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Morphological Variation among Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) in Eastern North America

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Abstract.—Herring Gull (*Larus argentatus*) and Great Black-backed Gull (*L. marinus*) morphometric data from various eastern North American locations was collected to examine the sources of variation in body size within and among geographic regions. For Herring Gulls, significant differences in all commonly taken measurements at local and regional scales were found. However, most of the variation in measurements was due to sex differences and the natural variance seen within local populations. Herring Gulls breeding in the Arctic did not show any evidence of being morphologically different from other groups. A discriminant function derived from a Newfoundland, Canada, breeding population of Herring Gulls successfully assigned the sex of birds in Atlantic Canada and Nunavut, Canada, further emphasizing that most of the variation seen is between sexes and not among local or even regional populations. It also indicates that the evitable variation introduced by inter-individual differences in measurements was insufficient to compromise the utility of the discriminant function. The correct classification rate was lower for Great Lakes breeding Herring Gulls, indicating that these birds have different morphologies than those of populations in easterly regions. In contrast, few differences and no clear geographic patterns were found in measurements for Great Black-backed Gulls. These results were consistent with recent genetic information, suggesting an older west to east radiation of Herring Gulls across North America and a lack of isolation among Great Black-Backed Gull populations. *Received 18 June 2014, accepted 29 August 2015.*

Key words.—body size, discriminant function, Great Black-backed Gull, Herring Gull, *Larus argentatus*, *Larus marinus*, morphometrics.

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Body size variation within a species generally has some genetic basis (Boag and van Noordwijk 1987), so differences among sites or across a species' range could indicate genetic differentiation (Ross and Bouzat 2014). Variation in adult body size can also be driven by ecological forces; in particular, conditions experienced during the growth

of young can lead to different adult phenotypes (Cooch *et al.* 1991; Genovart *et al.* 2003).

Gulls (Laridae) have a complicated phylogenetic history and the taxonomic placement of their populations, subspecies and species is being revised continually (Pons *et al.* 2005). The Herring Gull (*Larus ar-*

gentatus) complex, and closely related species such as Great Black-backed Gull (*L. marinus*), has received specific attention due to their genetic complexity (Liebers *et al.* 2004; Liebers-Helbig *et al.* 2010). It is not well understood if size variation exists within Herring Gull populations throughout the species' North American range; however, size differences have been identified across the Herring Gull complex. Significant differences exist between the size of British (*L. argentatus argentatus*) and Newfoundland (*L. argentatus smithsonianus*) birds (Threlfall and Jewer 1978). In contrast, discriminant analysis of Norwegian (*L. argentatus argentatus*) and eastern Canadian Herring Gull populations revealed the size of individuals in both groups is almost identical, though belonging to different subspecies (Threlfall and Jewer 1978). Early research found no clear morphometric differences between European and North American populations of Great Black-backed Gull (Dwight 1925), but little is known about morphological variation within North America (Mawhinney and Diamond 1999).

Discriminant function analysis is a method used to assess body size variation and provides the ability to correctly assign an individual to a group. In certain instances, discriminant functions can be used to confidently determine sex of seabirds (Granadeiro 1993), including Herring and Great Black-backed gulls in North America (Shugart 1977; Fox *et al.* 1981; Evans *et al.* 1995; Mawhinney and Diamond 1999). However, these functions have to be used cautiously when applied to species exhibiting a high percentage of overlap and/or variability in measurements (Jakubas and Wojczulanis 2007). If a discriminant function is applied more broadly across populations that exhibit important body size variation, it may not perform well (Genovart *et al.* 2003).

The purpose of this study was to examine the variation in morphological data in Herring and Great Black-backed gulls from breeding locations within their North American ranges to examine whether evidence exists of differences in body size measures

and how widely discriminant functions to assign sex can be used across regions.

METHODS

Study Area

We solicited data on morphometrics from researchers who have recently, or currently are, studying Herring and/or Great Black-backed gulls in North America. We obtained data sets for 13 sites for Herring Gulls and eight sites for Great Black-backed Gulls (Tables 1 and 2; Fig. 1). We did not consider data from non-breeding birds; only data collected during the breeding season between the months of April and July were examined. Data from live birds (except where indicated) were collected at nine Canadian sites: 1) eastern Newfoundland, where data were collected from two main locations with live birds captured in the Witless Bay Ecological Reserve (47° 15' N, 52° 46' W) and dead birds sampled in urban areas around the City of St. John's (47° 36' N, 52° 41' W); given their proximity these two sampling areas were considered as one site (Robertson *et al.* 2016); 2) Gannet Islands Ecological Reserve, Labrador (53° 56' N, 56° 30' W; Veitch *et al.* 2016); 3) Sable Island, Nova Scotia (43° 55' N, 59° 54' W; Ronconi *et al.* 2016); 4) Brier Island, Nova Scotia (44° 15' N, 66° 22' W); 5) Kent Island, New Brunswick (44° 34' N, 66° 45' W; Steenweg *et al.* 2011); 6) The Wolves Archipelago, New Brunswick (44° 56' N, 66° 44' W; Gilliland *et al.* 2004); 7) a suite of islands along the New Brunswick Bay of Fundy coast ranging from 45° 03' N, 66° 55' W to 45° 09' N, 66° 01' W; 8) Corossol Island, Québec (50° 05' N, 66° 23' W; Lavoie *et al.* 2012); and 9) East Bay Migratory Bird Sanctuary near Southampton Island, Nunavut (64° 00' N, 81° 59' W). In the USA, data were collected from live birds at two sites: 1) an urban population in Portland, Maine (43° 39' N, 70° 15' W; Perlut *et al.* 2016); and 2) Appledore Island, Maine (42° 59' N, 70° 36' W). We also included previously published information on birds collected from South Manitou Island, Lake Michigan, Michigan, USA (Shugart 1977), Presqu'île Provincial Park near Brighton, Ontario, Canada (Fox *et al.* 1981), and Ram Island in Buzzards Bay, Massachusetts, USA (Fox *et al.* 1981; Evans *et al.* 1995). Additional published information was available for Great Black-backed Gulls breeding in The Wolves Archipelago, New Brunswick, Canada (Mawhinney and Diamond 1999), and Herring Gulls breeding in eastern Newfoundland, Canada, in the Witless Bay Ecological Reserve during the 1960s (Threlfall and Jewer 1978). The years when birds were measured are provided in Tables 1 and 2.

