

# COLONY SELECTION AND COLONY SITE TENACITY IN RING-BILLED GULLS AT A STABLE COLONY

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**ABSTRACT.**—Long-term banding, wing-marker and retrapping data from one stable Great Lakes colony were used to establish whether or not Ring-billed Gulls exhibit a preference for colony sites at the time of first breeding or during subsequent years. About 13% of the adults captured were banded previously, of which 69% had returned to the natal colony. When calculated on the basis of banding year survivorship, the return rate ranged between 19 and 33%. Immigrants came primarily from colonies within a 64-km area. Of the 436 Ring-bills captured that had been banded as adults, 90% had returned to the colony of previous nesting. In addition, 60% of the wing-marked gulls nested for at least 2 years at Rogers City. The tendency to return to the natal colony is not well defined at this colony, but colony site tenacity after first breeding is well developed. Variability exists in data for less stable colonies, as birds are forced to move by high water levels or other environmental factors.—*Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115.* Accepted 25 November 1975.

SOME colonial larids select the natal colony as a site for first breeding (Harrington 1974). Thereafter they may return to this same breeding place year after year (Beer 1966). Colony fidelity or colony tenacity has been documented for several gulls, including the Herring Gull, *Larus argentatus* (Tinbergen 1961, Drost et al. 1961, Ludwig 1963); Silver Gull, *L. novaehollandiae* (Murray and Carrick 1964); Black-headed Gull, *L. ridibundus* (Svardson 1958, Beer 1961); Glaucous-winged Gull, *L. glaucescens* (Vermeer 1963); and Laughing Gull, *L. atricilla* (Stone 1937, Nobel and Wurm 1943, Bongiorno 1970). Occasional exceptions occur in species that use habitats subject to periodic destruction, such as the Black-billed Gull, *L. bulleri* (Soper 1959, Beer 1966), Franklin's Gull, *L. pipixcan* (Burger 1974a) and Brown-headed Gull, *L. maculipennis* (Burger 1974b). McNicholl (1975) recently reviewed the subject of larid site tenacity in relation to habitat.

Ludwig (1974) concluded that Ring-billed Gulls (*L. delawarensis*) nesting in the Laurentian Great Lakes attempt to return to the natal colony. In the same paper he referred to an absence of colony stability, which I have interpreted as including colony site tenacity, as resident birds are forced to move too often for site attachment by individuals to occur. Fluctuating water levels in the Great Lakes are the primary factors responsible for these moves. Ludwig (1974) depicted the history of Ring-billed Gulls on the Great Lakes as that of repeated movement of individuals from island to island. I find it difficult to accept Ludwig's implication that selection pressures have favored a return to the natal colony by Great Lakes Region Ring-bills when the environment he describes is so unstable that colony site tenacity is supposed to be absent in experienced breeders.

As some Great Lakes colony sites are less severely affected by high water, a dichotomous situation exists wherein some gulls have the option of returning to the same nesting location throughout their reproductive lives but others are periodically forced to move. A stable colony site, one where Ring-billed Gulls have nested annually for several decades, provides an opportunity to assess (a) the rate of return to a permanently available colony site, (b) the degree of colony site tenacity expressed by adults under these conditions, and (c) the rate of immigration and emigration. As competition for the remaining dry sites would be intensified during periods of high

water, the return rate of marked gulls at a stable colony site should be a reasonably stringent measure of the tendency for Ring-bills to develop colony site tenacity.

I have used band recoveries and wing-marker sightings accumulated over a 12-year period for a discussion of these topics for one of the most stable Great Lakes colonies. The data provide a baseline against which to compare similar information for new colonies, those subject to fluctuations in size, or those experiencing various types of disturbances.

