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Hybridization of a Lesser Black-backed Gull and Herring Gulls in Eastern North America

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ABSTRACT.—We present the first confirmed case of hybridization between a Lesser Black-backed Gull (*Larus fuscus*) and Herring Gulls (*Larus argentatus*) in North America (outside of Greenland). We discovered a Lesser Black-backed Gull × Herring Gull pair on Appledore Island, Maine in 2007. Nuclear DNA analysis indicated that the Lesser Black-backed Gull was the genetic parent of the chicks from 2008 to 2011. The offspring have not returned to breed, so we do not know if they are fertile. Increasing numbers of observations of Lesser Black-backed Gulls, including putative Lesser Black-backed Gull × Herring Gull hybrids along the Atlantic coast, indicate that Lesser Black-backed Gulls may be in the process of colonizing

North America. If so, additional hybridization with Herring Gulls is likely in areas of overlap. *Received 11 June 2013. Accepted 13 February 2014.*

Key words: avian hybridization, Gulf of Maine, large white-headed gulls, *Larus argentatus*, *Larus fuscus*, range expansion.

Lesser Black-backed Gulls (*Larus fuscus*, Linnaeus, 1758) breed primarily in northern and western Europe and have undergone a significant range expansion north and west as well as south during the past century (Cramp and Simmons 1983, Calladine 2004, Boertmann 2008). The species colonized Iceland between 1920–1930 and Greenland between 1986–1990. They also colonized the Netherlands, Germany, Spain, Portugal, and recently expanded to the Canary Islands (Cramp and Simmons 1983, Grande and Palacios 2002). This expansion mainly involved the subspecies *graellsii* (Post and Lewis 1995).

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The first record of Lesser Black-backed Gulls in North America (outside of Greenland) was in coastal New Jersey in 1934 (Edwards 1935). Records of this species in North America increased slowly from 1950 to the mid-1970s, with substantial increases thereafter. By 1994, Lesser Black-backed Gulls had been reported in all 31 states in the eastern half of the United States except for West Virginia (Post and Lewis 1995, Olsen and Larsson 2004). Particularly large concentrations (33% of all Lesser Black-backed Gulls found during annual winter counts 1996–2006) have been found in Pennsylvania (Hallgrímsson et al. 2011). Significant numbers have also been reported in Florida, New Jersey, Virginia and North Carolina (Rutt 2009). Most observations of Lesser Black-backed Gulls along the Atlantic coast of North America occur from September–May, but increasingly the species is observed June–August (Fogarty 2009). There is virtually no information on the origins of Lesser Black-backed Gulls in America. Only two firm records of banded Lesser Black-backed Gulls exist: a bird banded in Iceland that was resighted in Puerto Rico in 2002 and a bird banded in the Netherlands that was resighted in Cold Spring Harbor, New York in 1997 (Hallgrímsson et al. 2011).

In spite of increasing numbers of birds overwintering in eastern North America, no breeding had been observed. The one previous observation of breeding by a Lesser Black-backed Gull in North America was in 1993 (van Vliet et al. 1993) wherein a Lesser Black-backed Gull was observed near a Herring Gull (*Larus argentatus*, Pontoppidan 1763) sitting on a nest containing two eggs near Juneau, Alaska. The nesting attempt was apparently unsuccessful; the authors returned to the site on 25 July 1993 and found eggshell fragments near the nest along with both members of the pair. However, there was no evidence of juveniles at or near the nest.

Herring Gulls breed inland across Canada and Alaska and along the coasts of Alaska, the Great Lakes, and northeastern and mid-Atlantic U.S. (Pierotti and Good 1994). The species increased dramatically during the 20th century, leading to a southward range expansion along the Atlantic coast (Pierotti and Good 1994). However, in the past decade, numbers appear to have declined in the northeast U.S. (Welch et al. 2010). Recent genetic evidence indicates that the American Herring Gull is differentiated from the European

Herring Gull (*L. argentatus*) and that the two taxa are not each other's closest relatives (Liebers et al. 2004, Sternkopf et al. 2011). Hybridization between Lesser Black-backed Gulls and European Herring Gulls has been described (Tinbergen 1953, Harris et al. 1978), but the only record of potential hybridization between a Lesser Black-backed Gull and American Herring Gull is the observation by vanVliet et al. (1993).

