RECENT CHANGES IN THE RING-BILLED GULL POPULATION AND BIOLOGY IN THE LAURENTIAN GREAT LAKES

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SINCE World War II the Ring-billed Gull (*Larus delawarensis*) population of the Laurentian Great Lakes has been characterized by a massive increase in the number of nesting birds in all of the lakes. Published data on Ring-billed Gulls (Ludwig 1943) and Herring Gulls (*Larus argentatus*) (Paynter 1949; Hickey 1952; Ludwig 1962, 1966) were unable to indicate logical reasons for the enormous increases recorded; neither did published life tables suggest that such increases were possible in a *Larus* gull. Faced with the fact of an enormously increased gull population on the Great Lakes, it seemed clear that either parameters of population dynamics were incorrectly estimated, or the banding data on which the estimated mortality rates were based were inaccurate. Several workers (Hickey 1952, Hickey et al. 1966, Ludwig and Tomoff 1966) suggested that band loss could account for the unacceptable results. The incredibly rapid increase of this population that occurred between 1960 and 1965 simply could not fit even the most optimistically constructed model of population growth for the species based on field estimates of fledging rates and a reduced adult death rate (Ludwig 1966). Exploratory trapping data from 1965 showed that some birds raised in colonies of Lakes Erie and Ontario were recruited into Lake Huron colonies. This suggested that Great Lakes Ring-billed Gulls of breeding age may move from colony to colony and from lake to lake in some numbers.

Ecologists have long recognized that most animal populations tend to remain relatively stable, fluctuating about a mean number from year to year in undisturbed ecosystems. Beeton (1965, 1966) cited an example of disruption of the Great Lakes in the virtual disappearance of the *Hexagenia* sp. mayflies from Lake Erie and the appearance of huge populations of formerly rare tubificid worms, nematodes, and fingernail clams; these effects he attributed to pollution. Thus ecosystem disruption in the Great Lakes is characterized by irruptions of formerly rare or absent species as well as extinctions or decimations of formerly abundant species.

The recent explosive spread of the sea lamprey (*Petromyzon marinus*) and alewife (*Alosa pseudoharengus*) with the nearly simultaneous decline of the commercially valuable fish species underscores the fragile quality of these ecosystems (Miller 1956, Smith 1963). The species

 The Auk 91: 575–594. July 1974

diversity in these communities has always been low, largely owing to the recency of deglaciation and geological structure that prevented invasions of waterborne organisms. Possibly a more complex freshwater system would have evolved if these ecosystems had been permitted to develop naturally for enough time. The intrusion of European man into North America also increased the rate of introductions into these lakes. The formerly effective barriers to invasion by waterborne species were torn down, admitting Atlantic anadromous species. Others were introduced directly. These introductions, together with massive changes in these lakes' watersheds, have decimated much of the original fauna. Ever-increasing additions of industrial and municipal waste continue to disrupt the modern Great Lakes and to change the trophic structure on which Ring-billed Gulls depend.

Lakes in recently deglaciated areas tend to follow similar paths in succeeding from the oligotrophic condition to the filled-in bog. The oligotrophic lake with nutrient-poor watersheds becomes eutrophic and highly productive through gradual accumulation of nutrients that provide impetus to plant growth and the filling of lake basins. The Laurentian Great Lakes were deglaciated between 14,000 and 10,000 years ago, and attained modern water levels only about 2,000 to 2,500 years ago. When North America was discovered by European man each of the Great Lakes was in some stage of oligotrophy, developing no oxygen debts in summer, and supporting large populations of fishes, particularly coregonids. Eutrophication has been greatly accelerated by the growth of a huge technically oriented human population around the lakes, which has regarded running water as a vehicle for waste disposal. Beeton (1965, 1966) discussed the related problems of accelerated aging and pollution of the Great Lakes, noting that among them only Lake Superior has not had significant rises in nutrients and dissolved solids in the last half century. Harlow (1966) found that the human population surrounding the western Lake Erie basin contributed more than half of the nutrients to that grossly polluted and highly productive ecosystem. Most of the nutrient contribution was in the form of sewage. At the apex of food chains associated with these lakes are Ring-billed Gulls and other secondary predators. Adult Ring-bills are present on the Great Lakes during most of the year.

METHODS AND STUDY AREAS

Because banders have visited the Ring-billed Gull colonies in the Thunder Bay region of northwestern Lake Huron annually since 1932, colonies there were chosen for study trapping sites from 1965 through 1967. Ring-bill colonies in the Beaver Islands of Northern Lake Michigan were visited in 1965 in conjunction with a pesticide study of Herring

Gulls (Ludwig and Tomoff 1966), and were visited again in 1966 and 1967. The Charity Islands Reef colony in Saginaw Bay of Lake Huron was added in 1966 in conjunction with a study of the distribution of type E botulism in Ring-billed Gulls (Ludwig and Bromley 1967). Because data from these Lake Huron-Lake Michigan colonies proved that some birds were recruited from colonies of Lake Erie, Lake Ontario, and the St. Lawrence River, the 1967 research strategy included trapping in those areas to estimate the amount of exchange of gulls between colonies and lakes and to study colony social organization. The Mohawk Island colony in eastern Lake Erie near Port Maitland, Ontario, and two colonies in Lake Ontario (Little Gallo Island near Henderson Harbor, New York, and the Bluffs colony near Brighton, Ontario, within Presqu'ile Provincial Park) were added to the research design in 1967. The Chantry Island colony near Southampton, Ontario, in eastern Lake Huron between the Lake Huron and Lake Ontario colonies, was also included in 1967. Adult gulls were trapped in each of these colonies in 1967.

Large numbers of adult birds banded as chicks had to be captured to obtain an adequate sample of birds of known age and origin. I used a ¾-inch mesh cannon net, Dill cannons, and electrically fired 110-grain black powder cartridges for catching the gulls on their nests (Figure 1). Adult birds are most easily trapped in colonies when incubating or before the chicks are old enough to run. Inevitably some eggs and nests are destroyed during these operations, but clutches destroyed in the nesting season by careless stepping or falling projectiles are usually replaced. Adult birds are surprisingly little disturbed by cannon netting in their colonies early in the season. Unlike Southern (1967b), I found little evidence that cannon netting caused birds to abandon their colonies.

