MIGRATION AND DISPERSAL IN GREAT LAKES RING-BILLED AND HERRING GULLS

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Abstract.—Band-recovery data for Ring-billed (Larus delawarensis) and Herring (L. argentatus) Gulls were analyzed to determine the origins of gulls breeding within the Great Lakes region, the extent of lake and colony fidelity, and the winter and breeding season distributions of gulls of various age classes. Most Great Lakes Ring-billed Gulls wintered along the Gulf Coast, especially in Florida. Most Herring Gulls wintered along Lakes Erie, Ontario, and Michigan, although first-winter birds were more widely distributed and were recovered at greater distances than older birds. Movement into or out of the Great Lakes region by gulls of breeding age was minimal. However, movement among colonies and lakes was much more extensive; lakes and colonies do not define distinct populations. Gulls banded as chicks tended to return as adults to the lake, but not necessarily to the colony, where they where banded. Gulls banded as breeding adults were more likely to return in subsequent breeding seasons to the colony at which they had been banded than were chicks recovered as breeding adults. Gulls are probably not as colony-tenacious as previously believed, and natal dispersal plays a significant role in establishing or maintaining colonies. Management plans for Great Lakes Ring-billed and Herring Gull colonies should consider the effects of inter-lake and inter-colony dispersal.

MIGRACIÓN Y DISPERSIÓN DE *LARUS DELAWARENSIS* Y *L. ARGENTATUS* EN LOS GRANDES LAGOS

Sinopsis.-Se analizaron los datos de recuperación de anillas de Larus delawarensis y L. argentatus para determinar el origen de las aves reproduciéndose dentro de la región de los Grandes Lagos, la extención de la fidelidad al lago y a la colonia, y las distribución en temporadas invernales y reproductivas de aves de varias clases de edades. La mayoría de los individuos de Larus delawarensis de los lagos invernaron a lo largo de la costa del Golfo, especialmente en la Florida. La mayoría de los individuos de Larus argentatus invernaron a lo largo de los lagos Erie, Ontario y Michigan, aunque aves de un año estaban más ampliamente distribuídas y se recuperaron a mayores distancias que aves más viejas. El movimiento hacia o desde la región de los Grandes Lagos por aves de edad reproductiva fué mínima. Sin embargo, el movimiento entre colonias y lagos fué mucho más extenso; los lagos y las colonias no definen poblaciones distintas. Aves anilladas como pichones tienden a volver como adultos al lago aunque no necesariamente a la colonia donde fueron anilladas. Aves anilladas como adultos reproduciéndose retornaron más comúnmente a la colonia en que se anillaron en temporadas subsiguientes que los pichones recobrados como adultos reproductivos. Estas aves probablemente no son tán intensamente colonialistas como se creía previamente, y la dispersión natal juega un rol significativo en establecer o mantener las colonias. Planes de manejo para colonias de ambas especies en los Grandes Lagos deberían considerar los efectos de las dispersiones entre lagos y entre colonias.

In the last several decades, Ring-billed Gulls (*Larus delawarensis*) and Herring Gulls (*L. argentatus*) have shown dramatic increases in both

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numbers of colonies and numbers of nests in the Great Lakes region (Blokpoel and Tessier 1991, Scharf et al. 1994). Increased reproductive success associated with protection from persecution and the ability to exploit new food sources (landfills, introduced fish species) and new habitats (urbanized areas, dredge disposal islands) have contributed to these population increases (Belant 1993, Belant et al. 1993, Ludwig 1974, Patton and Hanners 1984). Unfortunately, burgeoning gull populations have resulted in a variety of conflicts with humans (Blokpoel and Tessier 1986) and other wildlife (Burness and Morris 1992, Nettleship 1972, Pierotti 1983). Therefore, an understanding of population dynamics and seasonal distributions of these migratory species is necessary for developing management plans to resolve these conflicts.

