# Breeding biology of California and ring-billed gulls

by Kees Vermeer

# Breeding biology of California and ring-billed gulls: a study of ecological adaptation to the inland habitat

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Cover photo by Robert V. Bocking

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# Perspective

Of the many forms of pollution, chemical contamination poses the greatest immediate threat to all organisms, including man. The most important and useful reason for studying gulls lies in their value as indicators of the health of the habitat. A recent survey (Vermeer *et al*, in press) on organochlorine residues in aquatic birds in the Canadian prairie provinces showed that California and ring-billed gulls are among the most contaminated. As gulls nest in colonies, changes in breeding populations can be readily detected and related to levels of chemical contamination. Ecological research on colonial birds is therefore valuable to monitor the effects of chemical pollution on the environment.

# Résumé

Le goéland de Californie *(Larus californicus)* et le goéland à bec cerclé *(Larus delawarensis)* ont fait l'objet d'une étude effectuée au lac Miquelon (Alberta), en 1964 et 1965, en vue de déterminer la période de nidification, le choix de lieux de nidification, le résultat de la reproduction, les habitudes alimentaires et le rythme de croissance de ces oiseaux, afin de savoir si ces espèces manifestent certaines aptitudes à nicher dans l'intérieur des terres.

Très peu de différences fondamentales ont été observées entre les espèces de Laridés qui vivent dans l'intérieur des terres et celles qui nichent dans les régions côtières. Les deux espèces du lac Miquelon nichent au sol, à la façon de maintes espèces côtières. Les rythmes de croissance et de reproduction du goéland de Californie et du goéland à bec cerclé sont semblables à ceux du goéland à ailes glauques *(Larus glaucescens)* de la côte de la Colombie-Britannique.

Les deux espèces en question semblent particulièrement adaptées à la nidification dans l'intérieur des terres, en raison de leur aptitude à profiter de l'abondance saisonnière de rongeurs trouvés dans ces lieux et de la brièveté de leur période de reproduction. Une expérience ayant pour but d'établir s'il existe quelque rapport entre la croissance et la survie des petits du goéland de Californie au moment de l'éclosion des œufs, n'a pas permis de déterminer si la durée de la période de reproduction de ces oiseaux, période relativement courte, est conditionnée par la pâture disponible.

# Abstract

The breeding chronology, reproductive success, nesting habitat, food, and growth rates of California gulls *(Larus californicus)* and ring-billed gulls *(Larus delawarensis)* were studied at Miquelon Lake, Alberta, in 1964 and 1965 to learn whether these species exhibit special adaptations to breeding in an inland environment.

Few basic differences between gull species breeding inland and those breeding on the seacoast were found. Both species at Miquelon Lake are ground nesters like many coastal species. Growth and reproductive rates of the California and ring-billed gulls are similar to those of glaucous-winged gulls *(Larus glaucescens)* breeding on the coast of British Columbia.

Apparent adaptations of the two species to breeding inland are the ability to exploit a seasonally abundant supply of rodents and a shortened breeding season. The results of an experiment to test the relationship of growth and survival to the time of hatching of California gull chicks did not show that the food supply governs the short breeding season.

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# Introduction

Fisher and Lockley (1954) state that the evolutionary radiation of gulls may have taken place from the North Pacific and North Atlantic. They list 42 species of gulls – 16 found in the North Pacific, 14 in the North Atlantic, 11 in the Arctic, 9 in the South Pacific, 6 in the Indian Ocean, 5 in the South Atlantic, and 2 in the Antarctic.

Most studies have concentrated on coastal colonies (Coulson and White, 1956, 1958, 1959, 1960, 1961; Drost *et al.*, 1961; Goethe, 1937, 1953, 1955, 1956, 1960; Harris, 1964; Kruuk, 1964; Moynihan, 1955, 1956, 1962; Paludan, 1951; Patterson, 1965; Paynter, 1947, 1949; Tinbergen, 1953, 1959; Ytreberg, 1956, 1960). This has obscured the fact that gulls also successfully exploit inland freshwater habitat. This study of California *(Larus californicus)* and ring-billed *(L. delawarensis)* gulls was undertaken to find out whether inland-breeding gulls depend on special adaptations in breeding biology. The two species were studied at Miquelon Lake, Alberta, at latitude 53° 15′ north and longitude 112° 55′ west, some 30 miles s.e. of Edmonton.

The California gull breeds only inland. The ring-billed gull also breeds inland except for a small eastern section of its range (Fig. 1). We do not know why these birds migrate from coastal wintering grounds to inland nesting grounds, but it may be because food is abundant there during the breeding season. Serventy (1960) suggested that the occurrence or availability of food and nesting sites governs the breeding distribution of sea-birds.

To learn whether the birds were adapted to the inland environment, I studied breeding chronology, reproductive success, nesting habitat, food, and growth of chicks to fledging. I chose the glaucous-winged gull *(Larus glaucescens)* as a coastal model because I had experience with this species, and because it breeds at a latitude similar to that of the California and ring-billed gulls which nest together at many locations in western North America.

In studying how the two species interact I watched for adverse effects of one species on the reproductive rate of the other; Paludan (1951) and Harris (1964) showed such effects in similar situations among gulls nesting together on the coast. Particular attention was paid to anti-predator mechanisms, especially those unique to the inland environment.

