a result of divergent and reticulate evolution between two ancestral lineages that originated around 100,000–600,000 years ago in two main refugia, the North Atlantic refugium and the continental Eurasian refugium. Genetic differentiation among taxa in these groups is also surprisingly low at nuclear loci, and shared polymorphism of mitochondrial DNA (mtDNA) is common (Crochet et al. 2003).

A secondary contact zone between Glaucous Gull (*Larus hyperboreus*) and the European population of Herring Gull (*L. argentatus*) has recently been established in Iceland (Ingólfsson 1970). Like several other gull species in northern Europe, Herring Gulls expanded in both population size and range during the 19th century and colonized Iceland, where Glaucous Gulls were already present, in about 1925. The distribution of Herring Gulls ranges from the Kola Peninsula in northern Russia west through Scandinavia, northern France, the British Isles, and Iceland (Olsen and Larsson 2004). The Glaucous Gull is an Arctic circumpolar species that has undoubtedly bred in Iceland for a long time, though early records are lacking or are not trustworthy. The first known records date back to the late 18th century (see Ingólfsson 1970). A recent study of mitochondrial sequence variation showed that the Glaucous Gull has two distinct phylogeographic lineages, one in North America and the other in Iceland and elsewhere in northern Europe (Vigfúsdóttir et al. 2008). In Iceland, both species breed in colonies, Glaucous Gulls usually on grassy slopes and cliffs by the sea and Herring Gulls more often on relatively level ground near the sea (Ingólfsson 1970, S. Pálsson et al. pers. obs.).

Ingólfsson (1970, 1987) described hybridization between the two species on the basis of morphological variation and observations of mated pairs. Using a hybrid index (HI) based on melanism patterns of the outermost primaries, Ingólfsson allocated HI scores to individual gulls and evaluated the extent of hybridization in different locations. He found that putatively pure *L. hyperboreus* predominated in western Iceland, whereas putatively pure *L. argentatus* and hybrids were common in southern and eastern Iceland. Variation in the melanistic patterns was extensive and indicated widespread hybridization. Studying allozyme and morphological variation, Snell (1991a, b) argued against hybridization, claiming that the variation found in Herring and Glaucous gulls in Iceland simply reflected natural variation within the species. Snell argued that the observed intrapopulation variability within Herring Gulls in Iceland resulted from a founder effect and suggested that the claimed hybrids in Iceland were light-winged Herring Gulls originating from Scandinavia (but see rebuttal by Ingólfsson [1993]). A study of mtDNA and microsatellite variation and geographic patterns revealed extensive haplotype and allele sharing in Icelandic Glaucous and Herring gulls (Vigfúsdóttir et al. 2008), supporting the conclusion that the two species hybridize in Iceland. Although

mitochondrial haplotypes could be used to distinguish the species, microsatellites failed to do so. Glaucous Gull mtDNA types were found to be a subset or branch within the larger mtDNA genealogy of the Herring Gull, and the genetic patterns pointed to asymmetrical introgression from the Glaucous Gull into the Herring Gull. A recent study by Gay et al. (2007) described a similar secondary contact zone between Herring Gulls and Caspian Gulls (*L. cachinnans*) in eastern Europe, where they observed variable rates of introgression among phenotypic traits and molecular markers. Here, we evaluate the extent of hybridization and introgression in the recently established contact zone in Iceland between Glaucous and Herring gulls, as reflected by morphological traits and genetic markers. The study covers a period of 40 years.

METHODS

Sampling.—Samples, listed in Table 1, were obtained from 250 adult individuals at breeding colonies in western and eastern Iceland (Table 1 and Fig. 1) over three periods: (1) collected by Ingólfsson, 1964–1973; (2) collected by Snell, 1985–1986; and (3) present study, 2005–2006. Samples from periods 1 and 2 were obtained from specimens at the Museum of Natural History in Reykjavik. These specimens had been collected mostly in breeding colonies using drugged bait. Sampling during period 3 (2005–2006) was done in the field by shooting or cannon-netting gulls attracted to bait placed near breeding colonies. Sample locations in western Iceland were in an area where Glaucous Gulls predominated, whereas sample locations in eastern Iceland were in an area where Herring Gulls and hybrids predominated, as described by Ingólfsson (1970). Mixed breeding pairs and presumptive hybrids were observed in all colonies, the presumptive hybrids being especially prominent in eastern Iceland during the first period, 1964–1973 (Ingólfsson 1970).