The role of dispersal in these population expansions, however, has not been adequately investigated. Gulls are generally considered to show a high degree of fidelity to their natal colony (Paynter 1947, Tinbergen 1960), but these observations are usually biased because colonies other than the colony of interest are seldom surveyed for marked individuals. Consequently, little information is available on the origins of gulls breeding in the Great Lakes.

I used band-recovery data to address: (1) the extent of emigration and immigration of Ring-billed and Herring Gulls into and out of the Great Lakes region, (2) the timing of migration of Great Lakes gulls, (3) winter distribution of different age classes of Great Lakes gulls, and (4) the extent of inter-lake and inter-colony movements of gulls within the Great Lakes region during the breeding season.

METHODS

Records for all Ring-billed and Herring Gulls banded in North America and recovered before 1994 were obtained from the U.S. Fish and Wildlife Service, Office of Migratory Bird Management, Laurel, Maryland. Records were excluded if the recovery site was not in North, Central, or South America, if the exact date or location of banding or recovery was uncertain, or if the "How Obtained" code was 50, 56, 96, or 98 (i.e., the exact date or location of recovery was not known). Those records with a "How Obtained" code of 16 (scientific collection) were also excluded, as these did not represent randomly obtained individuals. Only gulls banded as chicks (age code 4) or gulls banded as adults (age code 7 or 8 for Ring-billed Gulls, age code 8 for Herring Gulls) during the breeding season (May-July) (Ryder 1993) were used. This latter group was assumed to consist of adults breeding when banded. Gulls were assumed to hatch on 1 June, and became 1 year old the following May (during their second summer). Ring-billed Gulls were considered adults when 2 years old (third summer) and Herring Gulls when 3 years old (fourth summer). Yearlings were defined as <1 year old.

I defined the Great Lakes region as that area bounded by 75° and 93° W longitude and 41° and 50° N latitude following Weseloh (1984). Recoveries of gulls banded within this area were used to determine breeding

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and wintering areas and migration patterns. I also determined movements of potential breeding adults into or out of the Great Lakes using chicks banded within this area that were recovered during subsequent breeding seasons as adults.

To determine dispersal and movements of gulls among the five lakes, I defined each lake as series of contiguous 1° blocks. For gulls associated with each lake, distance to recovery site and distribution of age classes during winter (December–February) (Ryder 1993) and the breeding season were determined. For analyses of winter recoveries, only gulls banded as chicks were used. I identified North American wintering areas as New England (ME, VT, NH, MA, RI, CT, NY), Chesapeake Bay (NJ, DE, MD, DC, VA), Southeast (NC, SC, GA), Gulf Coast (FL, AL, MS, LA, TX), and Other. For analyses of breeding season recoveries, only gulls recovered ≥ 1 year after banding were used. Because the data did not satisfy the assumptions necessary for parametric analyses, recovery distances were analyzed using the Kruskal-Wallis χ^2 approximation in the NPAR1WAY Procedure (SAS Inst. 1988), with Dunn's multiple comparison tests to determine which means differed (Zar 1984). I used χ^2 tests to determine differences between proportions when necessary (Zar 1984).

RESULTS

Movement into or out of the Great Lakes.—Of 2427 Ring-billed Gulls banded as chicks in the Great Lakes region and recovered as adults during subsequent breeding seasons, 2375 (97.9%) were recovered within the Great Lakes. These recoveries accounted for 98.6% of the 2409 Ringbilled Gull chicks recovered as adults in the Great Lakes. Of 900 Herring Gulls banded as chicks in the Great Lakes region and recovered as adults during subsequent breeding seasons, 891 (99.0%) were recovered within the Great Lakes. These recoveries accounted for 99.6% of the 895 Herring Gull chicks recovered as adults in the Great Lakes.

Annual cycle.—A total of 12,550 Ring-billed Gulls (55% recovered as yearlings, 11% as subadults, and 34% as adults) and 8404 Herring Gulls (63% recovered as yearlings, 16% as subadults, and 22% as adults) banded as chicks in the Great Lakes region was recovered through 1993.