We discovered a Lesser Black-backed Gull × Herring Gull pair on Appledore Island, Maine, in 2007 (Ellis et al. 2008). The individual was banded in 2008 and returned to breed on the island every year since, except 2012, when it did not appear on the island. Here we provide three lines of evidence (genetic, behavioral, phenotypic) that strongly suggest that the Lesser Black-backed Gull produced hybrid offspring with more than one Herring Gull.

METHODS

Study Site

A Lesser Black-backed Gull × Herring Gull pair was observed on Appledore Island, Maine (42° 59' N, 70° 36' W), in the Isles of Shoals. The Isles of Shoals is a nine-island archipelago located approximately 10 km from the coast of New Hampshire. Appledore Island is the site of a large, mixed-species colony of Great Black-backed Gulls (*Larus marinus*, Linnaeus, 1758) and Herring Gulls. In 2009, there were approximately 660 pairs of Herring Gulls and 539 pairs of Great Black-backed Gulls on the island (JCE, unpubl. data). A Lesser Black-backed Gull was observed on Appledore Island once prior to our study; this bird was seen on 11 September 2006 near the same location where it nested in 2007 (S. Mirick, pers. comm.).

Breeding Chronology and Banding

We first discovered the pair at a nest with two eggs in May 2007 on the southeast portion of the island (Ellis et al. 2008). The nest was located on a bare rock ledge in a sub-colony of Herring Gulls and was within ~1 m of the same location each year from 2008–2011. Adult gulls were captured for banding during incubation with a walk-in nest trap; chicks were caught by hand from the nesting territory. All birds were banded with one metal band (provided by the Bird Banding Laboratory, USGS) and one plastic field readable band. A website and blog were established to facilitate resights of banded birds by the public.

TABLE 1. Summary of genetic sampling conducted from 2007–2011. Samples are identified by the code on the field readable leg band placed on each bird. In 2010, the chick died and was not banded.

Sample ID	Identity	Year sampled	Source of DNA
F02, F03	Chick	2008	Feather pulp
F05	Lesser Black-backed Gull	2007, 2008	Feather pulp
F04, F06	Chick	2009	Blood
Dead chick (unbanded)	Chick	2010	Tissue
F07	Chick	2011	Blood
K75	Herring Gull	2011	Blood

In 2007, the pair produced two eggs and successfully fledged one chick, which was banded. In 2008, we banded the Lesser Black-backed Gull and Herring Gull mate, monitored the nest for offspring, and banded the chick. Each year from 2009–2012, we noted the presence of the Lesser Black-backed Gull, recorded the identity of the Herring Gull mate (as indicated by the leg band), recorded the number of eggs and chicks, and banded pre-fledgling chicks.

Tissue Sampling for Genetic Analyses

We collected feathers or blood from the Lesser Black-backed Gull, one of the Herring Gull mates, and all chicks except one that died before hatching (tissue was collected from this chick). DNA obtained from the Lesser Black-backed Gull and Herring Gull mate was used to confirm sex and for paternity analyses. DNA from the chicks was used in paternity analyses. In order to place the genotypic data in a broader context, we also obtained feather pulps from Herring Gulls across Appledore in 2004 that were part of long-term population studies (JCE, unpubl. data). None of the individual birds used in that study were known to be genetically related; in a few cases, both members of a mated pair were sampled. Blood was taken from a brachial vein; feather pulp was obtained by plucking a growing feather from a bird. The samples were stored in an EDTA–

DMSO–NaCl buffer (Seutin et al. 1991). We sampled a total of 66 Herring Gulls (65 from across Appledore and one from 2011 that appeared to be the mate of the LBBG). Genomic DNA was extracted from feather pulps with a DNeasy tissue kit (Qiagen, Valencia, CA). DNA from the male Lesser Black-backed Gull (LBBG) was extracted from a feather collected from the nest (2007) and from plucked feathers (2008) (Table 1). DNA from the Herring Gull associated with the male LBBG in 2011 was extracted from a blood sample; this is the only year that both putative parents were sampled. DNA from presumably hybrid chicks was extracted from feathers, blood, and tissue from live or dead chicks (Table 1).