#### STUDY AREA AND METHODS

The Calcite colony is located on a man-made peninsula near Rogers City, Presque Isle County, Michigan (Pettingill 1958) thereby making it unique in the Great Lakes Region. Gulls have consistently used the Calcite site for several decades, possibly since the mid-1930's (U.S. Steel Corp. employee's pers. comm.). Its stability results from the surface being about 2 m above the high water level and plant succession being retarded by a hard-packed limestone substrate. The periodically significant changes in Great Lakes water levels have little effect on the amount of annually available nesting space at Rogers City. Shoreline erosion caused by winter storms occasionally changes the peninsula's profile but repairs are made to severely damaged places by the property owners (U.S. Steel Corp.). The Calcite location is also unusual in that considerable space is available for expansion of the colony. In contrast, many islands in the lakes, particularly Huron and Michigan, are reduced periodically in size or eliminated completely during high lake levels (e.g. 1973 and 1974).

The late W. P. Nickell banded gull chicks at the Calcite colony from 1957 through 1970. I supplemented his effort between 1963 and 1970 and then expanded my banding program after 1970. Over 18 years Nickell and I banded 53,801 Ring-billed Gull chicks at this colony. Occasional visitors also banded a few chicks, thereby slightly enlarging the banded sample discussed herein. This long-term effort allows measuring the tendency of Ring-bills to return to a natal colony.

I sampled the breeding Ring-billed Gull population at the colony by cannon-netting (Southern 1972) on several days in May or June 1963 through 1974. Nets were fired at several locations to provide representative samples of gulls nesting in central and peripheral areas. Although netting sites were not identical each year, considerable overlap occurred because of restrictions imposed by colony size, shape, and changes in the pattern of equipment stored on the site by U.S. Steel. Most trapping was done after clutches were complete or within 10 days after hatching. This procedure provided some assurance that captured adults were actually nesting in the colony. Earlier in the season several hundred Ring-bills often are attracted to the colony, particularly peripheral areas, but most of these birds eventually depart. Inclusion of large numbers of these birds in a sample intended to represent adults breeding at Rogers City would result in an inaccurate measure of the tendency of adults to change colonies.

I cannon-netted 73 adults in 1963 for use in homing studies (Southern 1967a) and from 1964 through 1974 a minimum of 300 adults was captured annually. My firing regime was casual. To minimize disturbances that might cause desertions by adults (Southern 1972) I allowed sufficient time between firings to permit gulls to settle on nests, and seldom made more than five firings per day. These precautions were considered essential because I have found that even careful cannon-netting will cause some desertions, particularly during incubation, and I wanted to minimize this source of bias. Possible distortions in data caused by investigators or their techniques must be considered along with other perturbing and decimating factors rather than discounting their importances as Ludwig (1974) did.

All captured adults were checked for old bands. Unbanded Ring-bills were banded with standard USFWS bands. Those carrying old bands received an additional band on the opposite leg, thereby extending the time over which the data would be available. Worn bands were removed and the bird rebanded. These practices partly compensated for problems associated with band loss from wear (Ludwig 1967).

The number of adult Ring-billed Gulls banded as chicks at the Calcite colony and then recaptured there provided a measure of the tendency to return to the natal colony, whereas those banded in other colonies indicated the extent of immigration. Previously banded adults known to have died in the colony during the late incubation or early parental care stages of the nesting cycle were included in the sample; those found early in the cycle or in the vicinity of the colony were omitted because they may have been visiting and not breeding at the peninsula.

I (Southern 1971) wing-marked 1587 adult Ring-bills with orange tags between 1967 and 1972. Between 1969 and 1974 the 1339 tags I applied carried black numerals permitting individual recognition without