We sexed individuals sampled during 2005–2006 with the molecular method developed by Fridolfsson and Ellegren (1999), as described in Hallgrímsson et al. (2008). The sex of the individuals sampled previously had been determined by autopsy.

Morphometric data.—Plumage traits and morphometrics were measured on fresh specimens according to Ingólfsson's (1970) protocol. Measurements of museum skins were taken from field data sheets that were kept with the corresponding specimens collected by Ingólfsson and Snell. Hybrid indices (HI) had not been scored for gulls collected by Snell, so we scored them following Ingólfsson (1970). The HI scores the degree of black pattern on the outermost primaries (numbers 6–10), from no trace in Glaucous Gull (HI = 0) to black patterns with sharp edges in Herring Gull (HI = 5). Additional HI scores from previous studies by Ingólfsson (1970, 1987) were included to evaluate the distribution of the scores, resulting in values from a total of 639 individuals. Other measurements included culmen length from base of feathers on top of bill; bill height at the gonial angle; length of tarsus; length of the right wing in outstretched position; weight measured with a standardized Pesola scale; bill depth, measured at the proximal border of the nares; tail length; and length of the middle toe.

Genetic data.—Individual genotypes, based on sequences of an 850-base-pair segment of the mitochondrial cytochrome-*b* gene and genotypes of five microsatellite loci, were obtained for each of the samples in Table 1 from Vigfúsdóttir et al. (2008).

TABLE 1. Numbers (n) of individual Herring Gulls and Glaucous Gulls sampled from each location during three periods, to which the numbers under "Sample" refer: (1) 1964–1973, (2) 1985–1986, and (3) 2005–2006. The first letter refers to species assignment based on the BAPS analysis, and the letter after the number refers to east (e) or west (w) for samples outside their main distribution range. Location numbers refer to locations in Figure 1; the same number is given to locations that are close to each other.

Species	Sample	Location number	Location	Latitude (N)	Longitude (W)	n
Herring Gull	a1	5	Hrómundarey	64°35'	14°19'	45
Glaucous Gull		6	Horn	64°15'	14°59'	12
	a1w	4	Skrúður	64°54'	13°38'	1
	a2	1	Reykjanes	64°01'	22°40'	1
	a3	2	Bjarnarhafnarfjall	64°59'	23°01'	1
	a3w	4	Skrúður	64°54'	13°38'	31
		4	Reyðarfjörður	64°56'	13°41'	20
	h1	2	Grundarfjörður	64°55'	23°15'	3
		1	Reykjanes	64°01'	22°40'	3
	h2	2	Bjarnarhafnarfjall	64°59'	23°01'	43
	h3	2	Búlandshöfði	64°56'	23°28'	3
		3	Reykhólahreppur	65°30'	22°17'	3
	h1e	2	Bjarnarhafnarfjall	64°59'	23°01'	26
		2	Grundarfjörður	64°55'	23°15'	49
		4	Reyðarfjörður	64°56'	13°41'	1
		6	Horn	64°15'	14°59'	2
		5	Hrómundarey	64°35'	14°19'	6

Laboratory methods (isolation, amplification, and sequencing) and genetic analyses are described in Vigfúsdóttir et al. (2008). Individual associations between genotype and morphology were compared using a Bayesian clustering method and the admixture analysis implemented in BAPS, version 4.14 (Marttinen et al. 2006). Individuals were identified *a priori* by assignment to HI classes I–VI, representing HI values of 0, 0.1–1.7, 1.8–2.6, 2.7–3.5, 3.6–4.4, and 4.5–5.0, respectively (as defined by Ingólfsson [1987]). We used the Bayesian clustering method to define the morphological groups with respect to HI value on the basis of their genetic makeup.