**Figure 1**
**California gull**                                    **Ring-billed gull**
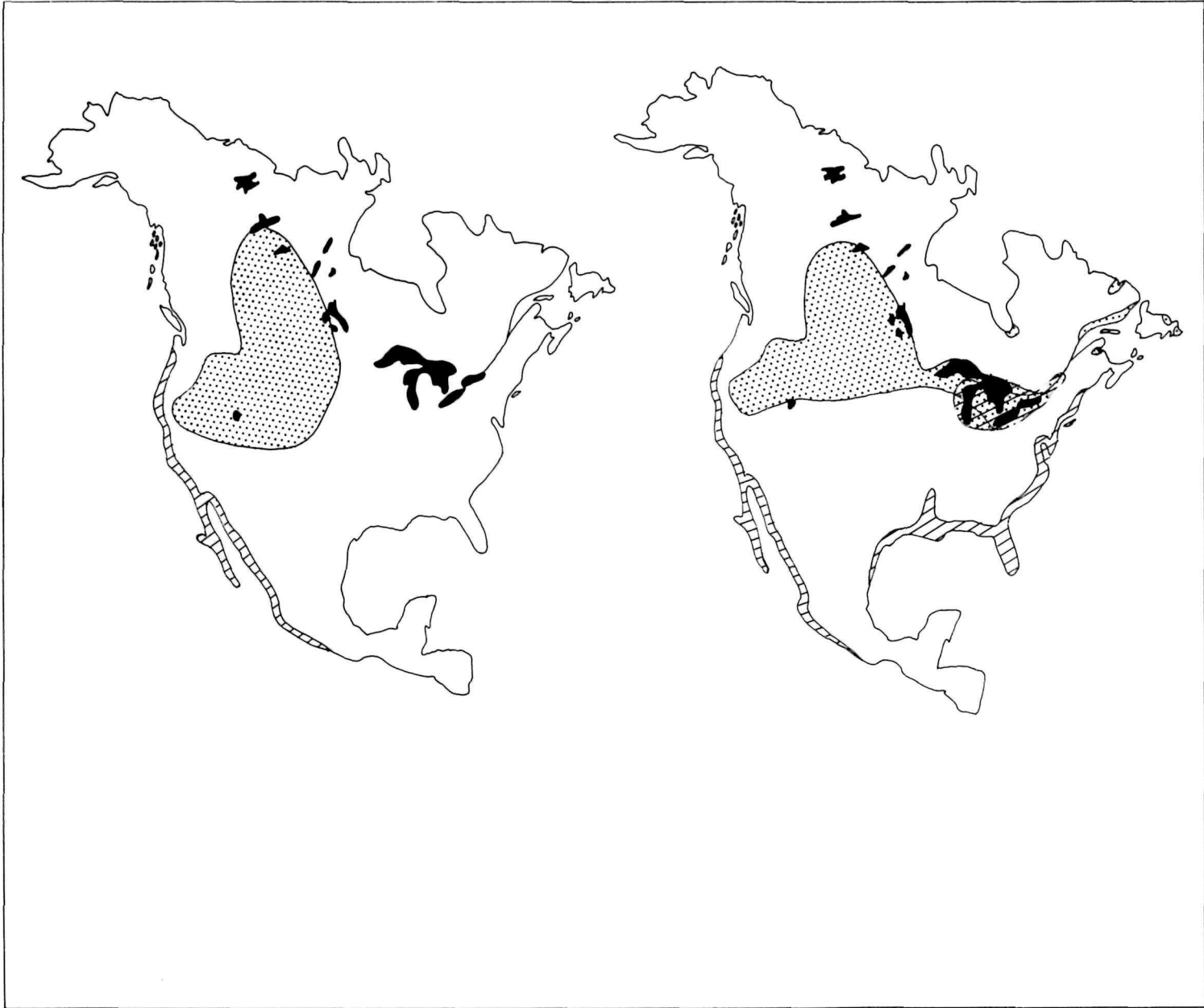


◩ Main winter range
⊡ Breeding range

# Methods

**Procedure in the colony and vicinity**

The study was conducted in the summers of 1964 and 1965 on islands of Miquelon Lake where California and ring-billed gulls nested. Figure 2 shows Miquelon Lake and the position of the islands in the study area. A cabin erected on island A in 1963 was observation tower cum living quarters.

Daily observations of gull colonies on island A were made from May 7 to August 8, 1964, and on islands A and B from April 23 to July 6, 1965. The time of arrival, and dates of laying, hatching, and fledging were recorded as well as the dates of the gulls' arrival at and departure from garbage dumps in the Edmonton area. Each nest was identified by the species attending it, its construction, and size of its eggs (Appendix 1); and was marked by a sturdy, one-foot-long wooden block bearing a numbered metal tag. The blocks were laid flat on the ground near each nest and thus could be positioned quickly.

The various stages in the reproductive cycle were recorded. From my arrival in the spring until hatching of all the chicks, nests were checked daily, as quickly and with as little disturbance to the gulls as possible. Nevertheless, my activities increased gull predation on eggs during the laying period. I have therefore omitted from my calculations of reproductive success those nests from which eggs were lost during the first days of the study – whether they had disappeared, or were broken and eaten. The birds became used to me after three or four days and frequently did not flee their nests during incubation until I was within five feet of them.

Upon hatching, the young were marked on their legs with individual combinations of binder tape which were later replaced with individually numbered coloured plastic bands and standard Canadian Wildlife Service aluminum bands. The fate of these marked chicks was followed through a daily search of the study area.

Since egg-laying was well advanced at the start of the study on island A in 1964 and on island B in 1965, the dates of clutch commencement were obtained by subtracting the average periods of egg-laying and incubation from the hatching date. These periods of egg-laying and incubation were derived from clutches observed from egg-laying to hatching. I visited island B during the egg-laying period, on May 7 and 11, 1966; and on May 6 and 13, 1967. In those years, the first date of laying for both species could be calculated from average time intervals between the laying of the eggs of a clutch.

The behavioural interaction of the gull species was studied at the time of territorial establishment. The vegetative cover and topography were analysed and their influence on the gulls' choice of nest-sites investigated. All the gull nests were plotted on maps of the islands; distances between individual nests and between nests and the water measured; and elevation of the nests above the level of the lake estimated.

**Food Analysis**

To determine the food habits of both species, specimens were taken at Miquelon and Beaverhill Lakes in 1965 and the contents of the oesophagus and proventriculus preserved. Adults were collected in May, June, and July; chicks in the first week of July. Since the regurgitated food did not differ from the food contained in the oesophagi, the samples were grouped for analysis. Gizzard contents were also analysed. The gizzard digests some foods more rapidly than others, hence the results would be biased if gizzards were the sole organs investigated.

Frequency of occurrence of specific food items was based on the number of times they were found in the total number of oesophagi and regurgitations. To measure volume to the nearest cm³ food was submerged in a graduated cylinder partially filled with water.

The indigestible residues were analysed separately from pellets collected on the breeding grounds. The gull species responsible for the pellets was determined by where they were found, a procedure with little chance of error in these spatially segregated colonies. Down feathers of gulls, grit, and such debris as glass, paper, cloth, fruit pits, and bottle caps were discounted.

From May to July 1967, California and ring-billed gull colonies were surveyed in southern and northern Alberta from motor vehicle and hydroplane, respectively. In addition, food pellets were collected from 14 different colonies.

