COLONY SELECTION, LONGEVITY, AND RING-BILLED GULL POPULATIONS: PRELIMINARY DISCUSSION

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Pettingill (1958) described a man-made pier at Rogers City (Presque Isle County), Michigan on which several thousand Ringbilled Gulls (*Larus delawarensis*) and Herring Gulls (*L. argentatus*) now nest. When I first visited this colony in 1957, approximately 800 pairs of Ring-billed Gulls were present. The colony had enlarged to about 4,000 pairs by 1964 and remained at that size in 1965. Ludwig (1962) has discussed similar rates of population expansion for other Ring-billed Gull colonies in the Great Lakes during the 1960's as well as the establishment of several new colonies.

This rather recent Ring-billed Gull population explosion may have been associated with the somewhat cyclic low water levels of Lakes Huron and Michigan which would tend to provide additional nesting areas. However, perhaps an equally important factor contributing to their success has been the species' increased exploitation of insects as a major food source during the breeding season. Currently competition between breeding Ring-billed and Herring Gulls for food and feeding sites appears to be minimal. Previously ring-bills may have been more dependent upon fish as food and were, thereby, in more direct competition with the more dominant Herring Gulls. Such competition could have been severe enough to hold the ring-bill population at a relatively stable level. However, the invasion of a different niche (feeding on terrestrial, aerial, and aquatic insects) by ring-bills probably reduced competition to that associated with colony sites and this, apparently is not severe enough to be a major limiting factor to the Ringbilled Gull population during lows in the water cycle.

During the 1963 and 1964 breeding seasons I used gulls from this colony in orientation and navigation studies. One phase of my project necessitated the capture of numerous adult Ring-billed Gulls for use as experimental subjects. In addition to providing the necessary birds for homing trials, this operation provided a technique for sampling the population and (a) determining the proportion of banded individuals to unbanded ones, (b) the age stratification of the colony, and (c) the influx of individuals reared in other colonies. In 1965, I returned to the area and, during early June, cannon-netted about one-third of the colony in an attempt to obtain additional data pertaining to these topics.

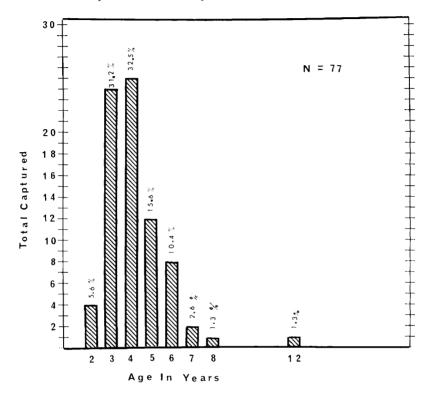
TRAPPING METHODS.—I found the cannon net trap to be the most satisfactory method for capturing the required number of Ring-billed Gulls. Traps of this sort have been described in the literature (see Mosby, 1963) and I will not elaborate upon them here. It should be stressed, however, that nets of relatively small mesh (three-quarter-inch) must be used for ring-bills in order to

prevent the entanglement of, and possibly damage to, flight feathers. Net sites and the pattern and number of firings were determined by my need for experimental birds. The maximum number of adult gulls caught at one firing was 40, but 12 to 15 made up the usual capture. Larger groups could probably be captured early during the nesting season when the birds are most concentrated, but the possibility of nest desertion would also be greatly increased. Many gulls, perhaps 25 per cent of those present, usually managed to fly out from under the net as it was being propelled over the birds. While the report of the cannon startled the birds, the effects in most cases were not lasting and often gulls started returning to nests within minutes after we retrieved and reset the net. Repeated firings (three or more) at the same site resulted in birds becoming hypersensitive to further disturbance and some desertion occurred at nests which contained eggs. Gulls at new colonies and subcolonies (small separate parts of a larger colony) reacted more violently to netting activities and only one or two firings were possible.

A few birds were killed by the cannon net but the rate of direct mortality (adults and young) did not exceed one per cent of all birds captured. If the number of birds actually before the net at the time of firing is used in mortality computations, the percentage of deaths and injuries caused by the operation would be considerably less. So long as precautionary methods are followed when selecting firing sites and placing the net, mortality rates should not exceed this level. Young, four weeks old or older, occasionally stood on the net and were killed when firing occurred. I was unable to determine if indirect mortality resulted from my 1963-64 netting activities since the captured adults were used in homing experiments and any losses of young or eggs were most likely attributable to the latter activity. In general, disturbances caused by periodic cannon netting were not greater than those caused by other banding activities (e.g., banding of nestlings), workmen in the area, etc. Our concentrated efforts during 1965 resulted in some nest desertions in areas where more than one firing occurred. In future attempts we will fire but once in areas having many nests still in the incubation stage. Repeated firings will be conducted when the young are between four days and three weeks old.