Genetic Analyses

Isolation of Microsatellite Loci, Primer Design, and Genotyping.—Microsatellite loci were isolated from libraries constructed separately for each gull species. We followed the protocol described by Hamilton (1999) and Pincus et al. (1999) with some modifications (Appendix 1). PCR primers flanking microsatellite repeats were designed by the program PRIMERSELECT (Lasergene, Madison, WI). Primers, dyes, and PCR fragment size of the clone are shown in Table 2; additional methodological details regarding primers can be found in supplemental material.

TABLE 2. Microsatellite locus name, primer sequences and 5' dyes, and PCR fragment size predicted from the cloned sequence. La and Lm indicate loci isolated from *L. argentatus* and *L. marinus* libraries, respectively.

Locus	Dye	Forward Primer (5'-3')	Reverse Primer (5'-3')	Fragment size (bp, clone)
La5	NED	gtcccaccaatccccactg	atcctaactgcaaatgtatcaccta	132
Lm7	VIC	tctgggaggtgcacaaggaata	gggggagaataaatggacaataata	259
Lm13	PET	ccaccaatccccactgagta	tccccttatagtttttctcctc	260
Lm17	VIC	gcagggtctgtttgaggtct	gcctgctaagtctttgtgtga	171
Lm23	NED	ggactctggcctggaaca	agaagcctaaccacaaaagtaacct	202
Lm25	6FAM	ccatgggagtcacctgcttac	agtagatcagtttggctttt	148

TABLE 3. Allele sizes and (frequencies) for six microsatellite loci genotyped from 65 Herring Gulls collected from Appledore Island, Maine in 2004.

La5ned	Lm7fam	Lm13pet	Lm17vic	Lm23ned	Lm25fam
134 (0.180328)	254 (0.3221)	265 (0.169)	172 (0.040)	192 (0.164)	157 (0.033)
136 (0.811475)	258 (0.139)	267 (0.822)	182 (0.774)	194 (0.057)	159 (0.016)
145 (0.008197)	260 (0.121)	275 (0.008)	184 (0.064)	195 (0.197)	161 (0.240)
	262 (0.322)		186 (0.073)	197 (0.115)	164 (0.198)
	266 (0.078)		190 (0.040)	204 (0.303)	165 (0.041)
	270 (0.017)		192 (0.008)	205 (0.049)	168 (0.215)
				206 (0.016)	170 (0.016)
				210 (0.016)	172 (0.066)
				211 (0.033)	174 (0.107)
				212 (0.049)	176 (0.033)
					180 (0.016)
					191 (0.008)
					193 (0.008)

Sex Determination.—We used PCR amplification and agarose electrophoresis following the protocol by Fridolfsson and Ellegren (1999) to determine sex of the Lesser Black-backed Gull and the Herring Gull mate from 2011.

Data Analysis

Microsatellite DNA allele frequencies were calculated with Microsatellite Analyzer (MSA) software (Dieringer and Schlotterer 2003). We compared the multilocus genotype of the male LBBG by eye to the multilocus genotypes of all sampled chicks to determine if he could have been the male parent in years 2008–2010. We also included F07 in this analysis in 2011, the year we sampled the Herring Gull mate as well.

RESULTS

DNA Analyses

Allele frequencies (MSA) for 65 Appledore Herring Gulls are shown in Table 3. The multi-

locus genotypes of the Lesser Black-backed Gull, chick or egg tissues, and adult Herring Gull from 2011 are shown in Table 4. The LBBG has two alleles not found in the Appledore Herring Gull population: allele 138 at microsatellite locus La5ned and allele 269 at microsatellite locus Lm13pet (Table 4). One fledged chick (F04 from 2009) and one dead chick (from 2010) exhibited both of these “private” alleles of Lesser Black-backed Gulls in their multilocus genotypes.

Molecular sexing confirmed that the Lesser Black-backed Gull is a male and the Herring Gull mate in 2011 was a female.

Copulation Behavior

On numerous occasions, we observed the Lesser Black-backed Gull copulating with his mates each year.