TABLE 1  
SUMMARY OF CAPTURE DATA FOR ROGERS CITY, 1963 TO 1974

Banding year	Total adults caught	Statistics for banded sample										Other colonies represented in sample No.
		Number w/bands		Proportion banded as chicks:				Proportion banded as adults:				
				At Rogers City		Other colonies		At Rogers City		Other colonies		
		Total	%	No.	%	No.	%	No.	%	No.	%	
1963	73	9	12.3	9	100.0	—	—	—	—	—	—	—
1964	390	31	7.9	17	77.3	5	22.7	9	100.0	—	—	2
1965	344	77	22.4	22	66.6	11	33.3	44	100.0	—	—	3
1966	309	93	30.1	42	85.7	7	14.3	44	100.0	—	—	2
1967	443	112	25.3	55	77.5	16	22.5	37	90.2	4	9.8	6
1968	314	75	23.9	23	62.2	14	37.8	31	81.6	7	18.4	2
1969	362	95	26.2	44	63.8	25	36.2	18	72.0	8	28.0	5
1970	459	99	21.6	44	62.0	27	38.0	18	64.3	10	35.7	6
1971	478	102	21.3	30	62.5	18	37.5	46	85.2	8	14.8	5
1972	455	123	27.0	49	71.0	20	29.0	50	92.6	4	7.4	5
1973	627	113	18.0	53	64.6	29	35.4	30	96.8	1	3.2	6
1974	623	152	24.4	55	64.7	30	35.3	65	97.0	2	3.0	5
Total	4877	1081	21.7	443	68.7	202	31.3	392	89.0	44	10.1	16

capture. I used the annual sightings of these marked gulls to supplement banding data on colony site tenacity, i.e. the tendency of adults to return to the colony of previous nesting. The amount of time spent looking for wing-marked gulls varied from year to year depending on the nature of my other projects. Some years I spent only a few hours looking for markers in May or June, but in other years I made periodic checks throughout the nesting season.

RESULTS

*Colony selection.*—During 12 nesting seasons (1963–74), I captured 4877 adult Ring-billed Gulls in the Calcite colony (Table 1). Of these, 645 (13.2%) were banded previously as chicks and 436 (8.9%) as breeding adults. Those banded as chicks included 443 (68.7% of the banded sample) that were reared at Calcite, the natal colony, and 202 (31.3%) that were raised at one of 16 other Great Lakes colonies (Table 1). These figures could be interpreted as showing that a large proportion of the captured adults had returned to the natal colony to breed, but this may not be the case as the origin of 86.8% of the birds is unknown. Only 13.2% of all adults captured at Rogers City are known to have returned to the natal colony. Neither of these figures is an accurate measure of the tendency of Ring-bills to return to the natal site.

Several factors contribute to the complexity of the above calculations: (1) as a thorough chick-banding program was conducted at Rogers City for 18 years, the proportion of the population banded may be greater than at most other Lake Huron colonies; (2) band loss through wear begins in the 4th year (see Ludwig 1967); (3) stability of the Calcite colony site may increase the likelihood that birds returning to breed for the first time will find a site familiar to them even though competition may be severe; (4) the portion of the colony sampled annually is small ( $\bar{x}$  = 5%), leaving the fate of many banded gulls unknown; and (5) differential mortality with age may be influencing recovery statistics. Interpretation is also hampered by the absence of information about the number of chicks and adults banded over this period at each of the other colonies.

The better to estimate the tendency of Ring-billed Gulls to return to the natal colony I adopted survival estimates published by Ludwig (1974) to calculate the

TABLE 2  
COMPARISON OF PREDICTED AND ACTUAL NUMBER OF SURVIVORS IN NATAL COLONY

Year sampled	No. chicks banded	Estimated survivors <sup>1</sup>	No. caught <sup>2</sup>	% of population <sup>3</sup>	Predicted no./sample	Actual no.	% pred. no.
1965	1632	345	1119	16	55	12	22
1966	1223	259	1135	16	41	9	22
1967	1333	282	1299	19	54	18	33
1968	1307	276	1392	19	52	15	29
1969	2260	477	1560	22	105	29	28
1970	1725	364	1250	18	66	20	30
Totals	12680	2679	9460	134	535	134	183
$\bar{x}$	1811	383	1351	19	76	19	26

<sup>1</sup> Number calculated to be alive in third year; 40% pre fledging mortality; 60% between fledging and 2 years; 12% between second and third year.

<sup>2</sup> Total captured during 3-year period when birds from this particular banding year would have been 2, 3, and 4 years old.