Seasonal distribution of recoveries and distance of recoveries from banding colony were similar among the three age classes of Ring-billed Gulls (Fig. 1). Northward migration of subadult Ring-billed Gulls began in April, one month after adults. During the breeding season, subadult Ring-billed Gulls were recovered an average of \geq 380 km from the banding colony, compared to \leq 161 km for adults. Migration of Great Lakes Herring Gulls was not as marked as Ring-billed Gulls. The mean distance from the banding colony for chicks recovered as adults peaked at 901 km during January. Recovery distance for subadult Herring Gulls remained relatively constant throughout the year, ranging from 316–745 km. Firstyear Herring Gulls showed the most distinct migration of any of the three age classes, with southward migration beginning in November and northward migration beginning in March.



FIGURE 1. Monthly mean distances from banding colony of Great Lakes Ring-billed and Herring Gulls banded as chicks. Number of recoveries/month for Ring-billed and Herring Gulls, respectively, were January 452, 159; February 339, 99; March 396, 151; April 323, 366; May 1284, 499; June 1010, 781; July 2454, 1258; August 3418, 2168; September 1394, 1327; October 854, 956; November 486, 523; December 501, 308.

Winter recoveries.—A total of 1235 Ring-billed Gulls banded as chicks was recovered during winter (799 first-winter, 184 second-winter, and 252 \geq third-winter); 547 Herring Gulls banded as chicks were recovered during winter (371 first-winter, 106 second- or third-winter, and 70 \geq fourth-winter).

In general, Great Lakes Ring-billed Gulls wintered farther from their banding colony than did Herring Gulls (Table 1). Mean distance to recovery site for Ring-billed Gulls was highest for those banded on Lakes Superior and Michigan. Overall, first-winter Ring-billed Gulls were recovered at a greater mean distance (1563 km) than second-winter (1419 km) or \geq third-winter (1265 km) gulls. Mean distance to recovery site for Herring Gulls varied widely among the 5 lakes. First-winter Herring Gulls were recovered at a greater mean distance (1037 km) than the other age classes (\leq 680 km).

The majority of winter recoveries of Great Lakes Ring-billed Gulls were from the Gulf Coast states (Table 2), with 54% from Florida alone. Most Great Lakes Herring Gulls wintered in the Great Lakes (Table 2).

A higher proportion ($\chi^2 = 31.87$, df = 1, P < 0.01) of first-winter Ringbilled Gulls were recovered in the Gulf Coast states than were \geq secondwinter birds (Table 3). More ($\chi^2 = 19.51$, df = 1, P < 0.01) \geq secondwinter Herring Gulls wintered in the Great Lakes than first-winter gulls (Table 3).

Breeding season recoveries.—Mean distance from banding colony to recovery site for both species decreased with age. Gulls banded as adults were recovered closer to the banding colony than were gulls banded as chicks (Table 4).

The proportion of Ring-billed Gull chicks returning as adults to the lake where banded ranged from 16% to 79% (Table 5). In comparison, between 27% and 70% of the subadults returned to the lake where banded. More adults than subadults returned to Lakes Huron, Michigan, Superior, and Ontario, but more subadults than adults returned to Lake Erie (Table 5). Overall, more Ring-billed Gulls returned as adults to the lake where banded than as subadults. The proportion of Herring Gull chicks returning as adults to the lake where banded ranged from 64% to 84%, compared to a range of 20% to 61% for subadults. Equal proportions of adults and subadults returned to Lake Superior. For each of the remaining four lakes, the proportion of chicks returning as adults was higher than as subadults (Table 5). Overall, more Herring Gulls returned as adults to the lake where banded than as subadults (Table 5).