**Growth**

In 1964, gull chicks on island B were weighed, to the nearest gram, on alternate days from hatching until fledging. Chicks up to 150 g were weighed with a spring balance, and subsequently, with a triple beam balance. The measurements were taken in a 300- by 100-foot fenced plot in which both species were nesting.

**Other study areas**

The breeding cycle of California and ring-billed gulls nesting on islands at the north end of Beaverhill Lake, 22 miles from Miquelon Lake, was investigated in 1965. The relationship of growth and survival to the time of hatching of California gull chicks was tested in 1967 on an island in Joseph Lake, six miles northwest of Miquelon.

**Statistics and data from other sources**

The Clark-Evans (1954) method was used to test whether the observed nesting distributions of the gulls departed from random with respect to the distance to the nearest neighbour. In all statistical tests, the null hypothesis was accepted if the probability level was below 0.05.

References to the glaucous-winged gulls are from my studies of this species on Mandarte Island (Vermeer, 1963) unless otherwise stated.

Figure 2. The study area on Miquelon Lake, Alberta.



0        100        200 Miles

● Location of Miquelon Lake study area in Alberta

0                    1                    2 Miles

A, B, C₁, C₂, C₃    Islands
C₄                  Peninsula

# Description of the study area

Miquelon Lake is an alkaline body of water with a total alkalinity in 1964 of 1383 parts per million (ppm) and a range in pH of 9.3 to 9.5 (Kerekes, 1965). It was then approximately 3 miles long by 2 miles wide, and averaged 9 feet deep. Its muddy and sandy shores are generally free of emergent vegetation and are strewn with pebbles and boulders piled up at various points into ridges. These ridges, created during spring breakup by wind-blown ice pushing rock and debris onto the shore, are also found on the islands.

Islands A and B (Fig. 2) are composed of boulders, sand, and clay mixed with decomposed vegetation. Island A, the main study area, was exposed in autumn 1949 by lowering of the water level. Information on how it was formed was obtained from a comparison of aerial photographs taken in different years, and from a former resident in the area. In spring 1964, island A was approximately 6 acres in area; and island B, 5 acres. Both islands were relatively flat, their highest point being 6 feet above the level of the lake.

## Vegetation

The flora of islands A and B was typical of islands in central Alberta (Moss, 1959). In the summer and autumn, plant growth was luxuriant, probably because the soil was enriched by the excrement of nesting gulls. A few small trees and shrubs including aspen (Populus tremuloides), willow (Salix), red osier dogwood (Cornus stolonifera), wild gooseberry (Ribes oxyacanthoides), and common wild rose (Rosa woodsii) grew on island A. A small group of aspen and a few wild gooseberry bushes grew on island B. Along the peripheries of both islands was a zone of fowl manna grass (Glyceria striata) and foxtail barley (Hordeum jubatum). A growth of sea blite (Suaeda depressa) on the muddy and sandy shore line indicated the saline nature of the lake water (Moss, 1959). The most common herbs in the interior of the islands were common nettle (Urtica gracilis), perennial sow thistle (Sonchus arvense),

absinthe (Artemisia absinthium), grey tansy mustard (Descurainea richardsonii), Canada thistle (Cirsium arvense), lamb's-quarters (Chenopodium album), three-square rush (Scirpus americanus), common great bulrush (Scirpus validus), Russian pigweed (Axyris amaranthoides), red-root pigweed (Amaranthus retroflexus), beaked sedge (Carex rostrata), common dandelion (Taraxacum officinale), and wire rush (Juncus balticus). To a lesser extent grew Fremont's goosefoot (Chenopodium fremontii), stinkweed (Thlaspi arvense), common yarrow (Achillea millefolium), silverweed (Potentilla anserina), aster (Aster), mountain goldenrod (Solidago decumbens), hemp nettle (Galeopsis tetrahit), red clover (Trifolium pratense), common plantain (Plantago major), hirsute fleabane (Erigeron lonchophyllus), wild morning-glory (Convolvulus sepium), brome grass (Bromus), common groundsel (Senecio vulgaris), fireweed (Epilobium angustifolium), agrimony (Agrimonia striata), and water smartweed (Polygonum amphibium). Only widgeon grass (Ruppia occidentalis) grew on the lake bottom.

## Vertebrates

The relatively common stickleback (Eucalia inconstans) and the scarcer yellow perch (Perca flavescens) were the two species of fish found in the lake (Kerekes, 1965).

Mammals recorded on island A were least weasel (Mustela rixosa), cinereous shrew (Sorex cinerus), deer mouse (Peromyscus maniculatus), and meadow vole (Microtus pennsylvanicus).

Table 1 shows the nests found on islands A and B in 1964 and 1965. One old nest of a crow (Corvus brachyrhynchos) was found in a young aspen tree on island A. Crows did not nest on the islands during the field study, presumably because of my presence. Nests of savannah sparrows (Passerculus sandwichensis) were not found; however, they were probably nesting there. If so, they would have been the only passerines breeding on the islands in those years.

**Table 1**
Number of nests of birds found on islands A and B, 1964-65

| | No. of nests | | | |
| | Island A | | Island B | |
| Species | 1964 | 1965 | 1964 | 1965 |
|---|---|---|---|---|
| California gull | 470 | 87 | 300* | 44 |
| Ring-billed gull | 315 | 58 | 1,200* | 378 |
| Canada goose (Branta canadensis) | 0 | 0 | 1 | 1 |
| Lesser scaup | 41 | 44 | 26 | 32 |
| Gadwall | 26 | 15 | 3 | 10 |
| Mallard | 9 | 3 | 3 | 3 |
| White-winged scoter (Melanitta fusca) | 9 | 2 | 2 | 7 |
| American widgeon | 3 | 1 | 2 | 1 |
| Pintail | 2 | 4 | 4 | 6 |
| Common tern | 1 | 0 | 0 | 0 |
| Marbled godwit (Limosa fedoa) | 1 | 0 | 0 | 0 |
| Spotted sandpiper (Actitus macularia) | 0 | 1 | 0 | 0 |

*Estimates

Six California gull nests were found in region C (Fig. 2) in 1964; two of these were on peninsula C4. In 1965, 65 pairs of California gulls nested in region C. Common terns (Sterna hirundo) also nested in region C. Birds found breeding in association with the terns were avocets (Recurvirosta americana), Wilson's phalaropes (Steganopus tricolor), piping plovers (Charadrius melodius), pintails (Anas acuta), American widgeons (Mareca americana), and lesser scaup (Aythya affinis).