Seabirds are particularly mobile creatures. In the Great Lakes at least three species of terns, the Common (*Sterna hirundo*), Black (*Chilidonias niger*), and Caspian (*Hydroprogne caspia*) have established reproducing populations. Herring, Ring-billed, and Great Black-backed Gulls (*Larus marinus*) are also established. The Little Gull (*Larus minutus*) is establishing itself in Lake Ontario near Toronto and in Lake St. Clair. Great Black-backed Gulls nest at scattered locations in Lake Ontario and seem poised at the edge of the Great Lakes for an invasion. Bent (1921) recorded Herring Gulls, Common Terns, Black Terns, and Caspian Terns breeding on islands in the Great Lakes well back into the 19th century.

Bent (1921) thought, as did Barrows (1912), that the Ring-billed Gull disappeared as a breeding species from Great Lakes islands early in the 20th century. Whether or not it disappeared completely is not certain. If it was established between 1906 and 1925 it must have bred in small numbers in remote parts of Lake Huron (Georgian Bay). Lud-

Figure 1. A cannon-netted sample of Ring-billed Gulls, Chantry Island, 19 May 1967.

wig (1943) recorded the species' return to prominence in northern Lake Michigan and Lake Huron after 1926.

By 1941 at least 26 islands had supported colonies at least once during the previous 15 years. Several islands, including Scarecrow, St. Martin's Shoal, Halfmoon, and South Limestone in Lake Huron, apparently have supported colonies continuously since 1932 (see Ludwig 1962 for list of colonies and their locations). By 1940 colonies in Lakes Huron and Michigan supported a population approximating 20,000 breeding pairs, and this portion of the Great Lakes population apparently remained nearly stable at this level until about 1960 (Ludwig 1966). The reasons for this moderate reinvasion of the Great Lakes are obscured by the past and by a lack of study; furthermore the reasons for population stability between 1940 and 1960 are not apparent. Some shifting of gulls between islands during this period in Lakes Huron and Michigan took place, but no irruption of gulls occurred comparable to the incredible increase that came between 1960 and 1967.

In 1960 the Ring-billed Gull population of Lakes Huron and Michigan was estimated to be 27,000 nesting pairs (Ludwig 1962). By 1967 this

TABLE 1
ESTIMATES OF NESTING PAIRS IN RING-BILLED GULL COLONIES OF LAKES HURON AND MICHIGAN 1960–67

Year	Estimated number of pairs	Percent growth over previous year	Trend of the water level[1]
1960	27,000	—	Very high
1961	33,000	22.2	High, lowering
1962	49,000	48.5	Average
1963	61,000	29.5	Low
1964	79,000	29.5	Lowest ever recorded
1965	99,000	25.3	Lowest ever recorded
1966	108,000	9.0	Rise to average
1967	141,000[2]	10.2	High, rising

[1] Data from monthly water level reports, U.S. Corps of Engineers, Detroit, Michigan.
[2] At least 22,000 nests were inundated in this nesting season; percent growth is estimated on the basis of 119,000 nests.

part of the Great Lakes population numbered at least 119,000 nesting pairs (Table 1). The years of maximum growth (1962–65) were years of low water levels and the estimate of 119,000 nesting pairs in 1967 was unquestionably low because rising water levels in May and June 1967 washed out at least 22,000 nests. This certainly discouraged many adult birds from nesting. The Ring-billed Gull population of Lakes Huron and Michigan probably approached 300,000 adult individuals plus 60,000 to 80,000 nonbreeding immatures scattered throughout eastern North America (see Ludwig 1943, for maps of the juvenile and immature ranges). The Huron-Michigan segment of the Great Lakes population was roughly four times larger in 1967 than it was in 1960. Through the period 1968–73 the lake levels have continued to rise. Many marginal sites that supported thousands of nests from 1964–66 were totally covered and have been completely destroyed (Figure 2).

I have discussed part of this unprecedented population expansion twice (Ludwig 1962, 1966) noting that an earlier poorly documented expansion of the Lake Ontario-Upper St. Lawrence River Ring-billed Gull population had taken place (Belknap 1961). The first Ring-bill colony in Lake Ontario was established in 1927. More colonies appeared in the Thousand Islands region of the St. Lawrence River in the 1930s. The population extended to available islands in the New York portion of Lake Ontario in the 1940s (Kutz 1946). The Little Gallo Island colony near Henderson Harbor, New York, was first recorded in 1945 with approximately 1,000 pairs of gulls "mostly Ring-bills" (Kutz 1946) covering less than an acre. Through regular expansion, this colony grew to occupy more than 30 acres of this 43-acre island by 1961 (Belknap MS, 1961). The breeding population in 1967 was estimated at 82,000 pairs covering 39 acres. About 1963 this colony approached saturation of the available nesting space (Table 2).

Figure 2. Flooding of a Ring-billed Gull colony by a natural rise of Lake Huron's water level, Chantry Island, 19 May 1967. On this date the water level was about 1 foot above the low water datum reference mark (576.8 feet above sea level). In June 1973 the water level was approximately 3.1 feet higher than when this photograph was made.