Intermediate Phenotype of Offspring

One of the offspring (field readable band: F02; Table 1) was observed by members of the public

TABLE 4. The multilocus genotypes of the Lesser Black-backed Gull male (band code, F05), chick (F02, F03, F04, F06, F07) or egg tissues, and adult Herring Gull (K75). Alleles in the chicks presumed to originate from the Lesser Black-backed Gull are in bold.

Sample ID	Year sampled	La5ned	Lm25fam	Lm17vic	Lm23ned	Lm7fam	Lm13pet
F02	2008	134/136	165/170		192/194	254/262	265/267
F03	2008	134/136	165/170	182/182	192/194	254/262	265/267
F04	2009	136/ 138	159/165	182/182	192/194	254/262	267/ 269
F06	2009	134/136	161/170	182/182		254/262	265/267
Dead chick	2010	136/ 138	159/159	182/182	192/206	254/262	267/ 269
F07	2011	134/136	159/161	182/182	192/206	262/262	265/267
F05	2011	134/ 138	159/170	182/182	192/194	262/262	265/ 269
K75	2011	136/136	159/161	182/182	204/206	254/262	267/267



FIG. 1. Presumed Lesser Black-backed \times Herring Gull hybrid (field readable band, F02) observed at (A) Provincetown, MA standing next to a Herring Gull (photo by B. Nikula) and (B) a landfill in Florida (photo by M. P. Harris).

after dispersing from Appledore Island. Both observers indicated that the bird initially attracted their attention because it looked like a hybrid gull (based on mantle color, leg color and body structure) (Fig. 1). On 13 December 2009 the bird was observed in Provincetown, MA (B. Nikula, pers. comm.). The observer indicated that the mantle was too pale for a Lesser Black-backed Gull, but the wings were shorter and the body was stockier than is typical for a Lesser Black-backed Gull (Fig. 1A). This gull was also observed at a landfill in Florida in February 2010 (M. P. Harris,

pers. comm.; Fig. 1B). The observer indicated that F02 had an unusual appearance and stood out among the crowd of over 40,000 gulls (including ~200 Lesser Black-backed Gulls and ~600 Herring Gulls) at the landfill.

Another gull, banded as a chick (field readable band: J06) in 2009 near the nest of the Lesser Black-backed Gull, was seen by two separate observers on the coast of Alabama in 2010 (C. McCready, M. J. Iliff, pers. comm.) (Fig. 2). One observer suggested that the bird was a Lesser Black-backed Gull \times Herring Gull hybrid based



FIG. 2. Presumed Lesser Black-backed \times Herring Gull hybrid (field readable band, J06) standing next to a Laughing Gull (*Leucophaeus atricilla*) observed in coastal Alabama (photo by C. McCready).

on its coloration and body structure (M. J. Iliff, pers. comm.). Specifically, the base of the bill was black, rather than pale as is the case for Herring Gulls. Additionally, the bird was dark above and pale below (and pale-headed), a pattern typical of Lesser Black-backed Gulls rather than Herring Gulls. J06 was not identified as one of the two offspring of the Lesser Black-backed \times Herring Gull pair in 2009. Instead, two chicks (field readable band: F04 and F06) were observed being fed by the Lesser Black-backed Gull at the nest after banding, confirming their status as offspring. J06 was banded near the nest but was not seen at the nest in subsequent observations.

DISCUSSION

In this study, we provided three lines of evidence that strongly suggest that a male Lesser Black-backed Gull produced viable hybrid offspring with at least two Herring Gulls on Appledore Island. First, analysis of microsatellite DNA is consistent with the Lesser Black-backed Gull siring all the chicks genotyped from the Lesser Black-backed Gull \times Herring Gull nest between 2008–2011. Even more definitively, two offspring sampled (chick F04 from 2009 and embryonic tissue from 2010) each carried alleles (138 at locus La5 and 269 at locus Lm13) that to this point are specific to the Lesser Black-backed Gull male and have not been found in the

Appledore Herring Gull population. We also observed the Lesser Black-backed Gull copulating with its mates each year. Third, one of the known offspring was observed after it dispersed from Appledore Island; it exhibited an intermediate phenotype, suggesting hybrid status. This study represents the first observed case of hybridization between these two species in North America. The formation of mixed pairs and the breakdown of isolating mechanisms are likely to occur when one species (in this case, Lesser Black-backed Gull) attaches itself to a colony where there are no conspecific mates available (Tinbergen 1953). Additionally, low levels of post-mating isolation may be a general phenomenon among large gulls (Gay et al. 2007).