Other waders and waterfowl nesting along the shore of Miquelon Lake were killdeer (Charadrius vociferus), willets (Catoptrophorus semipalmatus), red-necked grebes (Podiceps grisegena), mallards (Anas platyrhynchos), gadwalls (Anas strepera), pintails, blue-winged teals (Anas discors), lesser scaup, shovelers (Spatula clypeata), and redheads (Aythya americana).

# The breeding schedule: chronology

## Migration

Figure 3 depicts the winter recoveries of juveniles[1] raised at Miquelon Lake in 1964. Juveniles of both species have the same winter range, chiefly southern California and the west coast of Mexico. Farley (1932) found that the California and ring-billed gulls raised at Bittern Lake, 15 miles from Miquelon Lake, also wintered mainly in southern California. Although the ring-billed gull is a common fall migrant to Vancouver, British Columbia, it is rarely observed there in the spring. In contrast, the California gull is numerous in fall and spring. From observations cited by Houston (1963), California gulls migrate north in the spring along the west coast from California to southern British Columbia and then inland to the interior; in the fall they presumably use the reverse route southward. The ring-billed gulls, however, generally migrate north through the interior of the continent.

The first white-headed gulls (California or ring-billed, but definitely ring-billed gulls in 1967) were observed in the Edmonton area on March 29, 1964; March 30, 1965; March 28, 1966; and April 2, 1967, by R. Lister, J. C. Holmes, D. Newman, and R. Lister respectively (pers. comm.). In the first week of April of those four years I observed only ring-billed gulls in the Edmonton area.

The change of day-length, because of its precision, seems to be used by many mid- and high-latitude migratory birds to time their arrival (Farner, 1964; Wolfson, 1960). Besides the increasing daily photoperiod as a primary timer, such modifying factors as climatic conditions may also govern the time of arrival.

The mean snow depth in Edmonton in the last week of March, before the gulls arrived, was 1.8 inches in 1964, 11.0 in 1965, 3.3 in 1966, and 9.6 in 1967. Since snow depth differed greatly from 1964 to

[1] "Juvenile" is a fledged gull, from the same season, which has left the nesting colony. "Fledgling" denotes a gull which has fledged but has not left the nesting colony.

**Figure 3**



Banding location at Miquelon Lake
△ California gull
☐ Ring-billed gull

A August recovery
S September recovery
O October recovery
D December recovery
J January recovery
F February recovery

**Figure 4**



Mean daily temperature (F°)

● Arrival of first gulls

1965, and the arrival time differed by only one day, it was not a deciding factor.

Figure 4 relates the time that gulls arrive in Edmonton to mean daily temperature there. Since the daily temperatures were much higher in the last week of March 1966 than in 1964, 1965, and 1967, air temperature was apparently not the only factor affecting migration. It may, however, be important as a threshold factor; that is, the birds may not arrive unless a certain temperature has been surpassed at points along the migratory route and at the terminus of their flight.

Observations at the Edmonton garbage dump in autumn of 1963, 1964, 1965, and 1966 indicated that the last California gulls

left in mid-September, whereas the last ring-billed gulls left in the first week in November (Table 2).

**Colony occupation**

The gulls occupied the islands in Miquelon Lake before snow (Table 3) and ice disappeared. Ice disappeared from Miquelon Lake on April 30, 1964; May 8, 1965; and May 7, 1966. Snow disappeared from the islands on April 12, 1964; April 30, 1965; and sometime in the second week of April 1966. Ring-billed gulls returned to nest earlier than California gulls, possibly because different migratory routes were used.

At more southerly latitudes, where spring arrives sooner, the California gulls arrive

**Table 2**

Autumn observations of the numbers of California and ring-billed gulls at the garbage dump in Edmonton

| Date | No. of birds seen | |
|------|-----------------|---|
| | California gull | Ring-billed gull |
| Aug. 15, 1964 | ca. 500 | ca. 1000 |
| Aug. 29, 1966 | 10 | 190 |
| Sept. 6, 1965 | 4 | ca. 500 |
| Sept. 18, 1964 | 0 | ca. 500 |
| Sept. 18, 1966 | 2 | 155 |
| Oct. 16, 1966 | 0 | ca. 500 |
| Oct. 30, 1963 | 0 | ca. 400 |
| Nov. 3, 1964 | 0 | 100 |
| Nov. 6, 1963 | 0 | 6 |
| Nov. 7, 1964 | 0 | 0 |
| Nov. 8, 1965 | 0 | 0 |
| Nov. 10, 1964 | 0 | 0 |

on the breeding grounds earlier than they do at Miquelon Lake. They also begin laying earlier. They arrived at Great Salt Lake, Utah, in late February, and started laying about the second week of April (Behle, 1958). They reached Freezout Lake, Montana, on March 12, 1959, and began laying on April 22 (Rothweiler, 1960).

Table 4 compares the pre-egg periods of gulls at Miquelon Lake with pre-egg periods of California gulls in Montana and Utah, and of coastal glaucous-winged gulls on Mandarte Island. The pre-egg period is the time between the appearance on the breeding ground of the first individuals of a species and the laying of the first egg.

The pre-egg period in Montana and Utah is longer than at Miquelon Lake, but much shorter than on Mandarte Island. Short pre-egg periods seem to go with more northerly gull populations as well as inland environment which generally has a colder and longer winter than the marine habitat.

In the three years of the study, ring-billed gulls arrived at Miquelon Lake on similar dates (exact dates for California gulls are not known). Paludan (1951) found that unusually low temperatures and dull weather may cause herring gulls *(L. argentatus)* to delay occupation of the colony on Graesholm Island in the Baltic for a month. According to Bergman (1939), herring and mew gulls *(L. Canus)* occupy colonies on islands in the Baltic after the ice has melted. This view is supported by Ytreberg (1956) who, in three years of observation, recorded a two-week difference in the black-headed gull's *(L. ridibundus)* arrival at a colony on the outer edge of a vegetation belt skirting a lake near Oslo, Norway. The black-headed gulls did not occupy the colony until the ice had become perforated, and Ytreberg states that the delay was caused by the late thaw. Coastal gulls depend to a greater extent upon aquatic food which is available only after the ice melts. The case of the California and ring-billed gulls at Miquelon Lake is, however, different for they arrived there long before the ice thawed.