In 1953 another colony, the Bluffs, was established at Presqu'ile Provincial Park near Brighton, Ontario, on a 13-acre island. By 1964 banders reported that the island was virtually covered with Ring-bill nests except for a small sector used by Herring Gulls, Common Terns, and an occasional pair of Black-backed Gulls or Caspian Terns. In 1967 an estimated 23,000 pairs nested over 11 acres. In addition Ring-

TABLE 2
RING-BILLED GULL NESTING AT LITTLE GALLO ISLAND, NEW YORK, 1945–67

Year	Estimated number of nesting pairs	Area the colony covered in acres	Source of data
1945	1,000	1	Kutz (1946)
1948	—	8	Belknap (1961, pers. comm.)
1949	—	10	"
1950	17,000	12	"
1953	34,000	15	"
1955	45,000	20	"
1961	60,000	30+	"
1963	75,000	35	"
1966	75–85,000	38	Ludwig (1968)
1967	82,000	38–39	"

TABLE 3
TOTAL ESTIMATED POPULATION OF RING-BILLED GULLS IN THE GREAT LAKES REGION

Area	Number of breeding pairs 1930	1945	1967	Total estimated number of individuals in 1967 adults + 25%
St. Lawrence R.	None	2,000	10,000	25,000
Lake Ontario	2,000	15,000	165,000	412,500
Lake Erie	None	60	6,300	15,750
Lake Huron	1,000	20,000	119,000	297,500
Lake Michigan	None	None?	33,300	83,250
Lake Superior	None	None	1,400	3,500
				837,500

bills nest regularly on nine other islands in Lake Ontario, and on sites in the St. Lawrence River at least as far northeast as Montreal. The world's fair "Expo '67" was built on an island that Ring-bills used from 1961 to 1963 (L. Grey in litt.). At Toronto the gulls nest inside the main harbor on artificial islands made from dredgings. At least one colony exists in Lake Erie at Mohawk Island. It began in 1945 with 60 nests (Holroyd 1965) and grew to 6,300 nests (the saturation point) in 1964. In summary, the Ring-billed Gull population of Lakes Erie and Ontario began steady population expansion in the early 1930s, growing from an initial population of probably no more than a few thousand breeding pairs to the immense population attained between 1962 and 1964 when the island sites available for nesting were covered with nesting pairs. In 1967 the population was at least at 130,000 and perhaps as many as 200,000 breeding pairs. Including immature birds, this portion of the Great Lakes Ring-billed Gull population probably consisted of 350,000 to 500,000 individuals in 1967.

So far as is known, only a single colony of 1,400 breeding pairs existed in 1967 in Lake Superior, at Round Island near Sault Ste. Marie, Michigan (Table 3).

Like most seabirds the Ring-billed Gull is colonial, but its colonies are unusual for several reasons. Seabirds usually nest in stable colonies at the same site for many seasons, but the history of the Ring-billed Gull on the Great Lakes is one of repeated movements from island to island. Of the 26 islands that Ludwig (1943) listed as supporting colonies from 1926 to 1941, only four had Ring-bills nesting on them in 1967. During this 10-year study 23 new islands were taken over as colony sites and 11 were abandoned. Three islands had birds nesting for a season or more and then were abandoned for one or more seasons; later the gulls reestablished colonies at these same sites. Such repeated movement be-

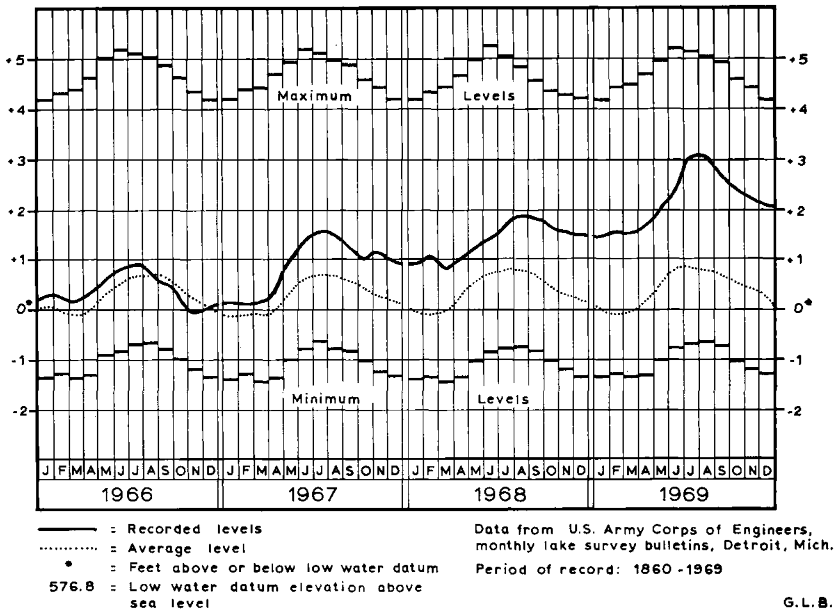

Figure 3. Average monthly water levels of Lake Michigan-Huron from 1966 through 1969.

tween islands is well-documented (Ludwig 1962) but remains unexplained.

Southern (1967a) and Ludwig (1962) each noted that low water levels were involved in the recent population increase in Lakes Huron and Michigan. In June 1960 the waters stood at a very high level, some 31 inches above the low water datum (L.W.D., 576.8′) level for these lakes. (The term low water datum refers to the average of 10-year low water levels for these waters. It is used by The National Oceanic and Atmospheric Administration to provide a reference point for navigation.) In June 1964 the level dropped to the all-time mean monthly low of 11 inches below L.W.D. through 1965 in Lakes Huron and Michigan, but in 1966 rose 10–11 inches to the L.W.D., 13 inches above this reference mark in 1967, and was 24–52 inches above L.W.D. in the summers of 1969 through 1973. Commonly the water levels of each of the Great Lakes cycle annually from a summer high, usually reached in July, to a winter low in February. This variation is usually about 1 foot in terms of mean monthly levels (see Figure 3). Superimposed on the annual cycle is a longer irregular fluctuation that may take from 5 to 11 years to complete. In the period of record (1860 to 1971) the difference between the highest and lowest June water levels was 6 feet, the long-term variation in June mean monthly level was 63 inches during my 13-year study.