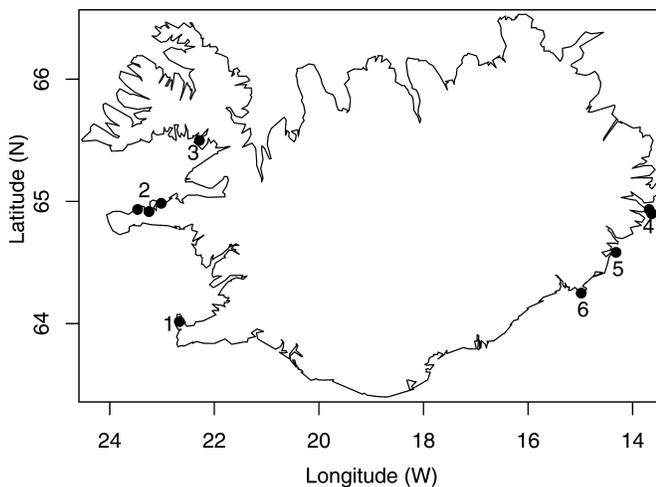


FIG. 1. Sampling locations of Herring Gulls and Glaucous Gulls in Iceland. Numbers refer to locations listed in Table 1.

Analysis of genetic and morphological data.—Associations between the measured variables and HI score and weight were estimated with the Pearson correlation coefficient. Admixture coefficients (q_i), obtained for each individual with the Bayesian analysis, were also compared with morphological variation. Variance in measured variables was analyzed with linear models, run separately on both species (classified either with HI score or solely with the genetic analysis) with respect to different periods, areas, sexes, and dependency on the HI score and the genetic admixture coefficient. Linear discriminant analysis (LDA) incorporated all variables measured. The principle of the method is to find a linear combination of the variables that maximizes the ratio of between-group variance to within-group variance (Quinn and Keough 2002). To avoid any differences between the sexes and systematic deviations attributable to differences among periods and the dependency between variables (or the collinearity), the LDA analysis was based on residuals from an analysis of variance. Measured variables, except weight, were fitted with the analysis of variance by including weight as a covariate. The residuals for weight were from a model that included HI as a covariate. The contribution of each variable to the discrimination observed in the LDA analysis was assessed by correlating it with the first two discriminants.

Measurements of individuals that were assigned incorrectly to morphological groups by the HI score, as revealed by the genetic analysis (BAPS, $P < 0.05$), were compared with those of the other individuals of the same morphological group. The comparisons were done with Mann-Whitney U tests, separately for the residuals from the analyses of variance of each measured variable (where the effect of period, area, sex, and their relationship with the HI score had been taken into account), and for the estimated values of the first linear discriminant (LDA1).

All statistical tests were performed using the statistical software R (see Acknowledgments).

RESULTS

Classification.—Assignment of individual genotypes by the Bayesian clustering method (BAPS) gives an optimal partition into two clusters, one including the morphological classes I and II and another with classes III–VI (Fig. 2A; as defined by Ingólfsson [1987]). The log likelihoods for different numbers of clusters k from 2 to 4 were $-2,854.6$, $-2,887.5$, and $-2,912.0$. The two clusters, 1 (I, II) and 2 (III–VI), correspond well with the bimodal curve observed in the HI (Fig. 2A), which reflects the two morphological groups, one close to Glaucous Gull and the other to Herring Gull. Distribution of HI values from a larger data set supports this division (Fig. 2B): only 8 of 639 individuals (or 0.0126%) have HI values between 1 and 2. Three individuals with the highest scores (1.0, 1.2, and 1.4) in class II were assigned to cluster 2. Individuals with lower values in class II were generally more likely to be classified with cluster 1, which indicates that the genetic division of the two morphological groups corresponds to an HI score of 1.0. BAPS analysis of modified classes in which the boundary between classes II and III is set at $HI = 1$ results in a lower likelihood for the two clusters ($-2,846.4$) than was obtained with the previous analysis. We refer those two groups to Glaucous Gull ($HI < 1$) and the other to Herring Gull ($HI \geq 1$). This division was also supported by a BAPS analysis when the mtDNA was omitted from the analysis. The admixture coefficients q_i (here, the probability of being assigned to the Herring Gull group) were strongly correlated with the HI scores ($r = 0.665$, $P < 2.2 \times 10^{-16}$). However, several individuals had genotypes that did not correspond to their morphology as shown in Figure 2. Eighteen of 117 individual Herring Gulls ($HI \geq 1$) had Glaucous Gull genotypes (BAPS, $P < 0.05$). Most (11) of these individuals were sampled during period 1, in eastern Iceland. Five individuals were sampled during period 2, in Skróður (eastern Iceland), and two individuals in period 2, in Grundarfjörður (western Iceland). Fifteen of 133 individual Glaucous Gulls ($HI < 1$) had Herring Gull genotypes (BAPS, $P < 0.05$). Six of them were from period 1, two from eastern Iceland, two from period 2, and 7 from period three. The proportions of incorrectly classified individuals in the two species (18/117 and 15/133) was not significant (Fisher exact test, $P = 0.3554$).