<sup>3</sup> Based on an estimated colony size of 7000 adults.

proportion of chicks banded at Calcite that would be alive when 2, 3, and 4 years old. These ages were selected as band loss is not believed to be a problem until the latter part of the 4th year (Ludwig 1967). The part of the population that was 2–4 years old represented by cannon-netted samples was used to estimate the number of natal colony survivors to be expected in the whole colony. Estimates from these calculations are probably high, i.e. represent the maximum number of individuals possibly returning to the natal colony (Table 2). On this basis, the rate of return to the natal colony by survivors of each age class ranged from 19 to 33%. This procedure shows the tendency to select the natal colony, even when a site is stable and band loss is not a factor, to be lower than estimated by other methods. For instance, Ludwig (1974) reported that 41% of 717 banded Ring-bills he captured had returned to natal colonies. About 8% of his captured sample of 9025 gulls carried bands and some of these had been banded as adults.

It is impossible to state which set of figures most accurately depicts the tendency for Ring-bills to return to the natal colony. If the return rate at Rogers City is 68.7% (natal proportion of banded sample), then Ring-bills have a preference for the natal colony that is not evident throughout the Great Lakes because of changing water levels. If my calculation based on survival rates is correct, Ring-bills apparently select a colony site from those available at the time of first breeding. This selection occurs primarily within a rather narrow range of latitude and longitude as indicated by the colonies at which Calcite Ring-bills have been recovered (Fig. 1).

In Figure 1B the origin (banding site of chicks) of gulls not banded at Rogers City is shown together with the proportion of those represented in the Rogers City sample from each site. About 65% of the foreign gulls were banded as chicks in Thunder Bay in Lake Huron, about 64 km (40 mi) away, where several colonies have existed. Another 10% were banded at various other Lake Huron colonies and most of the remaining birds came from northern Lake Michigan. This supports my (1967b) earlier suggestion that Ring-billed Gulls tend to return to a range of coordinates (i.e. possibly representing the lake where reared). Ludwig's (1974) results reinforce this position as he found that 87% of the gulls in his sample had returned to the lake where raised.

Ludwig (1974) reported that 2-year-old Ring-billed Gulls returned to the natal colony with a greater frequency (54%) than other age groups and concluded that one-third of the 2-year-olds in the population attempted to breed. During 12 years of cannon-netting at the Calcite colony the proportion of 2-year-olds I caught never