The lowering water after 1960 exposed new territory and allowed "new" islands to emerge from the lake that, devoid of vegetation, made ideal nesting sites for Ring-billed Gulls. The bushy plants that compete with gulls for ground surface had been drowned and scoured away. Two related factors prevent gull colonies remaining stable. First, rising water forces out resident birds; then with the lowering of the water level and reestablishment of a colony, the succession of land plants that tolerate gull feces begins. As the bushes grow, particularly willows (*Salix* sp.) and red osier (*Cornus stolonifera*), plant succession enters a stage in which the plants start to crowd out the gulls. During this study, plant succession in colony sites that had been inundated in 1960 proceeded to the bush stage approximately five to six seasons after lowering water levels left them dry. Many of these bushes were again destroyed by the rising waters after 1966. Although this kind of oscillation has not been followed for more than one cycle, it must proceed after each major water cycle in Lakes Huron and Michigan, and perhaps also in the other Great Lakes according to their water cycles. Belknap (MS) commented that rising water had an adverse effect on Ring-billed Gull colonies in Lake Ontario.

The small, low-lying islands in the Great Lakes are regularly covered with water in each long cycle. For example the Charity Islands Reef in Saginaw Bay, Lake Huron was completely awash in 1960 and was first colonized in 1961. By 1963 almost 2 acres of land had emerged from the lake and grasses, cinquefoil (*Potentilla* sp.), and thistles (*Cirsium* sp.) invaded. In 1965 at the low point of the water cycle, 2.5 acres had emerged from the lake; willows, nettles (*Urtica* sp.), and some red osier were well-established. In 1966 the willows were about 8 feet tall and the water level had risen 11 inches above the previous year but not enough to destroy nests in the colony: 1.56 acres supported 7,500 nests, a density of 4,700 nests per acre. In 1967 a sharp 20-inch rise in water level destroyed most of the colony, leaving only 400 nests remaining above water through the nesting season. In 1971 this site was completely awash again. Established plants were scoured away by winter ice movements in 1970. When the water level drops again another cycle of plant succession will begin. Such instability of the Great Lakes water levels and island sites, upon which the Ring-billed Gull depends, prevents birds from nesting at the same sites long enough to allow extensive organization by individuals or for year-to-year stability of the nest sites to develop.

The density of nests depends on the substrate, the vegetation, and the stage of succession of the resident plants. Completely open colonies such as the Little Gallo and Bluffs Island colonies in Lake Ontario have few rocks, bushes, and sticks lying about to break up the islands' surfaces; such islands are like the rough of a golf course. Under these conditions each nesting pair defends as much as a square yard of surface. The average nesting density of these colonies in 1967 was 2,208 nests per acre. However at Mohawk Island where the substrate was broken slabs of limestone, the birds defended territories only so far as they could reach. The uneven ground, though naked of plant cover, was sufficient to permit the gulls to divide the available ground into smaller units and the density was estimated at 4,670 nests per acre in 1967. The highest nest density ever seen was in 1967 at Chantry Island where very broken ground of fist-size glacial rocks, driftwood, and some short plants combined to create a habitat that held an estimated 5,170 nests per acre. The distance between nests in very dense colonies may be as little as 11 inches center to center when the nests are offset slightly from each other. This occurs only on broken substrate.

In 1952 and 1953 Emlen (1956) found that a Lake Michigan colony fledged 0.67 chicks per pair when its population was stable. Ludwig (1966) found an average fledging rate of 1.74 chicks per pair from 1963 through 1965 in selected colonies of Lakes Huron and Michigan when their populations were growing rapidly. Various investigators have found fledging rates in Herring Gulls ranging from 0.31 to 1.47 chicks per pair depending on local conditions (Paynter 1949, Paludan 1951, Drost et al. 1961, Ludwig and Tomoff 1966).

The rates of reproductive success are not easily reconciled with death rates computed from banding data for gulls. Paynter (1966), Hickey et al. (1966), Keith (1966), and Ludwig (1966) all expressed the opinion that band loss had biased Herring Gull banding data. None of the Herring Gull life tables produced by earlier investigators could balance reproduction measured in the field with the death rates measured by banding except that by Paludan (1951); Paludan's attempt balanced only if the maximum rate of fledging measured in the field was used to balance the 15% annual death rate estimated for breeding birds. I found that loss of bands from Ring-billed Gulls of the Great Lakes population seriously distorted the life table by reducing the number of recoveries from 5 years after banding onward. Individual band loss raised the estimated death rate for breeding birds computed from recoveries from the real 13% annual loss to 50%. Calculation of the number of fledgings needed to keep the population stable using the uncorrected data provided an estimate of 1.78 chicks per pair of breeding gulls per year. These results are virtually identical to banding studies of Herring Gulls (reviewed by Paynter 1966). Correcting my raw data by subtracting estimated band loss showed only 0.63 chicks per

TABLE 4
RETURN TO NATAL COLONY AS A FUNCTION OF AGE IN RING-BILLED GULLS

Age in years	Number of gulls returning to natal colony	Number of gulls leaving the natal colony	Total number captured	Percent of age class returning to natal colony
2	44	37	81	54
3	106	128	234	45
4	58	122	180	32
5	41	72	113	36
6	28	44	72	39
7	5	15	20	25
8	1	6	7	14
9	1	4	5	20
10	0	1	1	0
11	0	2	2	0
12	0	0	1	0
13	0	1	1	0
14	0	1	1	0
TOTAL	284	433	717	

breeding pair per year needed for population stability. The corrected estimate agrees with Emlen's (1956) field estimate of 0.67 fledgings produced per pair, made in a Lake Michigan colony when this population was stable in 1952 and 1953. My study (Ludwig 1967) and that of Fordham (1967) show that band loss may seriously distort all banding data for long-lived seabirds.