Field Methods

Live adult individuals were aged based on plumage and sexed with genetic methods or observation of copulation behavior, or were assigned to sex when both members of the pair were captured and the male was assumed to be larger (Fox *et al.* 1981). For dead specimens, sex was assessed by internal examination of the

Table 1. Measurements of adult breeding Herring Gulls in eastern North America. All measurements in mm. Values are means (± 1 SD), with range below and sample size at the bottom of each cell. Data for Ram Island, Massachusetts, USA, are from Evans *et al.* 1995 (note that printed culmen estimate for males is incorrect and corrected here); for South Manitou Islands, Lake Michigan, USA, from Shugart (1977); for Brighton, Ontario, Canada, from Fox *et al.* (1981); for Witless Bay, Newfoundland, Canada, from Threlfall and Jewer (1978); and for Corossol Island, Québec, Canada, from Lavoie *et al.* (2012).

	South Manitou Island, Lake Michigan 1973-1974	Brighton, Lake Ontario 1978-1980	Eastern Lake Ontario 2001-2002	Ram Island, Massachusetts 1990	Portland, Maine 2011-2012	Appledore Island, Maine 2006	Kent Island, New Brunswick 2009	Bay of Fundy, New Brunswick 2001-2002	Brier Island, Nova Scotia 2014	Sable Island, Nova Scotia 2011-2013	Eastern Newfoundland 1999-2013	Witless Bay, Newfoundland 1966-1968	Corossol Island, Québec 2006-2007	East Bay, Southampton Island, Nunavut 1998-2013
Males														
Head-bill	127.2 \pm 3.0 32	126.7 \pm 4.2 67	129.1 \pm 3.6 12	131.4 131.4-131.4	133.4 \pm 2.0 16	134.0 \pm 3.6 134.0 \pm 3.6	130.1 \pm 3.1 130.1 \pm 3.1	128.0-138.8 127.9-132.3	125.3-136.5 124.6-141.2	125.3-136.5 124.6-141.2	125.3-136.5 124.6-141.2	125.3-136.5 124.6-141.2	125.3-136.5 124.6-141.2	125.3-136.5 124.6-141.2
Bill depth	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67	18.9 \pm 0.8 17.2-21.0 67
Bill depth at gonys	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9	20.7 \pm 1.1 18.6-22.4 9
Culmen length	56.7 \pm 2.2 32	56.0 \pm 3.5 49.5-60.9 9	56.0 \pm 3.5 49.5-60.9 9	62.2 \pm 2.3 56.0-70.0 169	63.9 63.9-63.9 1	60.6 \pm 2.5 55.6-66.2 63	60.6 \pm 2.5 55.6-66.2 63	60.6 \pm 2.5 55.6-66.2 63	60.6 \pm 2.5 55.6-66.2 63	60.6 \pm 2.5 55.6-66.2 63	60.6 \pm 2.5 55.6-66.2 63	60.6 \pm 2.5 55.6-66.2 63	60.6 \pm 2.5 55.6-66.2 63	60.6 \pm 2.5 55.6-66.2 63
Tarsus	68.3 \pm 2.7 32	76.9 \pm 3.2 71.2-81.5 9	76.9 \pm 3.2 71.2-81.5 9	71.1 \pm 2.2 65.0-76.0 169	67.4 67.4-67.4 1	73.0 \pm 5.1 64.1-83.7 59	73.0 \pm 5.1 64.1-83.7 59	72.3 \pm 1.9 70.2-75.4 9	70.7 \pm 1.6 69.6-71.8 2	70.7 \pm 1.6 69.6-71.8 2	71.5 \pm 2.4 67.1-77.7 80	69.9 \pm 3.6 59.80 180	67.2 \pm 3.2 61.1-70.4 7	68.8 \pm 3.3 64.3-76.3 16
Total tarsus						78.6 \pm 4.1 73.7-83.7 4					81.8 \pm 2.6 75.7-89.5 80			
Wing chord	432 \pm 11 32	448 \pm 11 420-475 66	449 \pm 13 428-466 12	429 \pm 10 400-460 169	453 \pm 9 439-469 21	448 \pm 6 444-452 2	448 \pm 6 444-452 2	453 \pm 7 441-460 9	448 \pm 6 441-460 9	448 \pm 6 444-452 2	449 \pm 11 422-474 80	440 \pm 11 41-470 180	439 \pm 7 426-446 7	445 \pm 12 417-460 14
Females														
Head-bill	116.8 \pm 2.4 22	115.6 \pm 3.2 107.3-124.3 84	119.7 \pm 3.4 112.0-123.9 9	125.8 \pm 3.2 123.6-128.1 2	121.2 \pm 3.3 115.3-127.0 9	118.6 \pm 2.5 113.5-123.1 24	121.5 \pm 1.2 119.3-122.7 7	119.9 \pm 4.2 114.1-129.4 13	121.5 \pm 1.2 119.3-122.7 7	121.5 \pm 1.2 119.3-122.7 7	122.1 \pm 3.4 112.8-136.4 248	121.2 \pm 3.1 117.0-127.2 12	120.2 \pm 3.1 114.6-125.6 23	

Table 1. (Continued) Measurements of adult breeding Herring Gulls in eastern North America. All measurements in mm. Values are means (± 1 SD), with range below and sample size at the bottom of each cell. Data for Ram Island, Massachusetts, USA, are from Evans *et al.* 1995 (note that printed culmen estimate for males is incorrect and corrected here); for South Manitou Islands, Lake Michigan, USA, from Shugart (1977); for Brighton, Ontario, Canada, from Fox *et al.* (1981); for Witless Bay, Newfoundland, Canada, from Threlfall and Jewer (1978); and for Corossol Island, Québec, Canada, from Lavoie *et al.* (2012).