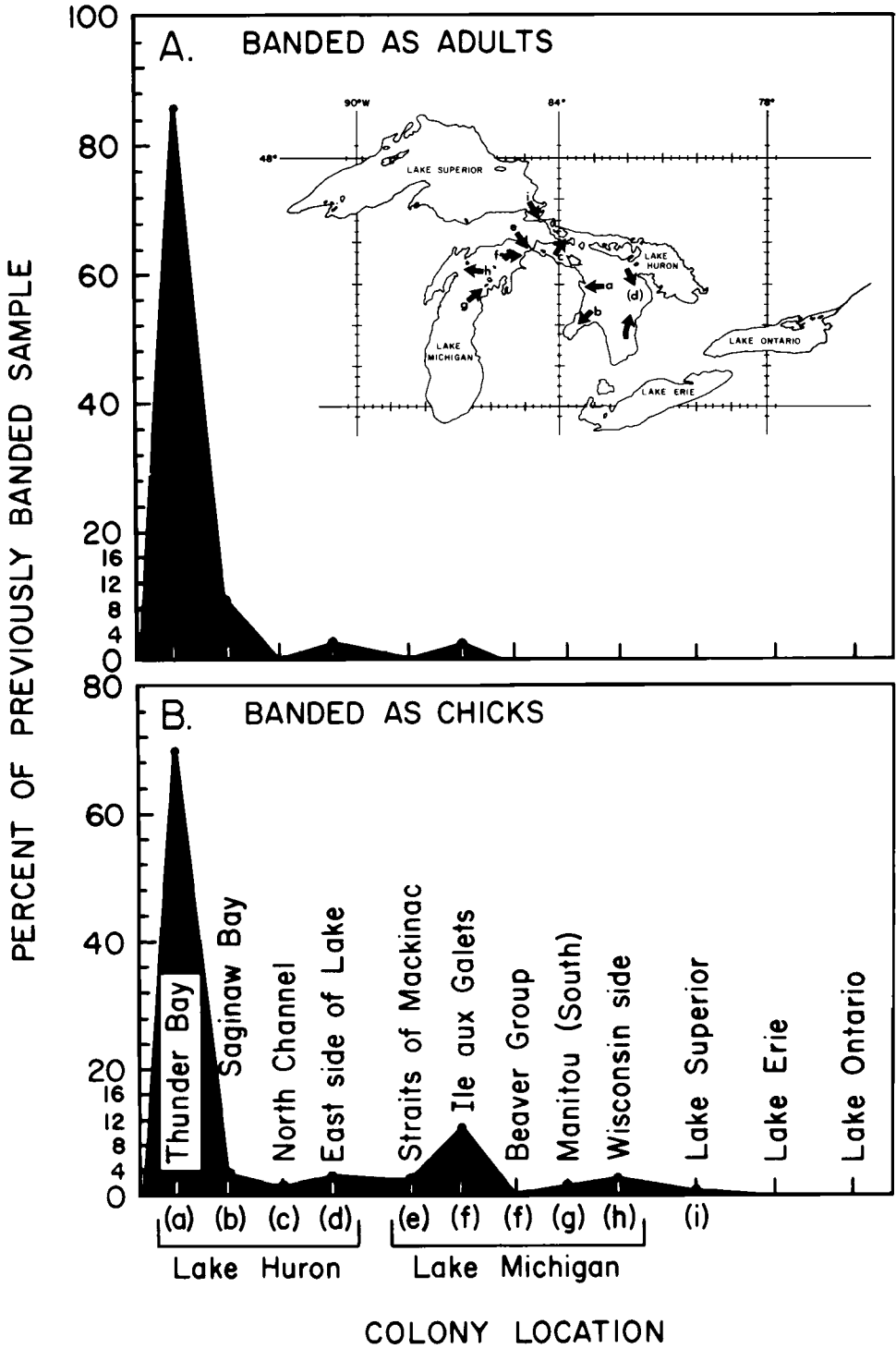


Fig. 1. Origin of Ring-billed Gulls captured at Rogers City that had been banded previously as adults (A) and chicks (B).

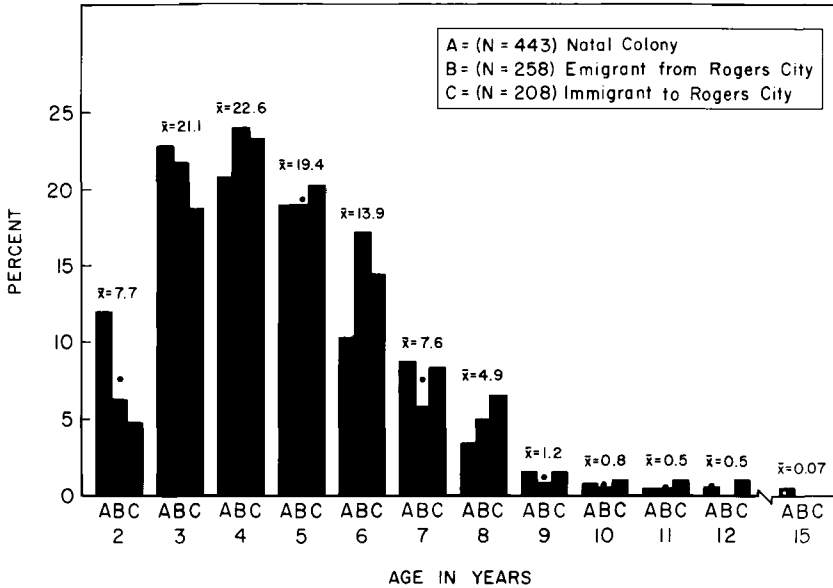


Fig. 2. Age of previously banded Ring-billed Gulls captured as adults at Rogers City or banded as chicks at Rogers City and recovered in another colony.

approached this level. Only 12% of the gulls captured (Fig. 2) that returned to the natal colony were in this age class. If the entire banded sample is used (natal and non-natal), the proportion of 2-year-olds decreases to 7.7%, which is considerably below that for 3- to 6-year-olds (Fig. 2) although band loss could influence this latter figure. This finding is notably different from Ludwig's indicating that his conclusion cannot be applied to all colonies, particularly stable ones.