Recruitment into various areas was estimated from banded gulls cannon netted or found dead in the nesting colonies. Cannon netting 8,916 adult gulls produced 608 recoveries of birds banded as chicks; 109 other banded adults were found dead in colonies. Of these 717 banded birds, 294 (41%) had returned to their natal colony to nest. Two-year-old gulls returned with the greatest frequency (54%). The data also suggest that roughly one-third of the 2-year-old birds in this population attempt to nest. These data (Table 4) clearly support the hypothesis that Ring-billed Gulls tend to return to their natal colony to breed for the first time. Although some gulls move great distances, most show a strong tendency to return to the natal lake to nest in a nearby colony; 86.5% of the banded gulls caught or found dead had nested in the same lake where raised. The birds nesting in each lake unit tend to maintain the colonies in their lake, although recruitment between these geographical units takes place regularly, and individuals do move from one end of the Great Lakes to the other (Table 5). Therefore these gulls are from a single immense Great Lakes population. These data definitely refute Southern's (1967a) suggestion that each colony is an independent population. Apparently there was a

TABLE 5
RETURN OF RING-BILLED GULLS TO COLONIES IN THE NATAL LAKE[1]

Lake where banded as a chick	Lake where captured as a nesting adult				
	Lake Ontario	Lake Erie	Lake Huron	Lake Michigan	Total number
Lake Ontario	29	0	17	0	46
Lake Erie	1	3	3	0	7
Lake Huron	11	0	501	33	545
Lake Michigan	2	0	15	7	24
TOTAL NUMBER	43	3	536	40	622

[1] For a more detailed casting of this table see Ludwig 1968.

considerable movement of individuals northwestward from Lakes Ontario and Erie into the colonies of Lakes Huron and Michigan, as the banding data gave a ratio of 16 birds moving into the northwestward colonies for each moving into the southeastern colonies. As a much higher proportion of the birds raised in Lakes Huron and Michigan was banded than in Lakes Ontario and Erie, probably the ratio of moving birds was actually closer to 50:1. A large portion of the population increase in Lakes Huron and Michigan recorded from 1960 to 1967 was unquestionably recruited from the colonies of Lakes Erie and Ontario.

Birds banded as breeding adults also were found to move between colonies. Of the 154 banded adults recaptured when nesting a second or third time, 46 (30%) had moved to a new colony. Three birds nested in three different colonies in 3 successive years. Southern (1967b) believed he could account for the moving adult birds he found as birds disturbed during homing trials and other experimental manipulations, but as only 8 of the 46 birds that moved in this study were banded as adults and manipulated in Southern's homing trials, this hypothesis is untenable. Rising water levels, plant succession at colony sites, and human disturbance explain this phenomenon adequately. As an example, 870 adult Ring-bills were banded at Charity Islands' Reef in 1966. In 1967 the rising water washed out all but 400 nests by July. A single cast of the cannon net in May 1967 caught 104 adult birds, 21 of which were banded there as adults in May 1966. Eight birds banded there in 1966 as adults were retaken nesting in three other colonies of Lake Huron in 1967 (Spoil's Island, Bird Island, Rogers City Calcite).

Southern banded about 900 adults at Rogers City between 1963 and 1966; we recaptured 23 of these in this study at three other colonies of Lake Huron and at two colonies of Lake Michigan. The Rogers City colony is too high to be inundated and dry enough so that plant

TABLE 6

AGE DISTRIBUTION OF RING-BILLED GULLS CAUGHT IN EIGHT CASTS OF THE CANNON NET AT BIRD ISLAND 23–24 MAY 1967

Cast numbers[1]	Number caught	Number banded	Average age of banded birds	Number in immature plumage	Percent with immature plumage
1 + 6 + 7[2]	294	37	4.00	17	5.8%
3 + 4 + 5[3]	190	22	3.27	48	25.3%
2 + 8[4]	136	26	2.77	89	65.0%
TOTALS	620	85	3.54	154	96.1%

[1] Refer to Figure 4 for details.
[2] All casts over previously used high density nesting sites.
[3] All casts over previously used low density nesting sites.
[4] All casts over area never used until 1967.

succession proceeds slowly, but being part of the mainland, this colony is unusually accessible to humans. It is visited occasionally by mammalian predators, regularly by Calcite Company workers, as well as three teams of scientists interested in Ring-billed Gull biology. These disturbances may stimulate individuals to move to more isolated colonies.

Early in this study numbers of gulls with a subterminal black band in the tail were noted in growing and new colonies; these birds seemed to be most plentiful on the edges of colonies. Ring-billed Gulls vary greatly in the age at which they acquire fully adult plumage in which the head, body, wing linings, body feathers, and rectrices are white, the mantle and back feathers are gray, and the six outermost primaries each have a white spot (window) near their tips. Brownish or brown-edged coverts, lack of white spots in the primaries, a subterminal black band or spots in the rectrices, grayish wing linings, and black-tipped head feathers are all characteristics of gulls in immature plumage. Very few gulls attain the fully adult plumage at 24 months. Very rarely an individual may retain vestiges of immature plumage into its 5th year. As Ring-billed Gulls cannot be aged accurately by plumage criteria, only the capture of birds that were banded as chicks can be used to test the hypotheses that invasions of new sites are usually by young gulls nesting for the first time, and that these young gulls are largely confined to the edges of established colonies. In 1967 only the rapidly growing Bird Island colony was large enough and had enough banded birds to test these hypotheses.

The Bird Island colony started in 1963 with 600 nesting pairs, which increased to 10,200 pairs by 1966 when we visited it often during our study of botulism in gulls (Ludwig and Bromley 1967) and sketched the nest distribution. In 1967 rising water largely destroyed nesting