Morphological variation.—We observed a strong correlation between the measured variables and weight, both for species combined and within species (Table 2). Corresponding correlations with HI score were much weaker within species and were often nonsignificant. Partitioning the weight with respect to period, area, sex, and HI score within species produced a significant effect for nearly all factors (Table 3). Comparisons of samples with respect to weight and HI are presented in Figure 3. The difference in weight between the two species was evident, but so was a temporal effect, in that sampled individuals appear to decrease in weight with time, as seen for a1, a2, and a3 ($b = -3.658$, $P \leq 2.67 \times 10^{-5}$) and for h1, h2, and h3 ($b = -4.169$, $P \leq 7.69 \times 10^{-5}$) (Fig. 3A). Samples obtained when one species was sampled within the main range of the other (a1w, a3w, and h1e) also showed clear deviation from the mean of the sampled individual's conspecifics,

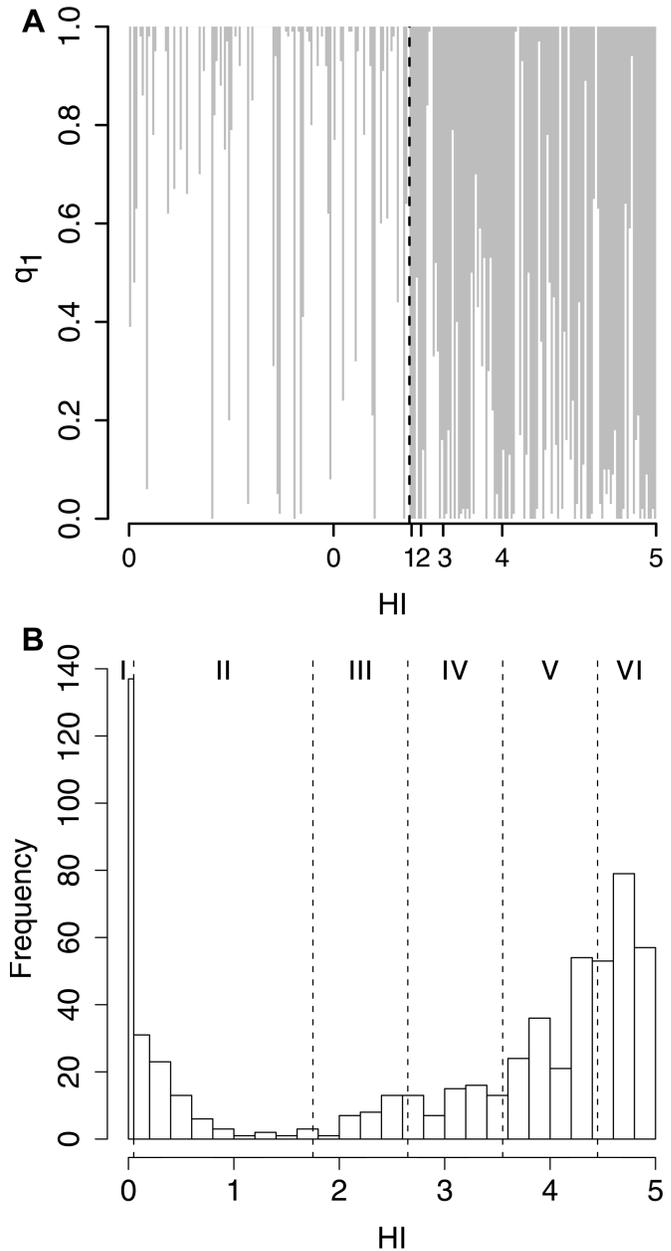


FIG. 2. Classification of individual Herring Gulls and Glaucous Gulls in Iceland. (A) Admixture analysis using BAPS (Marttinen et al. 2006). Vertical lines represent the admixture coefficients for each individual, where the proportional length of the white line is the proportion (q_1) of the genome of each individual that is traced to cluster 1. Individuals are ranked along the x axis according to hybrid index (HI) scores from 0 to 5. The broken vertical line at $HI = 1.0$ represents the division of the two groups obtained by the BAPS analysis. (B) Distribution of HI values obtained in the present study and by Ingólfsson (1970, 1987), totaling 639 individuals. Vertical lines mark classes I–VI (Ingólfsson 1987). The first interval represents only individuals with $HI = 0$.