	South Manitou Island, Lake Michigan 1973-1974	Brighton, Lake Ontario 1978-1980	Eastern Lake Ontario 2001-2002	Ram Island, Massachusetts 1990	Portland, Maine 2011-2012	Appledore Island, Maine 2006	Kent Island, New Brunswick 2009	Bay of Fundy, New Brunswick 2001-2002	Brier Island, Nova Scotia 2014	Sable Island, Nova Scotia 2011-2013	Eastern Newfoundland 1999-2013	Witless Bay, Newfoundland 1966-1968	Corossol Island, Québec 2006-2007	East Bay, Southampton Island, Nunavut 1998-2013
Bill depth	51.6 \pm 2.1 22	16.9 \pm 0.8 15.3-19.08 4						17.6 \pm 0.7 16.2-18.9 10					18.4 \pm 2.2 16.2-22.7 12	
Bill depth at gonyx			18.8 \pm 0.9 17.3-19.9 5		20.6 \pm 1.4 18.5-23.1 9	18.8 \pm 0.6 18.0-20.0 11		18.9 \pm 0.6 18.0-20.0 24	19.1 \pm 0.7 18.0-20.2 13	21.9 \pm 0.3 21.7-22.1 7	19.0 \pm 0.7 17.4-20.9 248	19.5 \pm 1.1 16-23 78		18.3 \pm 0.5 17.5-19.4 22
Culmen length	51.6 \pm 2.1 22		52.0 \pm 3.4 46.0-55.3 6	57.2 \pm 1.9 52.0-62.0 253	56.5 \pm 4.3 53.4-59.5 2			53.4 \pm 2.1 50.5-56.6 22	54.7 \pm 2.5 50.9-58.8 13	57.7 \pm 0.6 57.3-58.1 7		55.0 \pm 2.5 48-63 78	54.1 \pm 2.0 51.1-57.4 11	52.5 \pm 2.2 47.8-55.9 22
Tarsus	63.3 \pm 1.6 22		70.3 \pm 1.4 68.7-72.5 6	66.0 \pm 2.0 60.0-73.0 253	65.5 \pm 0.9 64.9-66.2 2	65.9 \pm 1.9 63.4-70.0 9	64.1 \pm 1.7 61.5-66.5 11	68.1 \pm 4.2 62.4-75.9 16	65.1 \pm 1.3 63.2-68.2 13	65.8 \pm 1.6 63.6-68.0 7	65.3 \pm 2.5 56.2-71.5 247	63.6 \pm 3.5 56-71 78	62.9 \pm 1.7 60.6-65.5 13	64.5 \pm 2.3 60.5-67.7 17
Total tarsus								73.3 \pm 2.2 70.9-75.9 6			75.1 \pm 2.5 65.3-82.4 247			
Wing chord	406 \pm 9 22	422 \pm 13 385-450 80	428 \pm 7 415-436 7	408 \pm 10 384-447 253	430 430-430 1	428 \pm 10 416-446 11	434 \pm 13 412-450 7	430 \pm 10 404-442 13	430 \pm 10 404-442 13	434 \pm 13 412-450 7	426 \pm 10 400-453 248	417 \pm 13 388-445 78	419 \pm 10 398-437 13	422 \pm 11 405-434 9
Unknown sex														
Head-bill			120.4 \pm 4.2 115.3-129.1 9		129.6 \pm 7.2 119.1-140.4 11		125.6 \pm 6.0 114.8-136.2 37	125.1 \pm 7.8 113.5-138.3 13	127.2 \pm 6.7 115.8-146.0 95	125.8 \pm 6.0 116.0-138.7 59	126.6 \pm 6.6 110.4-140.7 242			126.0 \pm 6.6 110.6-135.8 66
Bill depth									19.1 \pm 1.2 17.2-21.2 40					

Table 1. (Continued) Measurements of adult breeding Herring Gulls in eastern North America. All measurements in mm. Values are means (± 1 SD), with range below and sample size at the bottom of each cell. Data for Ram Island, Massachusetts, USA, are from Evans *et al.* 1995 (note that printed culmen estimate for males is incorrect and corrected here); for South Manitou Islands, Lake Michigan, USA, from Shugart (1977); for Brighton, Ontario, Canada, from Fox *et al.* (1981); for Witless Bay, Newfoundland, Canada, from Threlfall and Jewer (1978); and for Corossol Island, Québec, Canada, from Lavoie *et al.* (2012).

	South Manitou Island, Lake Michigan 1973-1974	Brighton, Lake Ontario 1978-1980	Eastern Lake Ontario 2001-2002	Ram Island, Massachusetts 1990	Portland, Maine 2011-2012	Appledore Island, Maine 2006	Kent Island, New Brunswick 2009	Bay of Fundy, New Brunswick 2001-2002	Brier Island, Nova Scotia 2014	Sable Island, Nova Scotia 2011-2013	Eastern Newfoundland 1999-2013	Witless Bay, Newfoundland 1966-1968	Corossol Island, Québec 2006-2007	East Bay, Southampton Island, Nunavut 1998-2013	
Bill depth at gonys			18.5 \pm 1.0 17.4-20.6 8				19.8 \pm 1.0 18.2-21.9 37	20.5 \pm 1.6 18.0-24.2 13	20.1 \pm 1.4 16.8-23.5 95	20.3 \pm 1.3 18.0-23.1 59	19.8 \pm 1.4 16.4-23.6 241			19.3 \pm 1.2 17.2-21.9 66	
Culmen length			53.0 \pm 3.1 48.5-58.2 9		59.1 \pm 2.9 53.8-62.3 11		57.7 \pm 3.3 51.0-63.6 37	56.2 \pm 3.4 51.1-61.5 8	58.2 \pm 3.8 50.2-66.8 95	56.6 \pm 3.3 50.9-63.4 59	56.6 \pm 3.7 47.0-68.5 129			55.9 \pm 4.2 49.5-69.3 66	
Tarsus			70.8 \pm 1.7 68.9-74.4 9		68.7 \pm 3.3 63.4-74.5 10		66.7 \pm 3.8 60.1-73.7 37	70.8 \pm 8.3 61.5-87.1 8	68.0 \pm 3.9 61.7-77.5 95	66.6 \pm 3.5 60.9-75.2 59	68.1 \pm 4.0 57.7-78.1 226			65.4 \pm 3.4 59.4-73.1 65	
Total tarsus															
Wing chord			420 \pm 16 402-450 9		432 \pm 13 420-445 3		448 \pm 14 419-483 36	440 \pm 24 416-470 4	437 \pm 15 410-475 95	439 \pm 15 401-470 59	435 \pm 16 395-474 242			434 \pm 21 395-500 58	

Table 2. Measurements of adult breeding Great Black-backed Gulls in eastern North America. Values are means (± 1 SD), with range below and sample size at the bottom of each cell. Data for The Wolves Archipelago, New Brunswick, Canada, 1996 are from Mahimney and Diamond (1999) (note the published SDs in the original paper are incorrect for wing chord and corrected values are presented here) and for Corossol Island, Québec, Canada, the data are from Lavoie *et al.* (2012).