Snares made from nylon monofilament fishing line were also used to capture individual gulls at nests or on perches. Such traps provided me with a means for capturing a particular bird for use in homing trials. Use of this technique was as likely to result in nest desertion by an incubating bird as was cannon netting. By means of these trapping techniques my assistants and I captured 134 adult Ring-billed Gulls in 1963; 433 during 1964; and 331 during three days in 1965 (total 898). Many Herring Gulls were also captured but comments in this paper are based solely on data obtained from ring-bills.

The cannon net trap provided an ideal means for sampling gull populations and many more birds could have been captured if this had been my primary purpose and if other studies were not being Fig. 1. Ages of 77 banded Ring-billed Gulls captured in the Rogers City colony during three summers. Presumably all were breeding therein. Data from banded individuals found dead within the colony were omitted since I did not know the time of death and it was possible that the birds did not represent a part of the breeding population. Note that almost two-thirds of the sample was made up of three- and four-year-old birds.



conducted in the same colony. This method might also be used at feeding sites or at other areas of gull concentration. A systematic cannon netting program, in addition to serving as a means whereby adult gulls may be banded, provides valuable information about gull populations, dispersal patterns, and longevity. One other banding group adopted this technique in 1965, and the combined efforts should eventually provide a complete answer to the questions discussed in this paper.

BANDING PROGRAMS AND NATAL COLONY CON-CEPTS.—Several extensive gull banding programs have been carried out in the Great Lakes colonies. The Ludwigs (1962) and others have banded nestling (local) gulls in most of the colonies of Lakes Huron and Michigan. Due to the extent of their task and to the unpredictability of the weather, they are often unable to spend the time necessary in each colony for thorough banding of the young. Nevertheless they have provided a sizeable working population of marked individuals for various studies. Walter P. Nickell has conducted a well organized banding program at the Rogers City colony. I estimated the thoroughness of Nickell's coverage to be between 70 and 80 per cent. Since several other banders also work in this colony, it is likely that no less than 80 per cent of the young ring-bills produced at Rogers City between 1957 and 1964 were banded. This is probably the best coverage given any of the colonies in Lakes Huron and Michigan. The degree of coverage may have been slightly less during 1957 and 1958. The product of these programs is a population ideally suited for determining whether or not Ring-billed Gulls return to their natal colony to breed.

Ludwig (1963) and others have stated that Herring Gulls normally attempt to return to their natal colonies for breeding. This conclusion has been generally applied to other gulls as well but in no instance has sufficient proof been presented. Ludwig (op. cit.) found that 40 per cent (based on 47 recoveries from 60,000 chicks banded over 32 years) of the Herring Gulls in his sample returned to the natal colony to breed. This figure was computed on the basis of band recoveries from several colonies and does not pertain to one population. If such a tendency existed, one would expect to find a large percentage, or perhaps even a majority, of the breeding Ring-billed Gulls at the Rogers City colony to be carrying bands as a result of the intensive banding of chicks. Such, however, was not observed to be the case. Of the 898 adult ring-bills I captured during the three summers, 129 had been banded previously. Fifty-two (40.3 per cent) of the 129 had been banded by me as adults during 1963 and 1964 (at Rogers City) and do not necessarily represent ring-bills reared in this breeding colony. Twelve of the remaining 77 gulls had been banded as young in Lake Huron colonies other than Rogers City. Therefore, the actual proportion of adults in my sample (65 out of 898) represented by birds positively banded as young in this breeding colony was only 7.2 per cent. I believe that this figure is also indicative of the percentage of banded individuals present in the colony. Thus my random sample representing about 22.5 per cent of the local population should be considered as representative.

On several occasions I randomly selected small sections of the colony and recorded the number of banded individuals sighted in each group of 25 adults. This technique indicated that 6.6 per cent of the colony's ring-bill population was banded. I am fairly certain, therefore, that the number of banded adults in the colony was not higher than my trapping results and predictions indicated. Furthermore, it is very likely that some of the birds banded by me as adults were included in these samples, therby biasing my calculations.

On the basis of these data I have concluded that Ring-billed Gulls do not necessarily home to their natal colony to breed. Instead, the apparent tendency is for three-year-old, and occasionally two-year-old, ring-bills to disperse with varying degrees of random-

ness upon returning to the breeding range. Dispersal may be restricted to a particular range of longitudes and possibly latitudes. My data, while admittedly limited, indicates that Lake Huron birds normally remain in that Lake or the adjoining Straits of Mackinac for breeding purposes. When the gulls return to this area to breed for the first time they randomly select a colony exhibiting suitable nesting sites. These birds may establish new colonies, enlarge old colonies, or compete with established adults depending on the existing environmental conditions. However. if there is a shortage of suitable colony sites, the probability of birds returning to their natal colony is greatly increased. Delayed fixed-goal homing to a particular breeding site until after the first breeding season permits the three-year-old birds to exploit fluctuating environmental conditions (i.e., water levels) resulting in new colony sites, range extensions, etc.