Most gulls (>75%) banded as breeding adults and recovered during subsequent breeding seasons were recovered ≤ 100 km from the banding colony (Fig. 2). For gulls banded as chicks, more than 55% of those recovered as adults were recovered ≤ 100 km from the banding colony; more than 60% of those recovered as subadults were recovered >100 km from the banding colony.

					Mean dist	Mean distance (km)			
	Acre at			Lake where banded	ded			All lakes	
Species	recovery	Erie	Huron	Michigan	Ontario	Superior	u	${ar{X}}^a$	SD
Ring-	0.5	1175	1653	1749	1407	1939	664	1563A	649
billed	1.5	1020	1483	1649	1327	1565	184	1419B	547
Gull	≥2.5	1352	1317	1378	1107	1829	252	1265C	599
Herring	0.5	775	1062	1046	147	1193	371	1037A	1499
Gull	1.5 - 2.5	*	595	521	122**	209	106	570B	564
	≥3.5	39	892	370	*	514	70	680B	1304

TABLE 1. Mean distances at which Ring-billed and Herring Gulls banded as chicks in the Great Lakes were recovered from their banding colony during winter (December-February).

J. Field Ornithol. Spring 1996

Species		La	ke where band	led	
Recovery region	Erie	Huron	Michigan	Ontario	Superior
Ring-billed Gull					
Lake Erie	8	3	1	1	0
Lake Huron	0	<1	0	<1	0
Lake Michigan	0	1	1	0	0
Lake Ontario	6	2	1	7	0
Lake Superior	0	0	0	0	0
New England	2	<1	1	3	0
Chesapeake Bay	9	8	12	12	15
Southeast	14	19	12	22	25
Gulf Coast	58	63	64	50	55
Other North America	2	2	7	3	5
Caribbean/South					
Central America	2	<1	1	1	0
Total recoveries	64	663	100	388	20
Herring Gull					
Lake Erie	44	22	12	13	8
Lake Huron	6	10	5	8	5
Lake Michigan	0	4	36	13	35
Lake Ontario	6	27	8	63	8
Lake Superior	0	<1	<1	0	8
New England	0	3	<1	13	0
Chesapeake Bay	11	3	<1	0	3
Southeast	0	3	4	0	3
Gulf Coast	22	12	13	0	15
Other North America	6	10	16	Ō	13
Caribbean/South					
Central America	6	4	3	0	3
Total recoveries	18	268	213	8	40

TABLE 2.	Distribution of winter recoveries (% of recoveries) of Great Lakes Ring-billed and
Herri	ing Gulls banded as chicks.

DISCUSSION

The number of nesting gulls in the Great Lakes, as well as the number of colonies, has increased substantially in the last two decades (Blokpoel and Tessier 1991, Scharf et al. 1994). Because band recovery data indicated minimal immigration of both Ring-billed and Herring Gulls into the Great Lakes during the breeding season, most of this growth was due to internal factors. Emigration was also minimal, indicating that this is essentially a closed system for both species (see also Weseloh 1984).

However, within the Great Lakes, gull movements among colonies appear to be substantial. Natal colony fidelity has been estimated to be about 40% for North American and European gulls (Blokpoel and Courtney 1982, Chabrzyk and Coulson 1976, Ludwig 1963, Parsons and Duncan 1978). Based on the band recovery data, at least 35–45%, and probably more, of gulls hatched in the Great Lakes do not nest at their natal colony.

		% of reco	overies	
	Ring-bi	lled Gull	Herrin	$ \begin{array}{r} 76 \\ 21 \\ 9 \\ 25 \\ 20 \\ 2 \\ 2 \\ 1 \\ 2 \\ 6 \\ \end{array} $
Recovery region	0.5 yr	≥1.5 yr	0.5 yr	≥1.5 yr
All Great Lakes	6	10	57	76
Lake Erie	2	3	16	21
Lake Huron	<1	<1	7	9
Lake Michigan	<1	<1	16	25
Lake Ontario	3	5	17	20
Lake Superior	0	0	<1	2
New England	<1	3	2	2
Chesapeake Bay	6	18	3	1
Southeast	21	17	4	2
Gulf Coast	65	48	17	6
Other North America ^a	1	5	13	11
Caribbean/South/Central America ^b	<1	<1	5	1
Total recoveries	799	436	371	176

TABLE 3.	Distribution of winter recoveries (% of recoveries) of two age classes of Ring-billed
and	Herring Gulls banded as chicks in the Great Lakes.