	Eastern Lake Ontario 2001-2002	Kent Island, New Brunswick 2009	The Wolves Archipelago, New Brunswick 1989	The Wolves Archipelago, New Brunswick 1996	Brier Island, Nova Scotia 2014	Sable Island, Nova Scotia 2012-2013	Eastern Newfoundland 2000-2006	Corossol Island, Québec 2006-2007	Cannet Islands, Labrador 2000-2001
Males									
Head-bill	151.9 \pm 6.1 145.9 - 172.0 15		149.7 \pm 2.5 145.2-154.8 16	149.2 \pm 3.6 78		147.1 \pm 3.0 141.9-150.0 6	151.6 \pm 5.0 148.1-155.2 2	154.1 \pm 6.1 147.7-161.5 5	
Bill depth	25.7 \pm 1.5 23.1-29.0 15		25.0 \pm 1.3 23.3-28.1 16					25.0 \pm 1.1 5	
Bill depth at gonys	27.4 \pm 1.0 25.7-29.0 15		26.7 \pm 0.8 25.3-28.1 16	26.5 \pm 1.6 78	26.4 \pm 0.8 25.7-27.5 6		25.9 \pm 0.1 25.8-25.9 2		
Culmen length	65.9 \pm 3.6 58.9-72.9 15		67.9 \pm 2.1 62.8-71.3 16	67.8 \pm 3.6 78	63.9 \pm 1.9 60.8-66.0 6		61.2 61.2-61.2 1	65.1 \pm 2.9 61.2-68.3 5	
Tarsus			81.8 \pm 3.9 72.6-87.5 16	82.7 \pm 4.6 78	82.3 \pm 3.0 77.5-85.3 6		81.5 \pm 1.1 80.7-82.3 2	83.2 \pm 3.2 77.2-88.8 11	
Total tarsus	93.3 \pm 3.4 88.8-101.3 14						95.6 \pm 3.0 93.4-97.7 2		
Wing chord	502 \pm 15 471-520 15		505 \pm 12 483-530 16	496 \pm 13 78	504 \pm 10 488-516 6		496 \pm 4 494-499 2	486 \pm 10 473-510 11	
Females									
Head-bill	139.7 \pm 4.0 135.2-145.4 9		138.5 \pm 2.4 134.5-142.2 12	136.4 \pm 3.4 108	137.1 \pm 0.6 136.4-137.8 5		134.4 \pm 0.1 134.4-134.5 2	137.2 \pm 10.2 130.0-144.4 2	

Table 2. (Continued) Measurements of adult breeding Great Black-backed Gulls in eastern North America. Values are means (± 1 SD), with range below and sample size at the bottom of each cell. Data for The Wolves Archipelago, New Brunswick, Canada, 1996 are from Mawhinney and Diamond (1999) (note the published SDs in the original paper are incorrect for wing chord and corrected values are presented here) and for Corossol Island, Québec, Canada, the data are from Lavoie *et al.* (2012).

	Eastern Lake Ontario 2001-2002	Kent Island, New Brunswick 2009	The Wolves Archipelago, New Brunswick 1989	The Wolves Archipelago, New Brunswick 1996	Brier Island, Nova Scotia 2014	Sable Island, Nova Scotia 2012-2013	Eastern Newfoundland 2000-2006	Corossol Island, Québec 2006-2007	Gannet Islands, Labrador 2000-2001
Bill depth	22.3 \pm 0.5 21.6-22.8 9		22.1 \pm 0.8 20.8-23.5 12					22.1 \pm 0.5 2	
Bill depth at gonyx	24.4 \pm 0.6 23.3-24.9 9		24.0 \pm 0.8 22.8-25.2 12	24.1 \pm 1.0 108		24.0 \pm 0.7 23.1-24.8 5	22.9 \pm 0.4 22.7-23.2 2		
Culmen length	60.6 \pm 1.8 57.2-63.3 8		60.9 \pm 1.4 58.8-63.4 12	61.3 \pm 3.5 108		61.5 \pm 1.2 60.1-62.9 5		60.5 \pm 0.9 59.8-61.1 2	
Tarsus			77.6 \pm 1.9 72.3-79.5 12	77.2 \pm 3.1 108		75.3 \pm 2.4 73.5-79.2 5	77.9 \pm 0.4 77.6-78.2 2	76.4 \pm 0.5 76.0-77.2 7	
Total tarsus	85.6 \pm 3.1 80.3-90.7 9						89.3 \pm 1.6 88.2-90.4 2		
Wing chord	482 \pm 14 465-510 9		481 \pm 11 460-494 12	468 \pm 14 108		471 \pm 11 458-484 5	468 \pm 4 465-470 2	464 \pm 10 449-482 7	
Unknown sex									
Head-bill	141.9 \pm 5.4 134.9-152.8 11	144.0 \pm 7.1 135.0-154.0 14			145.8 \pm 9.9 136.9-154.8 4	144.8 \pm 7.3 131.6-156.9 35	146.2 \pm 8.4 128.4-160.9 96		146.0 \pm 7.3 134.1-154.2 11
Bill depth	22.9 \pm 1.2 21.0-25.0 11		25.4 \pm 1.6 24.2-26.5 2						

Table 2. (Continued) Measurements of adult breeding Great Black-backed Gulls in eastern North America. Values are means (± 1 SD), with range below and sample size at the bottom of each cell. Data for The Wolves Archipelago, New Brunswick, Canada, 1996 are from Mawhinney and Diamond (1999) (note the published SDs in the original paper are incorrect for wing chord and corrected values are presented here) and for Corossol Island, Québec, Canada, the data are from Lavoie *et al.* (2012).