It appears that after a gull has nested in a particular colony, it returns to that same colony (and possibly to the same nesting site therein) each year thereafter, provided environmental conditions remain adequate. A partial basis for this conclusion resulted from my 1965 retrapping operation which showed that 55 per cent of the banded birds captured had been banded by me as adults in 1963 or 1964.

Modest support for the Initially Random Colony Selection Hypothesis was also obtained when I attempted to cannon net adult gulls in the Green Island colony (Mackinac County) in the Straits of Mackinac. Although the operation was scheduled too late in the nesting season when few young and adults were returning to brood areas (development of young was about one week ahead of the Rogers City colony), five adult ring-bills were captured, one of which had been banded as a nestling at Rogers City. Further indication of such colony shifts is presented by the 12 adults (15.6 per cent) retrapped at Rogers City that had been banded as nestlings in other Lake Huron colonies. While this represents a relatively small proportion of the total capture (1.3 per cent), its significance increases when we consider it possibly indicative of the origin of many of the unbanded individuals that are present. Unless these unbanded birds are ones which have lost bands (see later discussion), the majority probably represent immigrants from colonies wherein banding coverage was not very complete. These findings indicate the potential value of cannon netting projects in other Great Lakes colonies.

In 1965, J. P. Ludwig began cannon netting activities in several of the colonies visited for the purpose of banding chicks. This has provided a more extensive check on colony changes and also a more rapid means of testing my hypothesis. Among the adult Ring-billed Gulls Ludwig captured in the Grass Island colony (Alpena County) between 13 and 25 May he found five birds that I had previously netted as adults in the Rogers City colony. Initially this caused me to seriously doubt the validity of my original hypothesis. However, a check of my orientation data indicated that all five of these birds had been used in homing trials and that none of them had succeeded in returning from the experimental flights. Thus the resulting colony change cannot be considered normal under these circumstances. Factors associated with this behavior will be discussed in a later paper. It is, however, inter-esting to note that each bird returned to the Lake Huron region as previously predicted. It appears therefore that the hypothesis has withstood its initial test. Further increases in netting coverage may require modifications in this hypothesis. Colony shifts by adults that have bred previously must be carefully scrutinized with reference to environmental changes in their old colony. Particular colonies will undoubtedly be reduced in size as the lake levels once again rise toward their high mark, as ecological succession progresses (e.g., Green Island is no longer ideally suited for ring-bills), or as man-caused factors force the birds to move. While all of these may be considered as natural phenomena and while the birds' subsequent response might be normal, such shifts would not automatically negate the above stated hypothesis. I would predict in such instances that the birds would return to their new colony as faithfully as they had to their original one.

Three other possibilities exist as potential explanations for the small proportion of banded adults occurring annually at the Rogers City colony: (1) Unusually rapid band wear results in band loss a few years after the birds' first breeding season; (2) a high rate of population turnover (i.e., mortality) as a result of environmental factors, as yet unknown, which attain an accumulated lethal level by the sixth year of life or happen to exert their influences on this age class; or (3) insufficient returns are available for a thorough evaluation of the true situation. The first two points will be discussed in the following sections:

BAND WEAR AND LOSS.—The loss of bands during the early or mean years of a gull's life would bias my data in support of the above mentioned hypothesis. The possibility of this happening has been based on my examination of 117 bands carried by retrapped ring-bills, as well as some on museum specimens. Indications are that considerable band wear occurs during the first four or five years and after this period of time, many bands are thin enough to be easily removed by hand, and possibly by gulls. Only 12 banded individuals (15.6 per cent) over five years old were captured, one of which was banded 12 years earlier (see Figure 1). This latter bird was found dead in the colony in 1965 when it was 14 years old. Although there is general wear, greater wear appears to occur on the inner surface of bands. In all but two instances (seven- and eight-year-old birds), the band numbers were still legible when the birds were captured.

The reason for this rapid wear may be that size 5 bands, when first put on young (local) ring-bills, fit snugly but, as the birds near fledging age, the tarsi becomes less fleshy and the band slides up and down freely. As the birds reach adult size, the tarsal scales also become harder and protrude slightly thereby causing wear on the inside of the bands.

In 1965 I recaptured an individual I caught earlier (1963) when it carried a band placed on it as a chick in 1959. It was four-yearsold when I captured it the first time and the band was guite worn. I attached a new band to the opposite leg and left the old band on the bird (my usual practice). When recaptured in 1965, the sixyear-old gull carried only the newer band. Thus, had this bird not been rebanded, it would have been considered as a part of the unbanded population. A possible explanation for the larger proportion of unbanded individuals in the colony may, therefore, be that a large group of the breeding adults are six-years-old or older and have lost their bands. Our netting and rebanding program may eventually provide a more complete answer regarding the rate of wear. Also, it is likely that the newer band materials will wear longer. Obviously the existence of this possibility tends to cast a shadow of doubt over my original hypothesis. Nevertheless, I feel that it still provides us with a working concept.