Periodic variability in the proportion of 2-year-olds present in the breeding population is to be expected in response to environmental changes and population fluctuations. For instance, during periods when water levels are declining and nesting space is relatively abundant, there could be an influx of 2-year-olds trying to breed at locations where available space is not filled by older birds. If 2-year-olds show any tendency to return to a familiar geographical area at the time of first breeding, as possibly represented by the site of rearing, the probability that they would at least visit the natal colony at this time is high. At times when unoccupied nesting space is less plentiful, fewer 2-year-olds probably have an opportunity to breed at the natal colony and thus leave, but the pattern at Rogers City has not completely supported this view. Space apparently suitable for expansion of the colony has been available for many years but colony size remained at about 4000 pairs between 1966 and 1974. Water levels increased during this period and severely affected most of the island colonies. Throughout this period the proportion of 2-year-olds captured in the Calcite colony remained about the same each season. It thus appears that the availability of space for expansion is not influencing the difference between my results and Ludwig's.

Cannon netting early in the nesting cycle, as Ludwig (1974) did, may increase the likelihood of a large capture of visitors in this age class, but not necessarily a larger representation of nesting 2-year-olds. Many gulls frequent the Calcite colony each spring and participate in social encounters near the main colony, but usually they

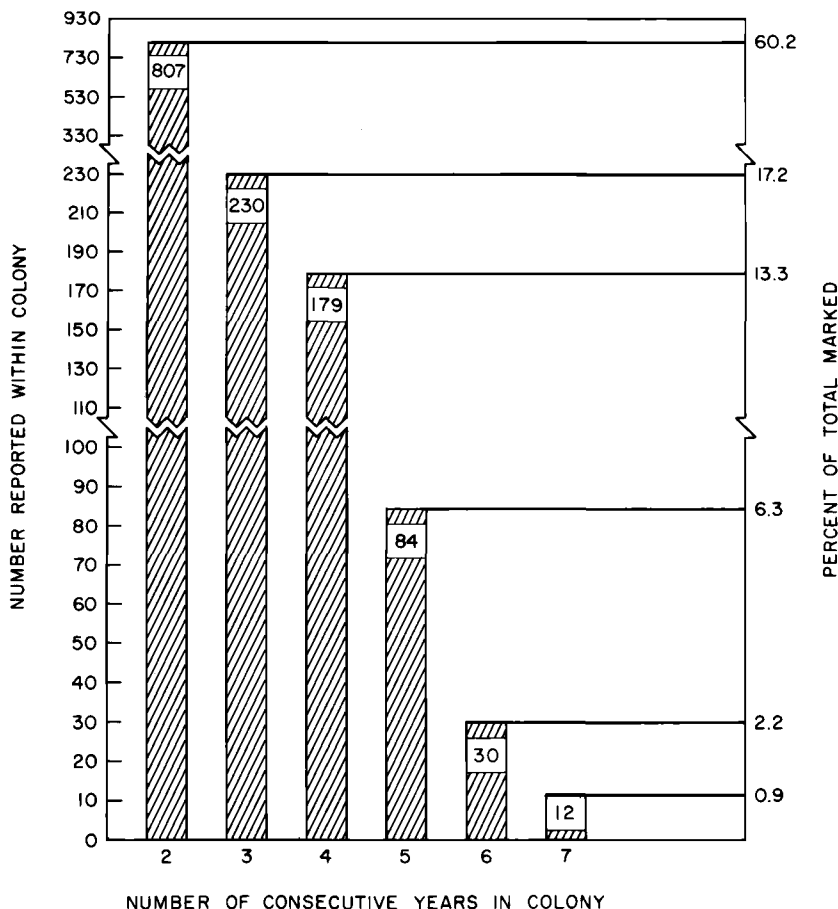


Fig. 3. Summary of sightings of wing-marked gulls nesting in the Calcite Colony.