being intermediate in weights (Fig. 3A). The four Herring Gulls sampled in western Iceland in period 3 (a3w) were significantly larger and lighter in plumage than Herring Gulls in other samples. The dependence on year of sampling was weaker for HI

TABLE 2. Correlation of measurements of Herring Gulls and Glaucous Gulls with weight and hybrid index (HI) score. Asterisks refer to P values: * $0.05 > P \geq 0.01$, ** $0.01 > P \geq 0.001$, *** $0.001 > P$, ns = nonsignificant.

	With weight			With HI		
	Glaucous Gull	Herring Gull	All	Glaucous Gull	Herring Gull	All
Culmen	0.77***	0.76***	0.85***	0.08ns	-0.21*	-0.59***
Gonys	0.76***	0.78***	0.80***	-0.08ns	-0.19*	-0.44***
Bill depth	0.68***	0.74***	0.70***	-0.05ns	-0.18ns	-0.30***
Tarsus	0.39***	0.23*	0.32***	-0.18***	0.17ns	-0.10ns
Wing	0.71***	0.81***	0.81***	0.05ns	-0.30**	-0.55***
Tail	0.61***	0.65***	0.76***	-0.33*	-0.001ns	-0.49***
Weight				0.01ns	-0.25**	-0.65***
Middle toe	0.48**	0.11ns	0.51***	-0.64***	0.20ns	-0.46***

TABLE 3. Analysis of variance of weight of individual Herring Gulls and Glaucous Gulls by hybrid index (HI) score, period, area, and sex based on the samples presented in Table 1. Two observations from both species were omitted because of incomplete data. (A) Species classified by HI. (B) Species classified by genetic analysis.

		Herring Gull				Glaucous Gull			
		df	SS	MS	F	df	SS	MS	F
(A)	HI	1	156,725	17.35	6×10^{-5}	1	212	0.02	0.88
	Time	2	117,713	13.03	9×10^{-6}	2	221,632	24.00	1×10^{-9}
	Area	2	147,809	16.36	6×10^{-7}	1	137,844	14.91	2×10^{-4}
	Sex	1	924,773	102.38	2×10^{-16}	1	2,019,313	218.68	2×10^{-16}
(B)	HI	1	1,045,654	122.23	2×10^{-16}	1	920,309	98.20	2×10^{-16}
	Time	2	125,203	13.44	7×10^{-6}	2	143,477	15.31	1×10^{-6}
	Area	6	87,556	9.40	3×10^{-8}	4	56,512	6.03	2×10^{-4}
	Sex	1	1,225,513	131.53	2×10^{-16}	1	1,607,034	171.48	2×10^{-16}
	Residuals	101	9,317			125	9,372		

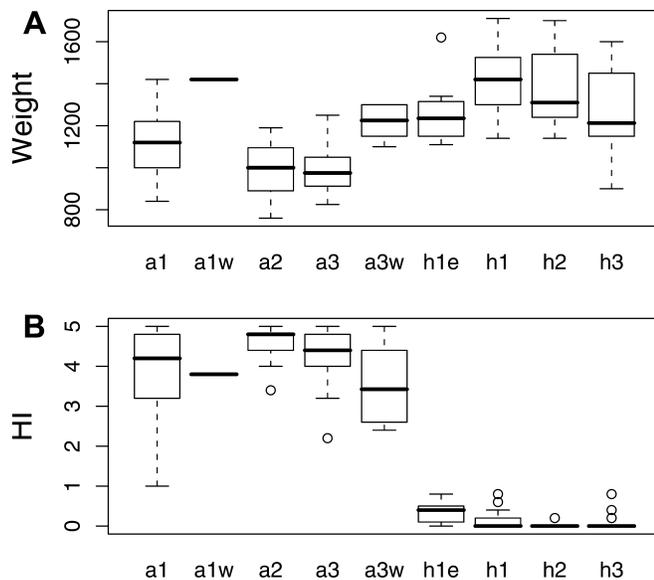


FIG. 3. Comparison of the morphology of Herring Gulls and Glaucous Gulls sampled in Iceland (A) based on weight and (B) based on hybrid index (HI). The labels on the x axis refer to samples listed in Table 1.