	Eastern Lake Ontario 2001-2002	Kent Island, New Brunswick 2009	The Wolves Archipelago, New Brunswick 1989	The Wolves Archipelago, New Brunswick 1996	Brier Island, Nova Scotia 2014	Sable Island, Nova Scotia 2012-2013	Eastern Newfoundland 2000-2006	Corossol Island, Québec 2006-2007	Cannet Islands, Labrador 2000-2001
Bill depth at gonyx	25.2 \pm 1.9 22.8-28.2 7	24.3 \pm 1.4 22.3-27.8 14			25.8 \pm 2.8 23.1-28.6 4	25.6 \pm 1.8 21.6-28.4 35	25.1 \pm 1.7 21.0-29.0 96		25.2 \pm 1.8 22.6-28.6 11
Culmen length	60.8 \pm 3.8 56.5-68.4 11	63.7 \pm 3.4 59.5-69.6 14			64.6 \pm 5.3 58.7-69.6 4	63.1 \pm 3.9 54.3-70.0 35	63.9 \pm 3.7 56.5-72.9 92		64.2 \pm 3.4 56.8-67.6 11
Tarsus		78.7 \pm 4.7 65.1-83.6 14			80.3 \pm 6.0 73.6-86.6 4	79.7 \pm 4.0 71.1-86.6 35	80.1 \pm 4.4 70.2-88.9 96		81.9 \pm 4.9 74.8-88.2 11
Total tarsus	88.3 \pm 5.4 81.6-100.1 11						93.6 \pm 5.4 83.4-113.1 96		93.6 \pm 4.5 88.1-100.3 11
Wing chord	478 \pm 25 452-525 7	500 \pm 11 485-519 7			483.0 \pm 34.1 450-519 4	491 \pm 17 453-517 35	488 \pm 17 448-522 96		493 \pm 22 463-524 11

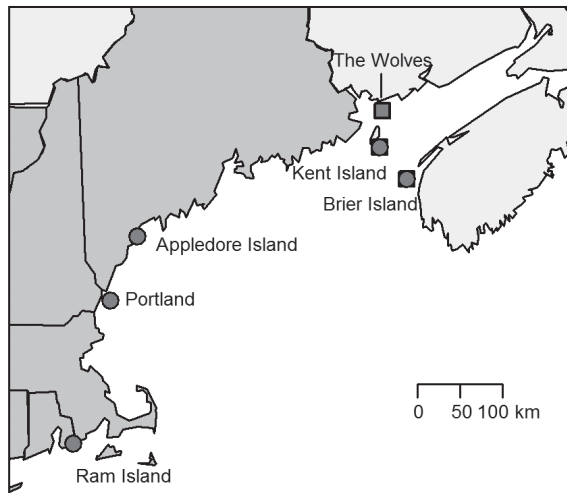
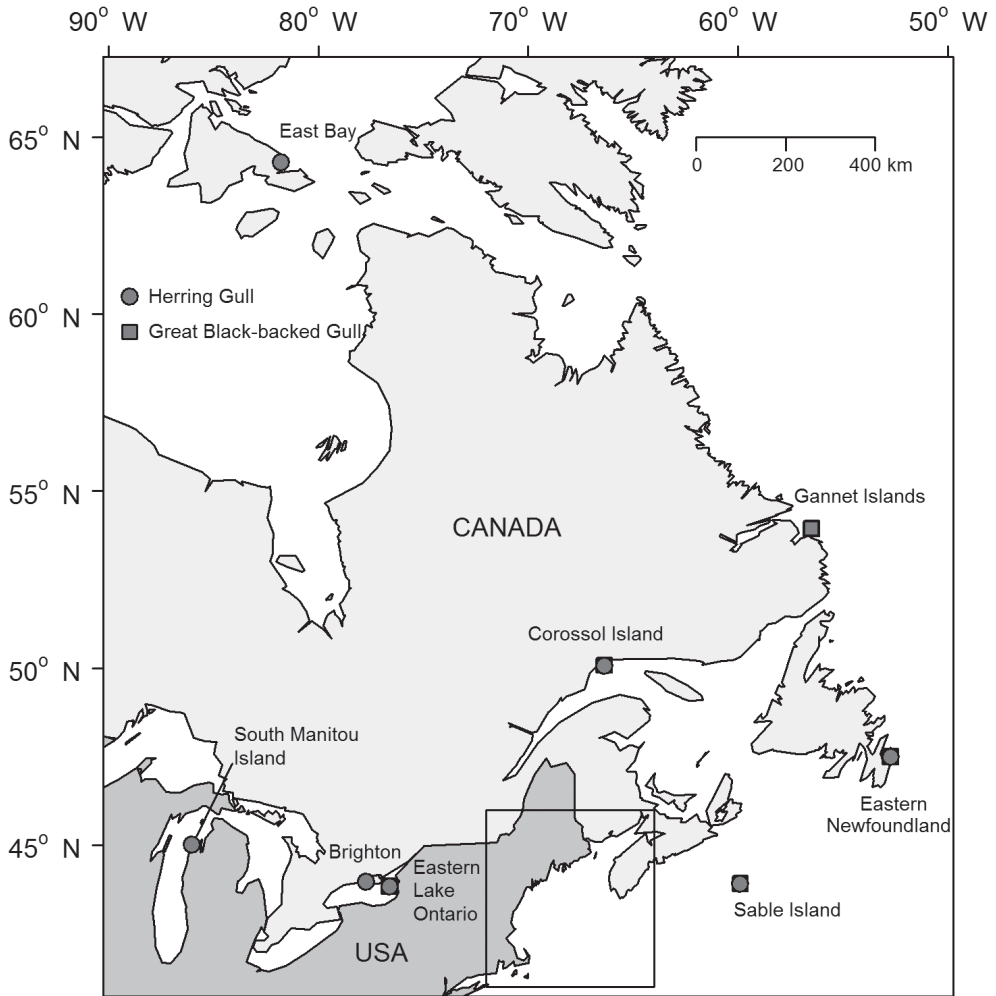


Figure 1. Sites where Herring and Great Black-backed gulls have been measured in eastern North America.

gonads. Measurements were taken of: 1) wing length, distance from the wrist to the tip of the wing with the wing flattened and flexed at the wrist; 2) head-bill, the maximum distance from the bill tip to the posterior extremity of the occipital process; 3) culmen, from the bill tip to the posterior extremity of the culmen; 4) bill depth at gonys, vertical height of the bill with the mandibles closed; 5) bill depth, minimum depth of the bill posterior to the gonys (Fox *et al.* 1981; Lavoie *et al.* 2012); 6) tarsus or tarsus bone, the length of the tarsometatarsus only; and 7) tarsus total, the total measurement from the two joints connecting the tarsometatarsus with the leg and the foot (Mawhinney and Diamond 1999).