^a Ring-billed Gull: Tennessee (8 recoveries), West Virginia (6), 11 states/provinces with ≤ 4 recoveries each; Herring Gull: Wisconsin (12), Tennessee, West Virginia (8 each), Ohio (6), Illinois (5), 11 states/provinces with ≤ 4 recoveries each.

^b Ring-billed Gull: Mexico (2 recoveries), 5 countries with 1 recovery each; Herring Gull: Mexico (9), Cuba (3), Bermuda (2), 6 countries with 1 recovery each.

Gulls banded as adults (and assumed to be breeding) were recovered in subsequent breeding seasons closer to their banding colony than were gulls banded as chicks and recovered as adults. About 1.3 times more gulls banded as adults were recovered ≤ 100 km from the banding colony than were chicks recovered as adults. Thus, adults of both species are more likely to return to a colony at which they have previously attempted nesting than to the colony at which they hatched, as has been found in Black-legged Kittiwakes (Coulson and Neve de Mevergnies 1992).

In recent years, the Great Lakes Ring-billed Gull population has continued to increase, whereas the Herring Gull population has remained relatively stable (Blokpoel and Tessier 1991, Chudzik et al. 1994), possibly because of a more varied diet and higher reproductive rate in Ring-billed Gulls. However, the role of dispersal in these population changes has been overlooked. Ring-billed Gulls appear less likely than Herring Gulls to return to their natal colony, as indicated by the longer mean recovery distances during the breeding season and lower percentage recovered ≤ 100 km of the banding colony. In certain mixed-species colonies, Ring-billed Gulls fledged more chicks than Herring Gulls (Chudzik et al. 1994) and nested in higher densities (C. P. Dwyer, unpub. data); thus their higher dispersal distances may be related to higher nest densities and fewer available nest sites at existing colonies. Furthermore, Ring-billed Gull colonies in the Great Lakes are frequently short-lived (Ludwig 1974), possibly due to changing water levels and plant colonization. High dispersal distances

Ring-billed and Herring G	ulls banded in the Great Lakes were recovered from their banding colony during subsequent	
	lled and Herri	

						Mean di	Mean distance (km)			
	Age at	Aore at		Lak	Lake where banded	ded			All lakes	
Species	banding	recovery	Erie	Huron	Michigan	Ontario	Superior	u	\bar{x}^a	SD
Ring-billed Gull	Chick	-	465	573	471	671	166	548	548A	620
	Chick	2	237	165	171	237	171	438	176B	233
	Chick	e)	101	140	163	138	60	595	141BC	229
	Chick	4	75	142	119	142	102	552	134BC	172
	Chick	5	131	121	110	135	321	329	126BC	178
	Chick	9≷	161	117	145	199	39	499	131C	174
	Adult	۱۷ گا	*	118	92	25	*	135	93D	155
Herring Gull	Chick	1	521	451	550	265	319	396	467A	722
	Chick	61	200	276	255	77	330	146	264A	342
	Chick	80	29	187	143	61	244	212	170AB	258
	Chick	4	12	162	110	14	140	189	130BC	180
	Chick	ъ	33	122	98	æ	60	155	98CD	174
	Chick	9≷	28	120	89	96	56	339	96CD	158
	Adult	≥4	137	43	54	13	*	51	41D	84
* Indicates () recoveries	ueries									

^{*} Indicates 0 recoveries. * Means with the same letter are not different (Ring-billed Gull: $\chi^2 = 365.97$, df = 6, P < 0.01; Herring Gull: $\chi^2 = 161.14$, df = 6, P < 0.01).