leave without trying to breed. Possibly these birds were stimulated to move because cannon-netting activities made the site appear unsuitable. Common Terns, *Sterna hirundo* (Austin and Austin 1956), and Forster's Terns, *S. forsteri* (McNicholl 1971), have been shown to return to examine a site and then move on if conditions are unsuitable. Netting early in the season might result in some established birds leaving as well, particularly if the firings are frequent.

Most Ring-bills nesting for the first time at the Calcite colony were 3-year-olds. About 95% of the 2-year-olds present in the colony have been males, or at least they have assumed the male's position during copulation.

*Colony site tenacity.*—During my study I caught 436 Ring-billed Gulls banded as adults at the Calcite colony. Of these, 392 (89.9%) were banded at Calcite while the remaining 44 (10.1%) were banded elsewhere (Fig. 1). Only a small proportion (about 9%) of the adults banded at Calcite is accounted for in this sample. But when data for banded and wing-tagged adults are combined, the documentation of Ring-billed Gull colony site tenacity at the Calcite colony is conclusive.

During four breeding seasons (1969–72) I gave 1339 adults captured on breeding territories serially numbered wing-markers. Also I retagged a few adults given un-

numbered markers in 1967 and 1968 with numbered markers when retaken in subsequent years. During the 1970–74 nesting seasons my research team recorded each positively identified marked adult. Each marker was counted but once each year for this purpose, although many marked gulls were recorded throughout the breeding season. During seven seasons (1968–74), 1342 sightings were recorded. I know that 60.2% of the marked gulls nested at the Calcite colony during at least 2 of the 7 years (Fig. 3). Some (0.9%) were reported during all 7 years, but tag and band loss prevents this from being a representative figure. The sightings listed in Figure 3 represent a minimal indication of birds actually returning because it is unlikely that every marked gull present in the colony was located each year. No comprehensive search for markers was conducted throughout the season, but whenever I surveyed the colony, I spotted previously unnoticed markers. For marker numbers to be discernable, gulls must be turned so the marked wing faces the observer, the marker must be preened into view and the numbers cannot be obscured by feathers. An unknown number of markers are lost annually and very few (possibly 10%) last more than 4 years.

Ring-billed Gulls also exhibit nest-site tenacity and mate fidelity, at least when provided with a stable colony site such as at Rogers City. These topics will be discussed elsewhere.

The data in Figure 3 substantiate that Ring-billed Gulls express colony site tenacity when environmental conditions permit. But even at a stable colony site, some adults move to other colonies. Factors associated with such moves are not well documented, but among the several possibilities are: (1) site tenacity may be linked with successful breeding, and birds unsuccessful for whatever reason (e.g. having a marginal nest site, mate incompatibility, unsuccessful competition) may move the next year (see Coulson 1966); (2) age-related circumstances may be involved, as in the case of Common Terns (Austin 1945, Austin and Austin 1956), wherein birds nesting as 2-year-olds may not become attached to a site until later, possibly as a result of very low nesting success as 2-year-olds, and an interim move occurs; (3) personality differences in individual gulls may make some more likely to desert the colony following traumatic experiences, such as predator attacks or human disturbance; (4) changes in site characteristics by forces such as shoreline erosion may stimulate a move; and, (5) unsuccessful competition by resident adults with experienced immigrating adults could precipitate nest site changes. Interpretation of banding data without concern for such contributing factors will produce questionable conclusions about colony site tenacity and other topics.