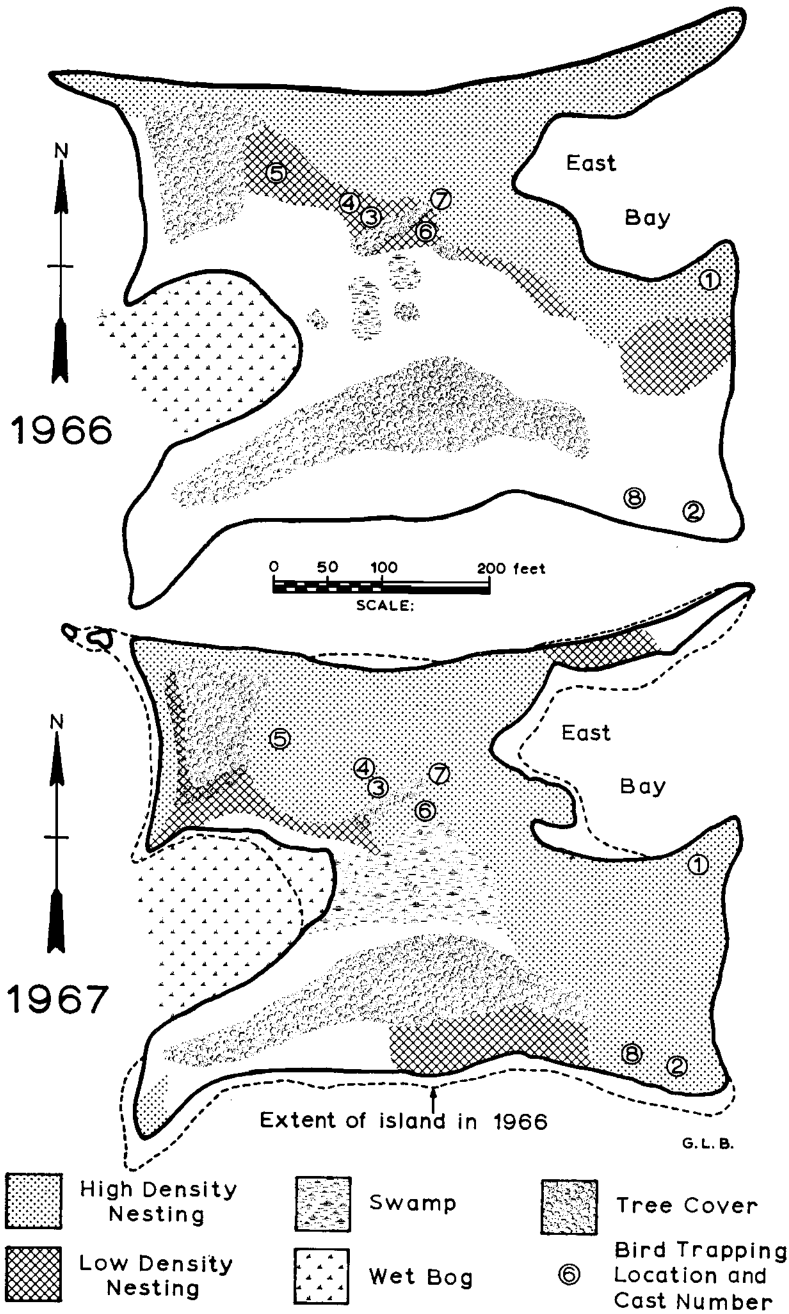

Figure 4. Ring-billed Gull nesting on Bird Island in 1966 and 1967.

on the northeast tip of the island, and expansion of the bogs in the islands' center forced the colony to move in a mass toward the southeast where its 13,200 nests filled up most of the available space (Figure 4).

Table 6, listing the results of eight casts of the cannon net, clearly shows the older birds concentrated near the center of the colony in territory that had been used for several seasons while the youngest birds were taken where nests were placed for the first time. Expansion of this colony was therefore largely carried out by the younger birds, many of them nesting for the first time (see Figure 4). These young gulls probably were unable to obtain a territory in competition with older established gulls and had to remain on the edge of the colony.

If gulls breeding for the first time do tend to enlarge old colonies and establish new ones, then the average age of birds nesting in a colony ought to reflect the length of time that the colony has been established or of stable size. Old colonies that have been saturated with nests for several seasons (those in Lakes Erie and Ontario, Chantry Island, Charity Islands' Reef, and Ile aux Galets) and that did not expand in 1967 ought to have older birds than unstable or new colonies. The banded birds in the five colonies trapped in 1967 that had not increased over their 1966 size averaged 4.77 years old. At Grass Island, where part of the colony was washed over and some new territory was occupied, the banded birds averaged 3.83 years old. The adults at two rapidly growing colonies at Bird and Spoils Islands averaged 3.49 years old. Each mean is significantly different from the others: The probability that the mean 4.77 is the same as the 3.83 mean is < 0.001 ($F_{2,297}$ is 23.16), while the probability that the means 3.83 and 3.49 are the same is < 0.05 ($F_{1,209}$ is 4.11). It is interesting to note that in 1967 not a single 2-year-old was then in a colony that had not expanded over its 1966 size; only the growing colonies had 2-year-old birds in the cannon net samples.

Most colonies of seabirds are relatively permanent and stable. Most Herring Gull colonies of Europe (Tinbergen 1960, Drost et al. 1961) have been permanent and stable through many seasons. The Ring-billed Gull population of the Great Lakes has been stable neither in size nor colony location. While many populations grow and disperse, such a rapid growth and dispersal among other Laridae is unknown. The exceptional growth rate certainly contributed to unstable colonies during the study period.

Discussion

Apparently this Ring-billed Gull population grew from a small number of gulls that reinvaded the Great Lakes ecosystems after 1925 and

TABLE 7
FISHES RECOVERED FROM RING-BILLED GULLS IN GREAT LAKES COLONIES, 1963-67

Species, number and % of sample	Lake Huron and Michigan	Lake Erie	Lake Ontario	Total all lakes
Alewives	527	7	110	644
Percent	71.4%	12%	33%	57.3%
American smelt	147	52	223	422
Percent	20.1%	87%	67%	37.6%
Yellow perch	5	0	0	5
Percent	0.8%	0	0	0.4%
Other species	51	1	0	52
Percent	7.7%	1%	0	4.7%

established themselves at scattered localities throughout the lakes (Ludwig 1943, Belknap MS). Their first notable successes were in Lakes Ontario and Erie, followed by expansion into Lakes Huron and Michigan with the population's rapid growth. The fledging rate of 1.74 I recorded (1966) in colonies of Lakes Huron and Michigan from 1963 to 1965 can now be judged as 2.75 times greater than needed to maintain a stable population. Unfortunately we have no data on fledging rates in colonies of Lakes Erie and Ontario. Considering the rate at which the species filled the island sites available and then expanded into the other Great Lakes, the fledging rate must have exceeded the 0.63 chicks per nesting pair needed for population stability.