than for weight, and nonsignificant for Herring Gull ($b = 0.015$, $P \leq 0.071$; Glaucous Gull: $b = -0.0028$, $P \leq 0.0031$; Fig. 3B). Herring Gulls showed a negative linear relationship between HI and weight ($b = -26.9$, $P < 0.017$). Corresponding relationships for Glaucous Gulls were not significant.

Linear discriminant analysis clearly separated the species along the first linear discriminant (LDA1), though several individuals (e.g., in samples a1, a3w, and h1e) were located between the main clusters (Fig. 4). The first axis explained 95.6% of the between-group variance, whereas the second axis explained 3.3%. A noteworthy distinction was also observed between h1 and h1e, mainly on the second axis. Classifying the individuals according to the prediction of the LDA, four Herring Gulls, all from a1, were grouped with Glaucous Gulls. All variables, except tarsus, showed significant correlation with LDA1 (with r values of 0.99 for HI, 0.7 for weight, 0.6 for culmen and wing, 0.5 for tail and middle toe, 0.4 for gonys, and 0.3 for bill depth; $P < 1 \times 10^{-5}$ in all cases). Two variables (tarsus and weight) showed significant correlation with the second axis ($r = 0.2$, $P < 0.001$).

No significant patterns resulted from comparing the morphological traits of the 33 individuals that were assigned to the other species by genetic evidence with those of conspecifics. Neither the ranks of the residual morphological trait values nor the LDA1-values differed significantly from the rest of the corresponding morphological distributions (U test, $P > 0.05$).

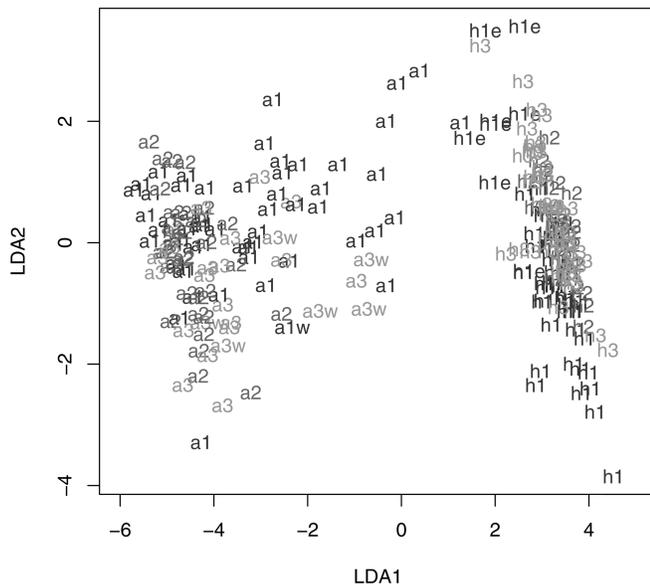


FIG. 4. Linear discriminant analysis of samples of Herring Gulls and Glaucous Gulls in Iceland, based on culmen, gony, weight, and the primary hybrid index scores. Individuals are identified with samples as presented in Table 1.

DISCUSSION

Morphological characters clearly distinguish Herring Gulls and Glaucous Gulls as traditionally defined, although, in the area of contact in Iceland, the exact boundary between the species is less clear. The observed variation led Ingólfsson (1970, 1987) to conclude that the two species were hybridizing extensively in Iceland. Snell (1991a, b) questioned that conclusion, arguing that the variation reflected the genetic legacy of light-winged Herring Gull founders. In response, Ingólfsson (1993) pointed out that both species in Iceland showed deviation in melanism scores (HI) from those of their conspecifics in Europe and Greenland and were more variable, which suggested introgression. A recent study of genetic variation in mtDNA and microsatellites (Vigfúsdóttir et al. 2008) supports Ingólfsson's conclusion, given that individuals of both species sampled in Iceland shared genotypes not found elsewhere. Considering the recent colonization of Iceland by Herring Gulls, the sharing of genotypes unique to Iceland points to hybridization after the colonization event rather than incomplete lineage sorting (Vigfúsdóttir et al. 2008). The observations in the present study provide further evidence that hybridization has occurred in Iceland.