Data Analysis

To allow us to include studies measuring bill depth instead of bill depth at gonys, we measured both on 47 Herring Gulls at Brier Island, 30 Great Black-backed Gulls in eastern Lake Ontario and 28 Great Black-backed Gulls at The Wolves Archipelago in New Brunswick. For Herring ($r = 0.91$) and Great Black-backed ($r = 0.87$) gulls, the correlation was high with a mean difference of 1.4 ± 0.5 (SD) mm for Herring Gulls and 2.0 ± 0.7 (SD) mm for Great Black-backed Gulls. We added these mean differences to each measurement of bill depth to convert that value to a bill depth at gonys measurement.

We only included birds showing definitive adult breeding plumage (4 years or older) in the analysis. To include previously published and summarized data, we created randomized data sets using the published mean, standard deviation and sample size to represent those sites. Data for Herring Gulls were quite rich, both in terms of the number of samples and the number of sites. Given the clustering of sample sites in the Great Lakes and the Gulf of Maine/Bay of Fundy (Fig. 1), we categorized sites as belonging to three different regions: Great Lakes, Gulf of Maine/Bay of Fundy (including Ram Island in Buzzards Bay) and a north-offshore region (Sable Island and all sites in Québec, Newfoundland and Nunavut) for the analysis of Herring Gulls. We used nested analysis of variance (ANOVA) (R Development Core Team 2015) to partition the variance in the four most commonly taken measurements (head-bill length, bill depth at gonys, tarsus and wing chord) to test for variation among regions, variation among sites within regions, and variation between sexes for Herring Gulls. The data for Great Black-backed Gulls were limited, so we simply used a standard analysis of variance (ANOVA) to test for variation in each measurement among sites and between sexes (R Development Core Team 2015). To understand how measurements covaried within individuals, we examined correlations among all measurements (except bill depth) for known-sex individuals with Pearson's correlation (R Development Core Team 2015). We did not include randomized data sets based on published summaries in this correlational analysis, as those correlations would be 0. For the same reason, we did not conduct multivariate ANOVAs on our data sets.

RESULTS

For the Herring Gull, differences were apparent among sites in known-sex birds, but clear patterns in the data were not apparent for the four most commonly taken measurements (Fig. 2). Head-bill length appeared to be smaller in the three Great Lakes samples (Fig. 2). ANOVA showed significant differences in the four most commonly taken measurements at all analysis levels, among regions, among sites within regions, and between sexes (Table 3). In terms of variance components, sex explained some of the variance in the data (39.5-62.0%); less variation was explained by differences among regions (5.2-16.7%) and even less among sites within regions (1.4-11.9%). Between a quarter and almost half of the variation remained unexplained (25.2-43.1%; Table 3).

We applied a previously created discriminant function based on Herring Gulls in eastern Newfoundland (Robertson *et al.* 2016) to other populations to determine its effectiveness at classifying sex over a wider geographic area. With an independent test data set from the same site, the function was 94.7% correct at classifying Herring Gulls to the correct sex. When applied to the data from East Bay, Nunavut, the success rate of correctly classifying birds to sex was similar at 95.7% ($n = 23$). For samples from the Gulf of Maine/Bay of Fundy, the function was also successful at classifying birds to sex: Brier Island, Nova Scotia (95.4%, $n = 22$); Bay of Fundy, New Brunswick (100%, $n = 32$); and Sable Island (100%, $n = 9$). The success rate of correctly classifying birds to sex from Lake Ontario was lower at 78.6% ($n = 14$).

In Herring Gulls, the correlations between measurements were somewhat lower than expected. Measurements of essentially the same body part did show high correlations, such as the two tarsus measures (tarsus and total tarsus), bill depth and bill depth at gonys, and to a lesser degree head-bill length and culmen length (Table 4). Even though both measure aspects of the head, bill-depth at gonys and head-bill length were not strongly correlated, and tarsus and wing showed only weak correlations with each