**Table 3**
Number of California and ring-billed gulls observed on the islands at Miquelon Lake during visits made before egg-laying

| Date | California gull | | Ring-billed gull | | Snow conditions on islands |
|---|---|---|---|---|---|
| | Island A | Island B | Island A | Island B | |
| March 30, 1964 | 0 | | 3 | | Present |
| April 2, 1966 | 0 | | 3 | | Present |
| April 3, 1965 | 0 | | 1 | | Present |
| April 4, 1965 | 0 | | 2 | | Present |
| April 8, 1966 | | 0 | | 120 | Present |
| April 12, 1964 | 10 | | 190 | | Absent |
| April 21, 1966 | 30 | | 70 | | Absent |
| April 23, 1965 | 80 | | 120 | | Present |

**Table 4**
Pre-egg periods of three gull species

| Gull species | Pre-egg period weeks | Location | Yr of study | Source |
|---|---|---|---|---|
| Glaucous-winged | 10-12 | Mandarte Island, B.C. | 1961, 1962 | Vermeer, '63 |
| California | 6-7 | Great Salt Lake, Utah | 1930-50 | Behle, '58 |
| California | 6-7 | Freezout Lake, Mont. | 1958, 1959 | Rothweiler, '60 |
| California | 3-4 | Miquelon Lake, Alta. | 1964, 1965 | This study |
| Ring-billed | 4-5 | Miquelon Lake, Alta. | 1964, 1965 | This study |

Island A was completely covered with snow on April 23, 1965. The gulls pursued their initial courtship and territorial activities on this snow cover twice a day. They were most active shortly after arriving at dawn (0400 hours), and most of them left after 0900 hours. They started to assemble on the island at 1700 hours and resumed activity, but at a lower peak. At sunset (2000 hours) all gulls departed for their roosting places. Only after they started to lay did they stay on the island overnight. I observed a similar daily rhythm during the pre-egg period in the glaucous-winged gulls on Mandarte Island.

One of the large nocturnal roosting places of California and ring-billed gulls was on Big Lake, 40 miles from Miquelon Lake, near Edmonton. The view that adult gulls roost on wide open mud flats and beaches for protection against predators (Tinbergen *et al.*, 1962) was confirmed by data on 1449 adult black-headed gulls killed by foxes (Kruuk, 1964). Except on extremely dark nights, gulls are safe from predators when roosting on open beaches, and are much more vulnerable when they roost on the breeding ground. Thus, by leaving the breeding colony during the pre-egg period, adult gulls are less exposed to predation at night.

**Clutch commencement**
Figure 5 depicts clutch commencement in 207 California and 275 ring-billed gull nests on island A in 1964, and in 140 California and 198 ring-billed gull nests on islands A and B in 1965. California gulls started clutches an average of 3.7 days later in 1965 than in 1964; ring-billed gulls started clutches an average of 2.4 days later. The differences between the years in the mean date of clutch commencement were statistically significant for each species and may have been due to differences in weather conditions. Table 5 compares weather data with the date of laying of the first egg of each species, as well as with the mean date of clutch commencement in both species.

Figure 5. Distribution of clutch initiation of
California and ring-billed gulls at Miquelon Lake.

**Figure 5**
**California gull**



**Ring-billed gull**
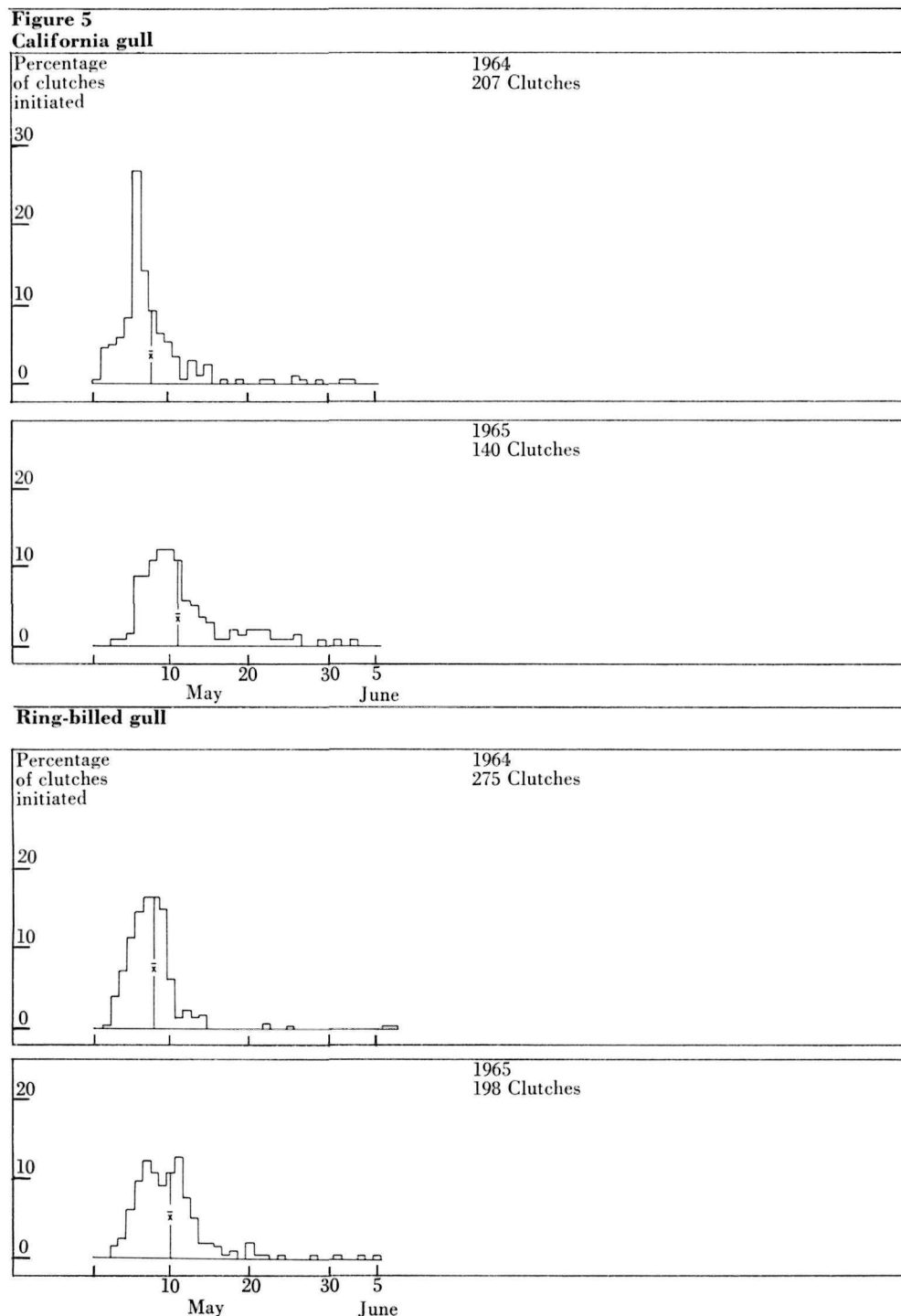
Delay in laying in 1965 (and 1966) co-incides with a decrease in mean daily air temperatures. Kirkman (1937) also found a correlation between low temperatures and late laying in the black-headed gulls in England. However, Bergman (1939) stated that clutch commencement in herring and mew gulls in Finland was dependent on the melting of the ice and not directly on the temperature. The presence of ice, per se, probably does not delay laying in the gulls at Miquelon Lake, since the thaw is a function of air temperature and since aquatic organisms are not their major food source in May.