The Herring Gull assemblage consists of more than 20 taxa, which occupy a circumpolar breeding range in the northern hemisphere. This assemblage has represented a significant systematic challenge because of the frequency of hybridization occurring between well-established species, the strong plumage similarity among some taxa, and the high level of phenotypic differentiation in some cases without apparent reproductive isolation (Crochet et al. 2002). Low levels of genetic differentiation at nuclear loci are thought to be explained by a combination of recent species origin and interspecific gene flow (hybridization) after speciation (e.g., Crochet et al. 2003, Sonsthagen et al. 2012).

The physical appearance of the Lesser Black-backed Gull in our study is consistent with the subspecies *L. f. graellsii*, and current thinking is that all, or almost all, North American Lesser Black-backed Gulls are this subspecies. However, it is not possible to conclusively eliminate *L. f. intermedius* as the subspecies because of the large amount of phenotypic variability among individuals of both subspecies. *L. fuscus graellsii* breeds in the Faroes, British Isles, Iceland, France, the Netherlands, Germany, and more recently the Canary Islands in the Macaronesian archipelago (Post and Lewis 1995, Grande and Palacios 2002). Numbers of this subspecies have increased substantially during the past decade (Hallgrímsson et al. 2011) and the breeding distribution has expanded to southwest Greenland (Boertmann 2008). It is quite possible that there are breeding populations of this subspecies in North America that have yet to be discovered.

A gull banded as a chick (band J06) in 2009 near the nest of the Lesser Black-backed Gull was resighted in coastal Alabama, USA, several months after it dispersed from Appledore Island. Based on its intermediate phenotype, this bird appeared to be a Herring Gull × Lesser Black-backed Gull hybrid. The bird was banded near the nest of the Lesser Black-backed Gull, but subsequent observations of the nest showed that it did not originate from the Lesser Black-backed Gull × Herring Gull pair. It is possible that this bird resulted from extra-pair copulation between the Lesser Black-backed Gull and a neighboring Herring Gull. Its phenotype was very similar to that of the confirmed offspring of the Lesser Black-backed Gull × Herring Gull, F02, also observed off the island. Compared to passerines, extra-pair paternity is low in seabirds, most likely because seabirds have long-term pair bonds with low divorce rates, very high paternal investment, and relatively small testes (Ashmole 1971, Furness and Monaghan 1987, Gilbert et al. 1998, Moller and Cuervo 2000).

There are several records of Herring Gulls breeding with other species of large white-headed gulls in North America including California Gulls, Glaucous-winged Gulls, Iceland Gulls, Glaucous Gulls, Thayer's Gulls, and Great Black-backed Gulls (McCarthy 2006). In a situation similar to the one we describe, Kelp Gulls, which are residents of South America, colonized islands off the coast of Louisiana in the early 1990s around the same time that the islands were

colonized by Herring Gulls (Dittman and Cardiff 2005). Hybridization occurred, and now both parental types and hybrids breed at these islands.

Increasing numbers of observations of Lesser Black-backed Gulls, including observations of putative Lesser Black-backed Gull × Herring Gull hybrids, indicate that Lesser Black-backed Gulls may be in the process of colonizing North America. If this is the case, hybridization with Herring Gulls is likely in areas of overlap. Additional research is required to ascertain the frequency of hybrid pairings in North America and to determine whether the hybrid offspring documented in this study are fertile.

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Testing for Behavioral Lateralization in Observational Data: a Monte Carlo Approach Applied to Neck-looping in American Flamingos

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ABSTRACT.—We applied a Monte Carlo approach to test for both individual and group level laterality

preferences in neck looping by American Flamingos (*Phoenicopterus ruber ruber*) at rest. We found no evidence of individual or group-level preferences, contrary to the results of previous studies. In the present data, the appearance of bias tended to decrease as the number of observations increased, suggesting that apparent lateral bias may be largely because of stochastic error. Pair members tended to loop the neck

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