Hybrids have traditionally been identified by their overall morphological or ecological intermediacy, though several studies have shown that numbers of intermediate and parental characters expressed in hybrids vary considerably among species, partly reflecting the choice of characters measured (see review by Rieseberg and Carney [1998]). The distributions of morphological traits in the present study were bimodal and linked with intermediate values in both HI scores and LDA and may represent some cases of F1 offspring. Although the HI scores are highly correlated with the LDA1, measurements such as weight and the admixture

coefficients showed more intermediate values than reflected by HI. The present study also uncovered several hybrid individuals that exhibited one parental type in morphology (e.g., HI score) but the other parental type in genotype. This may be a result of introgression, followed by generations of backcrosses.

Plumage variation within each species, as defined by the HI score, is partly reflected by variation in other traits, providing additional evidence for admixture. In general, Glaucous Gulls are heavier than Herring Gulls, but individual Herring Gulls with lower HI scores were heavier than those with higher HI scores. Classification based on genetic analysis revealed this admixture effect for Glaucous Gulls as well. Clear differences were observed among samples within species as defined by the BAPS analyses, whether for HI, weight, LDA scores, or admixture coefficients. It is noteworthy that samples from areas where both species breed (a1, a3w, and h1e) showed intermediate values, which suggested the presence of F1 or backcross individuals. Furthermore, temporal changes were observed, later specimens of both species being lighter than the earlier samples. The samples of Herring Gulls that Snell studied were similar in both weight and HI to the more recent Herring Gull samples from eastern Iceland. There could be several explanations for this slight increase in HI score from the earliest sample (a1), including the extinction of the colony of Glaucous Gulls (h1e) breeding in southeastern Iceland, selection counteracting the effect of hybridization, undetected population structure, and a possible influx of Herring Gulls migrating from Europe (Vigfúsdóttir et al. 2008). Interestingly, Glaucous Gulls are approaching the weight of Herring Gulls, even though the HI values of the former group are, on average, decreasing. This may reflect introgression of genes from Herring Gulls into Glaucous Gulls. The fact that pigmentation in the latter appears to be relatively stable suggests that dominance effects of pigmentation genes may mask introgression, though a better understanding of this effect is needed.

Ingólfsson (1970, 1987) found evidence of possible selection associated with hybridizing gulls in Iceland. Herring Gull-like individuals in southeastern Iceland, with high HI scores or small body size, had lower breeding success than other individuals, whereas individuals with intermediate HI scores were more frequently nonbreeders. Ingólfsson found no difference in adult mortality rates between individuals with different HIs. He also found that Glaucous Gulls molt their primaries earlier than Herring Gulls when living in the same area. However, the significant negative correlation between the advance of molt and HI in individuals from Horn, southeastern Iceland (Ingólfsson 1987), was not found in other colonies, which indicates that genes for these attributes were not closely linked with those forming primary pigmentation.

We did not observe asymmetric introgression, given that the numbers of individuals of both species that had genotypes assigned to the other species were similar. When taking the sample information (i.e., location and sampling year) into account, Vigfúsdóttir et al. (2008) reported more frequent introgression of genetic markers into Herring Gulls from Glaucous Gulls than vice versa. Such asymmetry is in accordance with results reported in a recent survey of the literature (Currat et al. 2008), in which asymmetric introgression from a local to an invading species was observed in 36 of 44 cases. A study including pure reference populations and

more genetic markers may be needed to clarify the state and frequency of introgressed individuals.

Our results suggest that the genes contributing to the reproductive isolation of Herring Gulls and Glaucous Gulls are few or that confounding effects of survival and mate choice counteract each other. A similar result was observed by Gay et al. (2007) in their study of the contact zone between Herring Gulls and Caspian Gulls. The lack of reproductive barriers may reflect the young age of the two species (Liebers et al. 2004). The Icelandic population of Glaucous Gulls may be especially vulnerable to mixing with Herring Gulls, given that both the population size and the range of the latter species have been expanding. Further climatic changes may enhance this process, resulting in further instances of hybridization at the contact zone of the two species in western Iceland.

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