Human disturbance may also influence the time of clutch commencement. In 1965, the California gulls started laying on islands A and B at the same time, but the ring-billed gulls started five days later on island A than on island B. The delay on island A may have been caused by my presence there. Ring-billed gulls are much more excitable than California gulls, and they began laying only after I had left the island temporarily.

The appearance of food, per se, did not appear to be a primary factor in the onset of egg-laying. Although an abundance of meadow voles and snow-free conditions provided much food in mid-April 1966, at least three weeks earlier than in the previous year, laying did not begin earlier. Belopolskii (1957) attributed regional difference in the onset of the breeding cycle in sea birds in the Barents Sea to food rather than to changing day-length. However, the influence of light and the effect of food on the time of egg-laying in birds are not mutually exclusive. Changing day-length not only stimulates the birds' sexual cycle, but also governs the increase of food at high latitudes. In regions closer to the equator, where seasonal light changes are not pronounced and may not be as important in controlling food sources as they are farther north, food may be the principal timer in the onset of breeding. Kahl (1964) reported that the breeding of wood storks

**Table 5**
Weather data and dates of the first egg and mean
clutch commencement in California and
ring-billed gulls at Miquelon Lake, 1964-67

| | Year | | | |
|---|---|---|---|---|
| | 1964 | 1965 | 1966 | 1967 |
| Mean daily air temp. (°F), Edmonton Int. Airport (25 miles from Miquelon Lake), April | 39.0 | 35.2 | 32.6 | 29.2 |
| Total hr bright sunshine, Edmonton Int. Airport, April | 232.9 | 209.1 | 213.7 | 237.7 |
| Islands in Miquelon Lake, snow free | Apr 12 | Apr 30 | Apr 2nd wk | May 2 |
| Miquelon Lake, ice free | Apr 30 | May 8 | May 7 | May 17 |
| First egg, California gull | May 1 | May 3 | May 9* | May 11* |
| First egg, ring-billed gull | May 2 | May 3 | May 4 | May 8 |
| Mean clutch commencement, California gull | May 8 | May 11 | | |
| Mean clutch commencement, ring-billed gull | May 8 | May 10 | | |

*Few gulls present

(*Mycteria americana*) in Florida coincided closely with food availability, which was influenced by declining water levels.

In Figure 6, clutch initiation of California and ring-billed gulls at Miquelon Lake is compared with that of herring and lesser black-backed gulls (*Larus fuscus*) on Graesholm Island in the Baltic Sea (Paludan, 1951); black-headed gulls on a freshwater body near Oslo, Norway (Ytreberg, 1956); and glaucous-winged gulls on Mandarte Island. The comparison is restricted to species studied at similar latitudes where at least two years' data on no less than 200 clutches were available. The greater degree of synchrony in laying in California and ring-billed gulls than that in coastal gulls can be seen from the shorter laying period, and the steeper slope and abrupt rise of the curves of clutch initiation. The distribution pattern of clutch commencement in black-headed gulls takes an intermediate position between that of the California and ring-billed gulls and that of the three species nesting in the marine habitat. That is, 80 per cent of the clutches were started within 10 days of the first egg by the California and ring-billed gulls; within 15 days by the black-headed gulls; and between 25 and 35 days by the three species nesting on marine islands. Clutch initiation was spread over a longer period in the four species breeding in habitats with a maritime cli-mate than in the two species nesting inland. The greater degree of synchrony of laying in gulls nesting inland than at the coast, at similar latitudes, may be an adaptation to breeding in the inland habitat.

In 1964, clutches were removed four weeks after the first egg was laid to test whether the parents would lay again. On May 28, 154 clutches of ring-billed and 63 of California gulls were taken from the centre of a dense group of nests on island B. The nests were checked on the next day to determine the degree of disturbance caused by removing the eggs. Both species occupied their territories as usual, although the nests were empty. One California gull clutch was started on June 3, and one ring-billed gull clutch on June 4. No clutches were laid in the area of the experiment or elsewhere in the colony after the first week of June. The apparent inability to produce clutches three weeks after the peak of laying appears to be characteristic of California and ring-billed gulls. Black-headed gulls in Norway (Ytreberg, 1956) and glaucous-winged gulls in British Columbia could readily renest as late as three weeks and one month respectively after the first hatching.

## Hatching

Figure 7 shows commencement of hatching in both gull species. The dates are based on the emergence of the first chick in each clutch. The mean dates on which California gull chicks began hatching were June 6, 1964, and June 13, 1965; and ring-billed gulls June 4, 1964, and June 14, 1965. In 1964, ring-billed gull chicks hatched an average of 1.7 days earlier than California gull chicks. This difference was statistically significant. The later hatching of the California gull chicks was due to the significantly longer incubation period in this species (Table 6). The difference in the hatching periods was not more than 1.7 days because the laying periods of the two species were similar. The mean dates of the commencement of hatching for California and ring-billed gulls were respectively 6.5 and 9.7 days later in 1965 than in 1964. These statistically significant differences are linked with later commencement of laying in 1965, increased human disturbance, and nocturnal predation. These disturbances may have prolonged incubation in 1965 when incubation periods of 20 clutches of California gulls were an average of 2.8 days longer than in 1964. Only two incubation periods of 28 days and 29 days were known in the ring-billed gulls in 1965. This compares with an average incubation period of 25 days in the previous year. Emlen *et al.* (1966) reported that nocturnal disturbance by a raccoon (*Procyon lotor*) delayed hatching in the ring-billed gulls. The late mean date of the start of hatching in the ring-billed gulls in 1965 may have resulted from early egg losses caused by a snowstorm during incubation.