The possibility of this type of rapid wear occurring is also supported by James P. Ludwig's (personal discussion) analysis of Caspian Tern (*Hydroprogne caspia*) band recoveries. This species retains fleshy tarsi as adults and, as a result, wear bands for much longer periods than Ring-billed Gulls.

The likelihood that my five-year estimate for the usual length of band wear represents an artifact of the start of Nickell's banding program (1957) was considered. However, my 1965 data failed to substantiate this possibility and a sharp increase in birds banded six years earlier by Nickell did not occur (only four were captured).

MORTALITY RATE.—If band loss is not entirely responsible for the apparent sharp decline in birds more than five-years-old, then a sudden increase in adult mortality must be considered as a possible cause. About 79 per cent of the ring-bills in my sample were between three- and five-years-old (see Figure 1). Possibly three or four years is the normal production period for Ring-billed Gulls in Lake Huron and replacement of individuals occurs in most instances prior to the sixth breeding season. If this is correct, reproductive success during recent years (the last decade) has been substantial enough to provide replacements within the diminished age classes as well as to result in a noteworthy expansion of the Great Lakes population (see Ludwig, 1962). The peak years of production appear to be between the ages of three and five years. If this is correct, a somewhat gradual decline towards the maximum age would be expected to occur. However, my data does not indicate this to be the case (see Figure 1). Obviously the potentiality of early band loss prevents me from drawing more definite conclusions at this time.

It may also be significant that the three-year-old group is not the largest. Since more gulls were produced in the Rogers City colony each year up to 1965, and since a more thorough banding coverage has been achieved during the years represented by returning three-year-olds, the probabilities of this age class being the largest should be the greatest. This may be further indication of random dispersal of the gulls returning to breed for the first time and gulls selecting the Rogers City colony are less likely to be banded.

DISCUSSION OF MATURATION.—Although Ring-billed Gulls may breed for the first time when they are two-years-old, most individuals do not begin until the third year of age. This phenomenon of prolonged sub-adult or non-breeding stages occurs in a number of birds and, to my knowledge, the survival values associated with this behavior have not been determined. The following discussion might indicate a partial solution.

The nesting requirements for Ring-billed Gulls are quite definite: rather open sand expanses without dense vegetation; a close proximity to water; seclusion from predators; and several more subtle factors. The occurrence of these conditions tends to limit nesting by these birds to small islands, or to portions of larger islands, in the Great Lakes. The Rogers City colony is an exception, being located on a point projecting from the mainland. The specific requirements above are met here nevertheless.

The average nesting success for ring-bills has been satisfactory, and maintenance as well as expansion of the Great Lakes population has been achieved. During this time competition for available nesting sites has not been as severe as it would have been if all of the ring-bills one-year-old or older had returned to the same general area (i.e., Lake Huron). Subadults, during the two years prior to breeding, inhabit suitable foraging areas outside of the breeding range, thus reducing to a minimum the amount of competition with the breeding adults for food, space, etc. At the same time, this behavior results in a much larger gull population being maintained as well as a more extensive geographical area being inhabited by the species.

On the basis of my available life table data (see Figure 1), it appears that a significant turnover in breeding adults occurs after the fifth year. The returning three-year-olds, besides replacing these individuals, are 'available' for establishment of new breeding colonies. Hence, during the current low levels of Lakes Michigan and Huron, many new colonies were formed, old colonies enlarged, and generally the ring-bill populations flourished. Since the threeyear-olds select colonies at random, even fewer of the Rogers City birds should be returning to the natal colony during this period. When the water returns to its 'normal' level more birds will return to the natal colony out of necessity.

SUMMARY

During three summers (1963-1965) cannon netting techniques were used to capture 898 adult Ring-billed Gulls at the breeding colony. Of these, 7.2 per cent had been banded as chicks in the same colony; 1.3 per cent as chicks in other colonies; 5.8 per cent by me as adults in the same colony during 1963 and 1964; and the remainder were unbanded. On the basis of the small number of banded individuals present in the colony, the capture of several birds banded as chicks in other colonies, and the recapture of the same adults, a hypothesis has been established which states that Ring-billed Gulls select their first breeding colony at random from those available within a particular range of latitudes and longitudes. After having once nested in a particular colony the bird usually returns thereto so long as environmental conditions remain suitable. However, limited data indicates that older adults will also, at least on occasion, change breeding colonies.

Influencing factors such as band wear, life span, lack of sufficient recoveries have also been discussed. A brief discussion of the selective value of delayed breeding (two or three years after hatching) in gulls is presented.

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