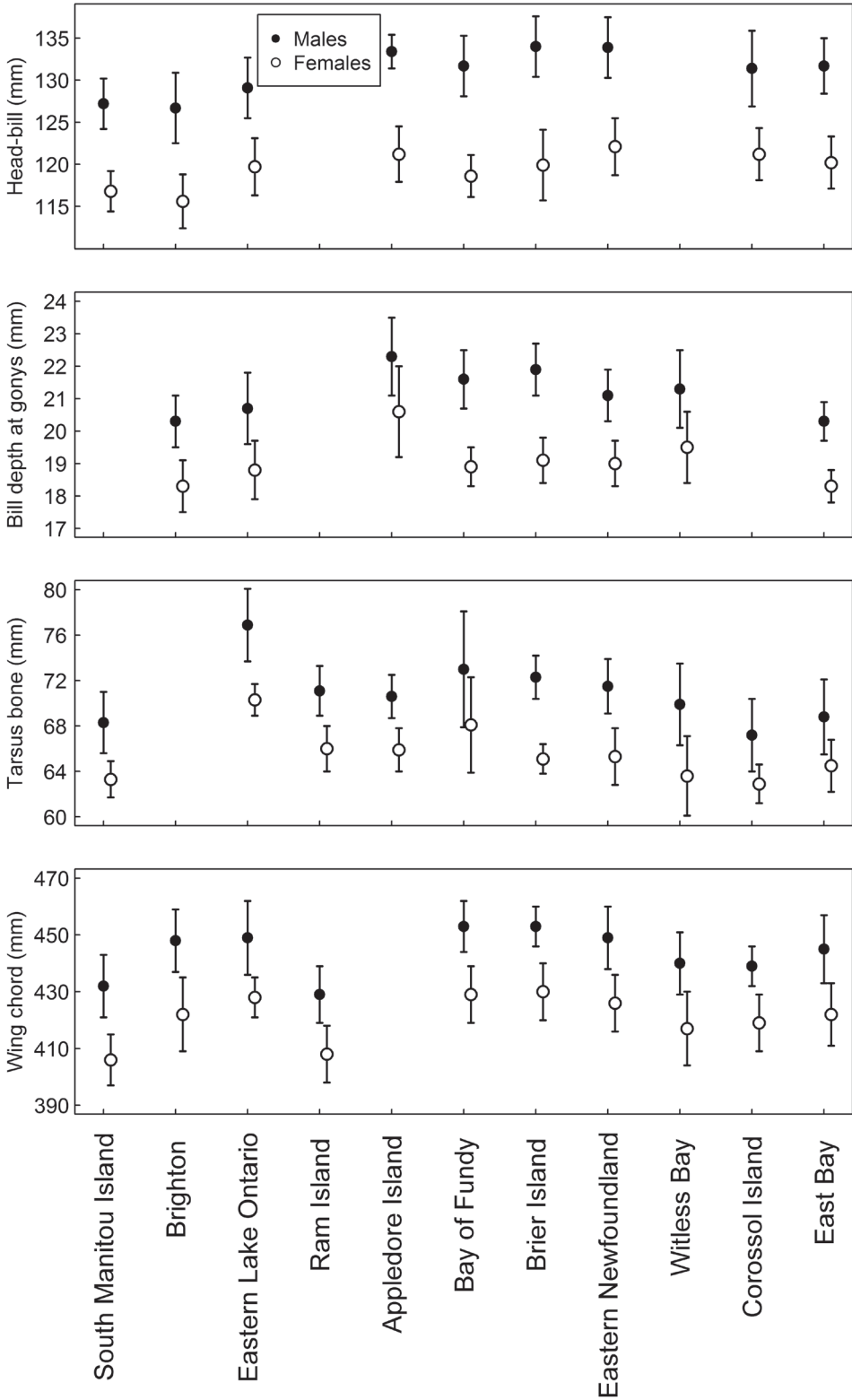


Figure 2. Measurements of Herring Gulls from 11 sites across eastern North America. Error bars represent ± 1 SD. Head-bill is the maximum distance from the bill tip to the posterior extremity of the occipital process.

Table 3. Proportion of variance explained in four measurements of adult breeding Herring and Great Black-backed gulls collected across eastern North America. For Herring Gulls, regions are Great Lakes, Gulf of Maine/ Bay of Fundy and offshore-north.

	Head-bill	Bill Depth at Gonys	Tarsus	Wing Chord
Herring Gulls				
Among regions	11.6% $F_{2,754} = 175.0$ $P < 0.001$	16.7% $F_{2,693} = 188.6$ $P < 0.001$	5.2% $F_{2,1012} = 60.9$ $P < 0.001$	11.8% $F_{2,1071} = 171.1$ $P < 0.001$
Among sites, within regions	1.4% $F_{8,754} = 5.1$ $P < 0.001$	3.6% $F_{6,693} = 13.5$ $P < 0.001$	7.9% $F_{9,1012} = 20.6$ $P < 0.001$	11.9% $F_{8,1071} = 43.1$ $P < 0.001$
Among sexes	62.0% $F_{1,754} = 1864$ $P < 0.001$	49.0% $F_{1,693} = 1105$ $P < 0.001$	43.8% $F_{1,1012} = 1029$ $P < 0.001$	39.5% $F_{1,1071} = 1148$ $P < 0.001$
Within sites and sexes (error)	25.2%	30.7%	43.1%	36.8%
Great Black-backed Gulls				
Among sites	4.7% $F_{4,253} = 13.2$ $P < 0.001$	3.6% $F_{3,247} = 6.3$ $P < 0.001$	0.4% $F_{3,242} = 0.55$ $P = 0.65$	4.1% $F_{4,264} = 5.2$ $P < 0.001$
Among sexes	73.4% $F_{1,253} = 845.7$ $P < 0.001$	50.0% $F_{1,247} = 265.8$ $P < 0.001$	42.9% $F_{1,242} = 183.4$ $P < 0.001$	44.9% $F_{1,264} = 232.1$ $P < 0.001$
Within sites and sexes (error)	22.0%	46.5%	56.7%	51.1%

other and the measurements associated with the head and bill.

For the Great Black-backed Gull, data from known-sex birds were limited (Table 2), with the published work from New Brunswick providing the most comprehensive data set (Mawhinney and Diamond 1999). Most

of the variation among the four commonly taken measurements was explained by sexual differences (42.9-73.4%) or remained unexplained (22.0-56.7%); site explained little variation (0.4-4.7%; Table 3).

Using Mawhinney and Diamond's (1999) published discriminant function based on

Table 4. Correlations (*r*) among measurements of known-sex adult Herring and Great Black-backed gulls across eastern North America. Males are below, to the left of the main diagonal and in bold and females are above and to the right. A correlation between tarsus and total tarsus could not be calculated for Great Black-backed Gulls due to low sample size ($n = 2$).

	Head-bill	Bill Depth at Gonys	Culmen Length	Tarsus	Total Tarsus	Wing Chord
Herring Gull						
Head-bill		0.24	0.55	0.34	0.49	0.18
Bill depth at gonys	0.32		0.30	0.18	0.28	0.23
Culmen length	0.65	0.28		-0.02	0.76	0.10
Tarsus	0.28	0.12	0.08		0.83	0.26
Total tarsus	0.38	0.22	0.60	0.93		0.27
Wing chord	0.19	0.16	0.22	0.34	0.28	
Great Black-backed Gull						
Head-bill		0.44	0.06	0.18	0.04	0.48
Bill depth at gonys	0.36		-0.02	-0.11	-0.41	0.12
Culmen length	0.40	0.39		-0.38	0.55	0.25
Tarsus	0.47	-0.06	0.03		—	0.19
Total tarsus	0.56	0.15	0.39	—		0.23
Wing chord	0.12	0.05	0.10	0.33	0.14	

head-bill length and bill depth at gonys for Great Black-backed Gulls, we successfully classified sex in 100% ($n = 28$) adults collected earlier (1989) in the same region. We also successfully classified 95.6% ($n = 23$) Great Black-backed Gulls from Lake Ontario to sex. Similarly, the function successfully classified 90.9% ($n = 11$) gulls breeding on Sable Island to sex, and correctly classified the four known-sex Great Black-backed Gulls from Newfoundland.