The recent dependence of Ring-billed Gulls on alewives for food in Lakes Huron and Michigan is documented elsewhere (Ludwig 1966). The alewife successfully invaded the Great Lakes approximately in 1950 (Miller 1956) following the sea lamprey's decimation of the predacious fish in the upper lakes. Table 7 lists the fishes collected from Ring-billed Gulls in Great Lakes colonies from 1963 through 1967. Almost three-fourths of the fishes recovered in colonies of Lakes Huron and Michigan were alewives. The food data collected from Lakes Ontario and Erie colonies suggest that fish populations in those ecosystems are quite different from those in Lakes Huron and Michigan. The alewife first established itself as an anadromous species in Lake Ontario. It was prevented from further invasion of the Great Lakes prior to the opening of the Welland Canal, and possibly by the presence of large fish predators. Other wide-ranging effects on the fish fauna of Lake Michigan were discussed by Smith (1963); obviously this fauna is not stabilized and is still changing rapidly. One may speculate that the irruption of Ring-billed Gulls has followed that of the alewives to the northwestward as these fishes have extended their range.

Population dynamics of large *Larus* gulls have long been misunderstood, basically because our knowledge of mortality rates came from banding. The difficulty of working with the raw banding data has been pointed out by many workers (Paynter 1949, 1966; Poulding 1954). Until my study (Ludwig 1967) no reliable estimate of mortality rates was obtainable from banding data. Fordham (1967) suggested the method I used but lacked a complete recovery series for the Kelp Gulls (*Larus dominicanus*) he studied. Most investigators, realizing that banding data were biased by band loss, either ignored the estimates and guessed at the real rate (Vermeer 1963, Ludwig 1966), or used other means to derive crude estimates (Drost et al. 1961, Keith 1966). Kadlec and Drury (1968) made an independent estimate of adult survivorship in the marine Herring Gull population of eastern North America. They estimated an adult death rate of 8% in this population and confirmed Ludwig's (1966) and Keith's (1966) speculation that dynamics of the real Herring Gull population were very different from those suggested by banding techniques. Lack (1954) accepted the mortality estimates for large *Larus* gulls in the range of 30% per year adult mortality rate and incorporated the erroneous information into his discussions of adjustment of clutch size in birds. The consensus among those investigators who have examined gull banding data in detail is that the real death rate of adults in the large *Larus* species lies in the range of 8 to 13% annually. Clearly the Ring-billed Gull, with a shorter generation time than the other large *Larus* gulls (2.7 vs. 4.0 years), a low adult death rate, and a low requirement of fledgings to maintain population size, is capable of irruptive increase when the fledging rate rises even slightly over several years.

Lack (1954) believed that clutch size in birds is adjusted to food supply and stated his premise as follows: "It is considered that clutch size of each species has been adapted by natural selection to correspond with the largest number of young for which the parents can, on the average, provide enough food." If this were true for gulls, they should, on the average, be able to find sufficient food to raise three chicks. Lack's argument is invalid on two counts. First if gulls usually produced that many chicks, quite clearly they would "need" a death rate of 30% of more to balance their birth rate. Secondly several investigators found that mortality of chicks in colonies with stable populations was greatest immediately after hatching and that the usual cause of death was predation or scalping, not starvation (Paludan 1951, Drost et al. 1961). Chick numbers in marine colonies are commonly reduced to one shortly after the brood hatches; rarely has food shortage been implicated in this process.

It may be of significance that those *Larus* gulls with a large clutch size occur in Northern Hemisphere habitats where repeated Pleistocene glaciations alternately destroyed and remade gull habitats. The ability to reoccupy recently deglaciated gull habitat would depend on how many chicks could be fledged. A clutch size reduced to one does not permit the birds to fledge more than a chick each year and thus the larger clutch size in combination with the reduced death rate could be strongly selected for. Gulls need a long life span to survive when nesting habitats are capriciously destroyed. Suitable nesting sites in the Great Lakes at least are at best only temporary phenomena. In times of rapid change the *Larus* gull is an irruptive species. Such a reproductive strategy is not unlike that of some marine fishes where a single year class may dominate the commercial catch for many years owing to exceptionally high fry survival in a single season (Lack 1954).

The Ring-billed Gull, often referred to as a prairie species (Bent 1921), may be similarly adjusted to catastrophic conditions (Vermeer 1968). Small kettle-hole lakes are notably unstable. The water level in such lakes varies enormously and the lakes may inundate colony sites between seasons. The long life span and large clutch size prepare the species to be irruptive when a large amount of suitable habitat develops. Apparently the Great Lakes represent such a habitat with their suitable islands, a new food source in the form of alewives, and other factors that remain to be discovered.

Acknowledgments

Most of the information presented in this paper is drawn from my doctoral thesis. The assistance of committee chairman Nelson Hairston and committee members Robert Storer, Francis Evans, and William Farrand is gratefully asknowledged. C. S. Tomoff, D. D. Bromley, and A. A. Kives participated as field assistants, while the patience and dedication of Catherine E. Ludwig made the work possible. F. E. Ludwig provided technical support. Funds were provided by the American Museum of Natural History's Mae P. Smith and Frank M. Chapman Funds. Many banders, especially W. Nickel, I. Sturgis, F. Novy, A. Bunker, allowed the use of their data for the analysis. All of the above mentioned persons contributed significantly to this study.

Summary

The Ring-billed Gull population breeding in the Great Lakes remained fairly stable from 1940 to 1960, when it was estimated at 27,000 pairs. By 1967 the population had exploded to at least 141,000 pairs and extended its breeding grounds westward from Lakes Ontario, Erie, and Huron to Lakes Michigan and Superior.