Since egg-laying was highly synchronized in the California and ring-billed gulls, incubation could become effective earlier in those species than in gulls nesting in a coastal habitat. For this reason, the amount of effective incubation during the laying period was calculated from differences in known time intervals in laying versus those in hatching between successive eggs of a clutch (Table 7).

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Figure 6. Cumulative distribution of clutch initiation in six gull species. Freshwater (upper): A. Ring-billed gull (this study) 53°15′N, inland, 473 clutches; B. California gull (this study) 53°15′N, inland, 347 clutches; C. Black-headed gull (Ytreberg, 1956) 59°55′N, coastal, 363 clutches. Marine (lower): D. Herring gull (Paludan, 1951) 55°18′N, coastal 214 clutches; E. Lesser black-backed gull (Paludan, 1951) 55°18′N, coastal, 273 clutches; F. Glaucous-winged gull (Vermeer, 1963) 48°38′N, coastal, 792 clutches.



Figure 6
Freshwater
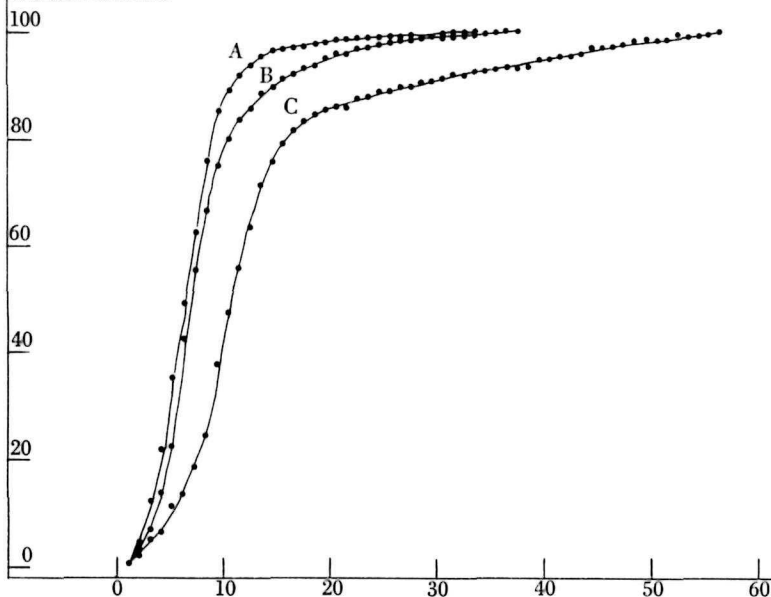
Marine
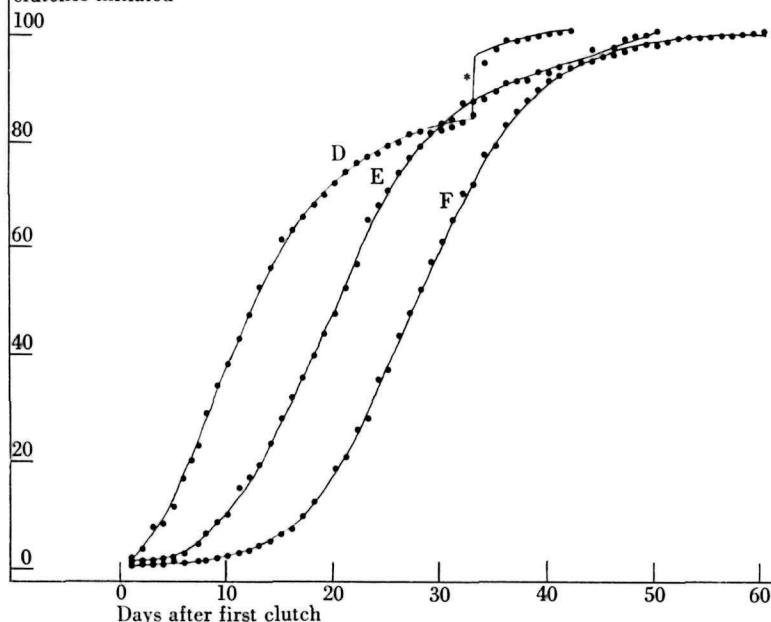
* Interference by snowstorm (Paludan, 1951:59)

It is evident that the hatching intervals are shorter than the laying intervals. Therefore, it can be deduced that incubation becomes fully effective not during the laying period, but when the maximum brood-patch temperature is applied to the eggs, approximately one week after clutch completion in herring gulls (R. H. Drent, pers. comm.). The amount of effective incubation applied to the eggs during the laying period was calculated with the following formula and expressed as a percentage.

Incubation effectiveness =

$$\frac{\text{Time interval between the hatching of successive eggs in a clutch}}{\text{Time interval between the laying of successive eggs in a clutch}} \times 100$$

For the Calfornia gulls, only 26 per cent and 51 per cent of the full incubation effectiveness was achieved after the first and second egg, respectively; and for the ring-billed gulls, 28 per cent and 54 per cent. The percentage of incubation effectiveness during laying in the inland-breeding California and ring-billed gulls is similar to that of four species of gulls breeding on marine coasts (Table 8).

Table 9 compares the incubation periods of California and ring-billed gulls at Miquelon Lake with those of marine-nesting gulls. Since incubation apparently takes slightly longer in larger gulls of the same genus, adult weights are shown. When weight differences are considered, there appears to be no adaptive shortening in the incubation periods of the inland-nesting California and ring-billed gulls.

**First flight and colony departure**
Table 10 shows the ages of California and ring-billed gulls at first flight in 1964. The average age was 40 days for California gulls, and 37.2 days for ring-billed gulls. On the average, California gulls hatched on June 6 were calculated to fledge by July 16; ring-billed gulls hatched on June 4, by July 11.