The behavioral variability in gull response to investigative techniques and other types of disturbances is difficult to assess objectively. I have noticed that some gulls (perhaps 50–60%) return to the nest immediately after release, others may be gone for minutes or hours, and still others may stay away for days or possibly never return. I have records for 11 wing-marked adults that apparently deserted the Calcite colony following cannon-netting, and I suspect others have responded similarly. In 1974 an adult deserted a nest with two eggs following netting and was not sighted for 2 weeks. Two gulls were reported from Thunder Bay (Lake Huron) colonies in 1972, a month after being marked at Rogers City. Another Ring-bill was reported about 400 km away in Ontario 3 weeks after being wing-marked. Seven others are known to have returned to the Rogers City area during the year following marking but they remained outside the colony as nonbreeders. Conversely it is possible that Ring-bills that have tolerated cannon-netting without desertion are less likely to desert during



subsequent experiences than are birds new to the colony. This is not considered to be a serious source of error, as 60.2% of the wing-marked adults are known to have returned to nest the year following marking.

I have records of gulls netted at Rogers City breeding at other colonies and Ludwig (1974) reported capturing adults from Rogers City (24 gulls) and several other colonies that moved between the colonies he studied. Some Ring-billed Gulls displaced by rising lake levels move to other colonies while others may form groups of nonbreeders outside of colonies. During 1965–67, Ludwig (1974) banded adult Ring-billed Gulls at several Great Lakes colonies. Water levels were on the increase in 1965 (see Chart No. 207, Marine Sciences Directorate, Dept. of the Environment, Ottawa, Ont.) and continued to rise through 1974, thereby reducing the amount of nesting space available for gulls. In 1965 and 1966 no adults Ludwig banded were captured at Rogers City (Table 1) but some have been captured each year since then. The number of Ludwig's birds caught at Rogers City increased each year from 1967 through 1970. After this the number declined, but band loss may have contributed to lower recapture rate. Only a small proportion of the adults displaced by rising waters are accounted for in the Rogers City data even though apparently suitable nesting habitat is available on the peninsula for colony expansion. No significant change in the number of breeding adults was noted until 1973, when about 300 additional pairs were present. In 1974 about 800 more pairs apparently tried to nest, but the actual number of clutches in mid-May (4067) was about the same as in 1971 (about 4000). Several thousand adults have remained in the vicinity (within 0.5 km) as nonbreeders from 1971 through 1974 and occasionally small groups (maximum of 200 pairs) have started nesting in 'subcolonies.' These satellite locations have produced no young. In 1975, about 1300 additional pairs of Ring-bills nested on the peninsula in places adjacent to the original colony and by increasing density in the existing colony. No nonbreeding adults loafed in the characteristic sites in 1975, suggesting that the birds present between 1971 and 1974 eventually accepted the peninsula as a breeding site. If this is the case, established birds that are forced to move by changes such as increasing water levels, may not be quick to adjust to the new circumstances and considerable time may be required for most Ring-bills to transfer to a new colony site.

Wing-marked Calcite colony gulls have been recorded visiting other colonies, particularly early in the season, but most departed without breeding. Twelve adults earlier tagged at Île aux Galets, a Lake Michigan colony near Cross Village (Emmet Co.), were subsequently recorded at Rogers City. All but one left after a few days. The exception was incubating a clutch of eggs in 1974 but apparently failed to produce young. The presence of a marked foreign gull in a colony is not adequate evidence of nesting nor is it necessarily indicative of desertion from another colony. It appears that colony site tenacity develops to a significant degree when colony sites are stable but adults occasionally change colonies as noted by the Austins (1956) for Common Terns. Unstable colonies, on the other hand, are periodically in a state of flux with fewer returning adults and high levels of group adherence among older birds (McNicholl 1975), but not among younger birds (Austin and Austin 1956). This finding for Ring-billed Gulls confirms the views of Austin (1945, 1956) based on Common Terns, and suggests that group adherence among experienced adults may be of selective value because it increases reproductive success through colony stability but it also contributes to continuing reproductive success by providing a nucleus of

experienced birds that can move to a new site and efficiently re-establish a new colony.

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