This explosion was encouraged by lowering water levels in the early 1960s that greatly increased the amount of suitable breeding territory available and by the successful invasion of the lakes by alewives in 1950 and their subsequent rapid increase and spread.

Band loss greatly distorts the mortality figures in birds over 4 years of age, but the annual adult mortality rate is certainly lower than 13%. The species' long life span and large clutch size enable it to be irruptive when large amounts of food and suitable habitat become available. Annual fluctuations in Great Lakes water levels constantly alter the amounts of available nesting space and prevent birds establishing the year to year stability of and fidelity to breeding grounds manifested by maritime-nesting larids. Consequently considerable shifting and exchange of individuals occurs between colonies. New colonies are composed essentially of younger adults.

Literature Cited

Barrows, W. B. 1912. Michigan bird life. Michigan Agr. Coll., Spec. Bull. Dept. Zool. Physiol.

Beeton, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10: 240–254.

Beeton, A. M. 1966. Indices of Great Lakes eutrophication. Univ. Michigan, Great Lakes Res. Div. Publ. 15: 1–8.

Belknap, J. 1961. Little Gallo Island revisited. Kingbird 2: 90.

Bent, A. C. 1921. Life histories of North American gulls and terns. U.S. Natl. Mus. Bull. 113.

Drost, R., E. Focke, and G. Freytag. 1961. Entwicklung und aufbau einer population der Silbermowe, *Larus a. argentatus*. J. Ornithol. 4: 404–429.

Emlen, J. T., Jr. 1956. Juvenile mortality in a Ring-billed Gull colony. Wilson Bull. 68: 232–238.

Fordham, R. A. 1967. Durability of bands on Dominican Gulls. Notornis 14: 28–30.

Harlow, G. L. 1966. Major sources of nutrients for algal growth in western Lake Erie. Univ. Michigan, Great Lakes Res. Div. Publ. 15: 389–394.

Hickey, J. J. 1952. Survival studies of banded birds. U.S. Dept. Interior, Spec. Sci. Rept. Wildl. 15: 1–177.

Hickey, J. J., D. A. Keith, and F. B. Coon. 1966. An exploration of pesticides in a Lake Michigan ecosystem. J. Appl. Ecol. Suppl. 3: 141–154.

Holroyd, G. L. 1965. Ring-billed Gulls of a Lake Erie colony. Ontario Bird-Banding 2: 19–33.

Kadlec, J., and W. H. Drury. 1968. Structure of the New England Herring Gull population. Ecology 49: 645–676.

Keith, J. A. 1966. Reproduction in a DDT contaminated population of Herring Gulls. J. Appl. Ecol. Suppl. 3: 57–70.

Kutz, H. L. 1946. Breeding of the Ring-billed Gull in New York. Auk 63: 591.

Lack, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

Ludwig, F. E. 1943. Ring-billed Gulls of the Great Lakes. Wilson Bull. 55: 234–243.

Ludwig, J. P. 1962. A survey of the gull and tern populations of Lakes Huron, Michigan and Superior. Jack-Pine Warbler 40: 104–120.

LUDWIG, J. P. 1966. Herring and Ring-billed Gull populations of the Great Lakes 1960–1965. Univ. Michigan, Great Lakes Res. Div. Publ. 15: 80–89.

LUDWIG, J. P. 1967. Band loss—its effect on banding data and apparent survivorship in the Ring-billed Gull population of the Great Lakes. Bird-banding 38: 309–323.

LUDWIG, J. P. 1968. Dynamics of Ring-billed Gull and Caspian Tern populations of the Great Lakes. Unpublished Ph.D. dissertation, Ann Arbor, Univ. Michigan.

LUDWIG, J. P., AND D. D. BROMLEY. 1967. Observations on the 1966 mortalities of fishes and birds in the Saginaw Bay ecosystem. Final report on contract #14–17–004–279. Ann Arbor, Michigan, U.S. Bur. Comm. Fish.

LUDWIG, J. P., AND C. S. TOMOFF. 1966. Reproductive success and insecticide residues in Lake Michigan Herring Gulls. Jack-Pine Warbler 44:77–89.

MILLER, R. R. 1956. Origin and dispersal of the alewife (*Alosa pseudoharengus*) and the gizzard shad (*Dorosoma cepedianum*) in the Great Lakes. Trans. Amer. Fisheries Soc. 86: 97–111.

PALUDAN, K. 1951. Contributions to the breeding biology of *Larus argentatus* and *Larus fuscus*. Videns. Medd. Dansk Naturh. Foren. 114: 1–128.

PAYNTER, R. A. 1949. Clutch size and the egg and chick mortality of Kent Island Herring Gulls. Ecology 30: 146–166.

PAYNTER, R. A. 1966. A new attempt to construct life tables for Kent Island Herring Gulls. Bull. Mus. Comp. Zool. 133: 489–528.

POULDING, R. H. 1954. Loss of rings by marked Herring Gulls. Bird Study 1: 37–40.

SMITH, S. H. 1963. Status of the deep water cisco populations of Lake Michigan. Trans. Amer. Fisheries Soc. 93: 155–163.

SOUTHERN, W. E. 1967a. Colony selection, longevity, and Ring-billed Gull populations: preliminary discussion. Bird-Banding 38: 52–60.

SOUTHERN, W. E. 1967b. The role of environmental factors in Ring-billed and Herring Gull orientation. Unpublished Ph.D. dissertation, Ithaca, New York, Cornell Univ.

TINBERGEN, N. 1960. The Herring Gull's world, rev. ed. New York, Basic Books Inc.

VERMEER, K. 1963. The breeding ecology of the Glaucous-winged Gull (*Larus glaucescens*) on Mandarte Island B. C. Occ. Pap. Brit. Columbia Prov. Mus. 13.

VERMEER, K. 1968. Breeding biology of California and Ring-billed Gulls: a study of ecological adaptation to the inland habitat. Canadian Wildl. Serv. Rept. 12.

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