Correlations among measurements produced a wide range of coefficients for Great Black-backed Gulls, including some negative correlations (Table 4). Even measures related to the head and bill were only weakly correlated ($r = -0.02$ to 0.44).

DISCUSSION

We found significant differences in all measurements at local and regional scales for Herring and Great Black-backed gulls. However, in terms of the proportion of variance explained, regional and local differences explained relatively little variation. Most of the variation in measurements was due to sex differences and the natural variance seen within local populations. There was some evidence that Herring Gull individuals in the Great Lakes may have smaller head-bill lengths, but other measurements such as wing and tarsus did not show obvious differences with birds in other parts of eastern North America. For Great Black-backed Gulls, there was no clear pattern of morphometric variation across eastern North America, and a discriminant function to sex birds created with birds from New Brunswick performed well on gulls from Lake Ontario.

Previous work using discriminant functions to discriminate Laridae according to sex have emphasized the importance of using locally collected data (Shugart 1977; Fox *et al.* 1981; Evans *et al.* 1995), and have led to high (> 90%) successful classification rates (Threlfall and Jewer 1978; Coulson *et al.* 1983; Mawhinney and Diamond 1999; Galarza *et al.* 2008). Our results show that there are differences within and among regions, con-

sistent with the caution expressed by these previous researchers. However, our ability to successfully use a function created with Herring Gulls breeding in Newfoundland at a number of study sites in Atlantic and Arctic Canada, and that the published function for Great Black-backed Gulls (Mawhinney and Diamond 1999) was useful at all sites examined, suggests these site differences, even though statistically significant, can be relatively small. A locally derived discriminant function will usually have a better ability to correctly classify individuals to sex, especially as some of the variation among sites is likely attributable to variation in technique among researchers (Arnqvist and Mårtensson 1998). However, the Great Black-backed Gull discriminant function developed in New Brunswick had a 100% success rate of classifying an independent sample from the same region, which suggests the function is robust to inter-individual differences in measurement technique. Future discriminant function analysis could use Bayesian approaches. By treating previously published discriminant functions as priors, a Bayesian approach provides a formal quantitative approach to allow the functions to be updated with more recently collected data. The relatively weak correlations among various measurements within individuals of the same sex, even for measurements of essentially the same part of the body (e.g., the head), suggests that in addition to considerable body size differences among individuals within sexes, there is also considerable variation in body shape among adult breeding gulls. Additionally, measurement error may weaken or alter correlations (Perktaş and Gosler 2010). Given these weak correlations, discriminant functions including a number of measurements are likely to provide greater accuracy.

At 78%, the correct classification rate was lower for Great Lakes breeding Herring Gulls, again indicating these birds may have different morphologies than populations to the east and may be reproductively isolated (Weseloh 1984). In addition to possible morphometric differences, the coloration of the tips of the outer primaries were less white in Herring Gulls at Niagara Falls compared to

birds in Newfoundland (Jonsson and Mactavish 2001), and birds at Niagara Falls appeared to be smaller, although these were mostly winter samples so breeding origins are not known. Similarly, Adriaens and Mactavish (2004) noted that differences among the wing tip patterns range across North America, with darker wing tips in populations to the west.

Early migration studies performed by Gross (1940), using band recovery data, indicate Herring Gulls migrate from breeding locations in the Great Lakes south to the Gulf of Mexico, while birds breeding on Kent Island, New Brunswick, mainly winter along the USA eastern seaboard similar to birds breeding in Newfoundland (Threlfall 1978). Within the Great Lakes, there are differences as well, with birds originating in the western Great Lakes moving to the eastern Great Lakes, while birds originating in the eastern Great Lakes were more likely to move to the USA eastern seaboard (Moore 1976). Unlike the younger cohorts, adult Herring Gulls in the Great Lakes remain in the region for the non-breeding season (Weseloh 1984), suggesting this population may be somewhat isolated from other populations. Genetic evidence also indicates differences between Great Lakes and Atlantic coast populations. Based on mitochondrial DNA sequencing of cytochrome b and nuclear mini-satellite variation, there appears to be genetic mixing within the Great Lakes, but some evidence of genetic isolation from the Atlantic Canada population (Yauk and Quinn 1999; Chen *et al.* 2001). These results are consistent with the suggestion that Herring Gulls in North America, which are not closely related to the European Herring Gulls, evolved from a radiation to the east from northeast Russia and across the Bering Sea to North America (Liebers-Helbig *et al.* 2010).

In contrast to Herring Gulls, no differences were apparent in Great Black-backed Gull populations. Current evidence suggests that Great Black-backed Gulls evolved in a northeastern Atlantic refugium, and have only recently colonized North America, probably during the last glacial retreat (Liebers-Helbig *et al.* 2010). Dwight (1925)

noted that this species was monotypic across its entire range, including Europe, and recent banding data show that young Great Black-backed Gulls from North America visit Europe (Wille *et al.* 2011), possibly facilitating current gene flow across the Atlantic. The population in North America also underwent a recent population reduction, and subsequent range expansion to the south along the USA Atlantic coast (1920s) and west to the Great Lakes (1950s) would have further homogenized the population (Krug 1956; Drury 1973; Good 1998).

There was relatively little variation in the morphology of Herring Gulls and Great Black-backed Gulls in eastern North America. The one exception was an indication that Herring Gulls on the Great Lakes may be different. These observations are generally consistent with known movements of Herring and Great Black-backed gull populations and recent colonization events. Local and regionally scaled genetic studies using modern methods (next generation sequencing), paired with studies using recent developments in lightweight high-resolution telemetry, will allow us to develop a better understanding of the current population structure, as well as breeding and non-breeding range affinities, of Herring and Great Black-backed gulls in eastern North America.

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