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Dispersal of Great Lakes Gulls

	Lake where	% recovered a	t natal lake (n)	
Species	banded	Subadult	Adult	χ^{2a}
Ring-billed Gull	Erie	53 (36)	16 (68)	7.73**
0	Huron	60 (586)	75 (1239)	41.39**
	Michigan	41 (127)	63 (302)	36.63**
	Ontario	27 (184)	66 (328)	5.24*
	Superior	70 (53)	79 (38)	4.42*
	All Lakes	51 (986)	70 (1975)	94.86**
Herring Gull	Erie	48 (25)	84 (31)	15.36**
0	Huron	48 (256)	73 (384)	42.62**
	Michigan	61 (186)	84 (360)	17.00**
	Ontario	20 (10)	64 (22)	74.95**
	Superior	55 (65)	71 (98)	0.95
	All Lakes	53 (542)	78 (895)	93.50**

 TABLE 5.
 Natal lake fidelity of Great Lakes Ring-billed and Herring Gulls banded as chicks and recovered during subsequent breeding seasons.

^a Comparison of proportion of adults returning to natal lake vs. proportion of subadults returning to natal lake. * = P < 0.05, ** = P < 0.01. All comparisons with 1 df.

may be a response to nesting in rapidly changing or unstable habitats (McNicholl 1975). Identification of the mechanism(s) by which gulls choose to nest at an established colony (natal or otherwise), or to establish a new colony, would help determine the relationships between dispersal, habitat availability, and population size.

Great Lakes Ring-billed Gulls, regardless of the lake of origin, frequently winter along the Gulf Coast, with the major concentration in Florida (Southern 1974, this study). Great Lakes Herring Gulls, particularly \geq second-winter individuals, generally winter along Lakes Erie, Michigan, and Ontario (Moore 1976, this study). Thus, individuals breeding on any one lake interact with conspecifics from the other lakes during winter. This mixing on the wintering grounds, combined with extensive inter-colony and inter-lake movements during the breeding season, supports earlier conclusions that lakes and colonies do not define distinct populations (Ludwig 1974). Rather, for each species, the entire Great Lakes region is comprised of one large population (Weseloh 1984).

Ring-billed and Herring Gulls were irregular or rare winter residents in the Great Lakes during the early part of the 20th century (Bent 1921), but have become increasingly abundant since the 1950s (Dolbeer and Bernhardt 1986). Based on band-recovery data, most \geq second-winter Herring Gulls now winter along the lower Great Lakes. This recent change in their winter distribution is possibly due to the ability to exploit anthropogenic food sources (Belant et al. 1995) and the abundant forage fish (Dolbeer and Bernhardt 1986) available along the shores of the lower Great Lakes.

Local management plans for widespread nuisance species are useful for solving specific problems, but are seldom long-term solutions. For example, Dolbeer et al. (1993) found that management actions directed



FIGURE 2. Distance of recovery from banding colony for Ring-billed and Herring Gulls banded in the Great Lakes, and recovered during subsequent breeding seasons. Solid bars indicate gulls banded as chicks and recovered as subadults; hollow bars indicate gulls banded as chicks and recovered as adults; stippled bars indicate gulls banded as breeding adults.

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towards a single colony of Laughing Gulls (*Larus atricilla*) reduced the risk of aircraft/gull collisions, but were ineffective at reducing the target colony size, due to immigration from surrounding colonies. Gull colonies generally are not distinct populations, due to considerable movement of individuals among colonies (Ludwig 1974, this study). Dispersal plays a significant role in maintaining or increasing existing colonies, and in establishing new colonies. Therefore management plans for Great Lakes gulls, such as modification of waste management practices or habitat modification, should consider the regional influence of emigration and immigration.

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