**Figure 7**

**California gull**

**Ring-billed gull**
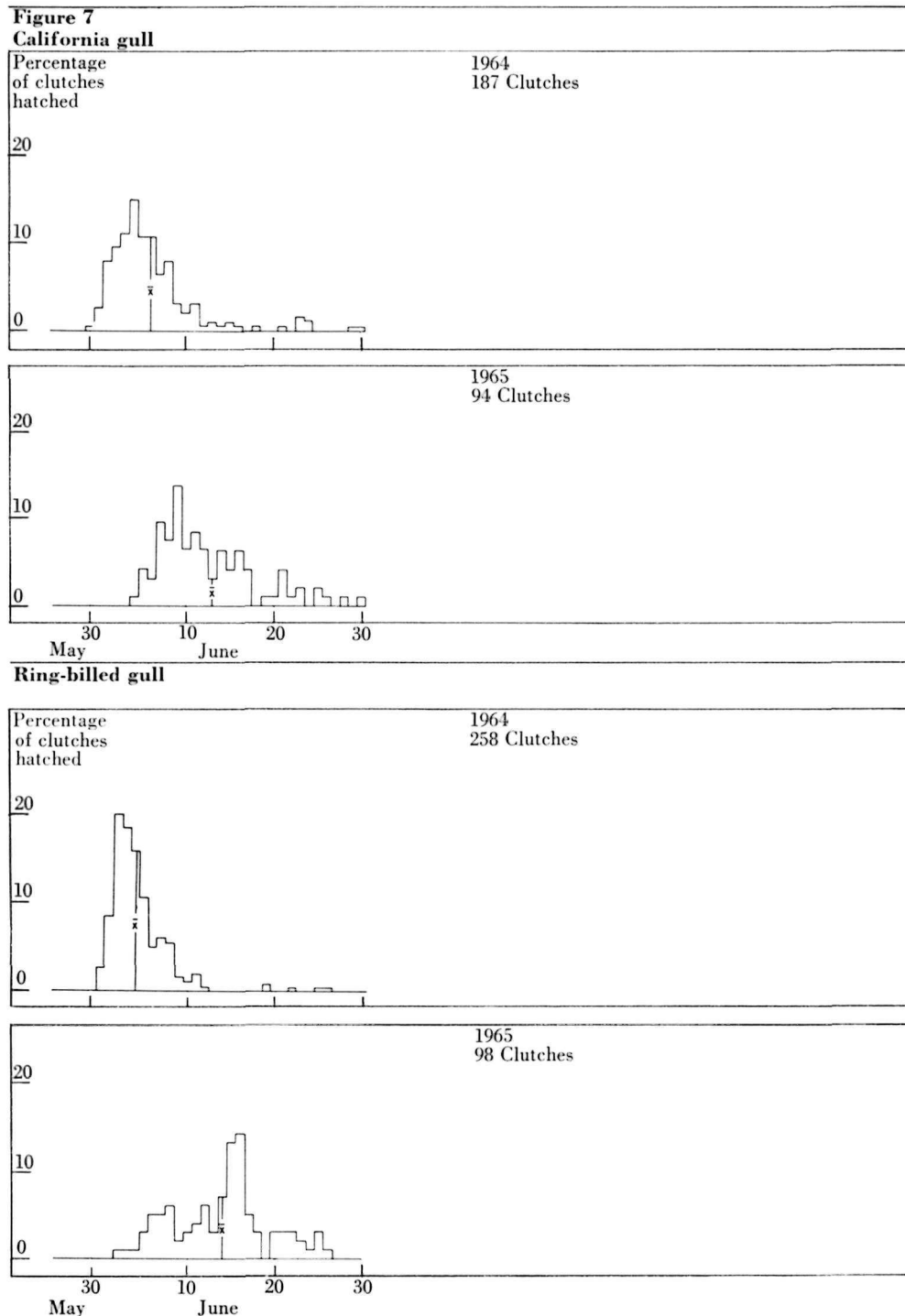
Observations made July 5, 9, 10, and 13, 1965, at two gull colonies at the north end of Beaverhill Lake showed that the chronology of the gull breeding cycles there were similar to those at Miquelon Lake. The first fledglings of both species at Beaverhill Lake were observed on July 9.

The chicks of the coastal-breeding herring gull (Paynter, 1949) and glaucous-winged gull on Mandarte Island fledged on the average at 42 and 44 days respectively. Since these two species are larger (Table 9) than California and ring-billed gulls, the slightly later dates are expected.

Every three days in July 1964, counts were made of the number of fledglings on island A. Fledglings of both species remained on the island for an average of 11 days after fledging, not much different from the average of 14 days during which glaucous-winged gull fledglings remained on Mandarte Island.

Most families of California and ring-billed gulls appear to break up at the colony. The counts made in 1964 show that the parents left island A just before the fledglings (Table 11).

The presence of the chicks appears to be the chief reason the adults remain on the nesting grounds. In 1965, no fledglings were produced. On July 2 of that year, only four adults of each species along with five California and three ring-billed gull chicks were on island A. On July 3, the eight chicks had disappeared and the adults had departed. Gulls had also left island B by that date.

The departure of the parents before the fledglings in 1964, and the much earlier disappearance of the adults from the breeding grounds in 1965 than in 1964 may indicate that the food supply was scarce at Miquelon Lake in July of both years. Surveys showed fish was scarce there (C. Hunt, pers. comm.). In contrast, at Lac la Biche (120 miles N.E. of Miquelon Lake) in the last week of August 1966, I observed many California gulls — adults and fledglings — near the nesting habitat. Continued residence so long after fledging may be related to abundant

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fish. More than one million pounds of fish are caught in Lac la Biche each year (C. W. Scott, pers. comm.).

I believe that once the fledglings leave the Miquelon Lake islands on which they were hatched they do not generally return, but go where food is readily available. The garbage dump in Edmonton attracts large numbers of gulls, and in August 1964 I saw several colour-banded juveniles, of both species, from Miquelon Lake. After the second week of August, no gulls remained on the islands of Miquelon Lake.

**Table 6**
The incubation periods* for 57 clutches of California and 64 of ring-billed gulls, 1964

| Gull species | Intervals between laying and hatching of the third egg, days | | | | | | Mean ± SE |
| | 23 | 24 | 25 | 26 | 27 | 28 | |
|---|---|---|---|---|---|---|---|
| California | | | 3 | 22 | 29 | 3 | 26.6 ± 0.09 |
| Ring-billed | 1 | 17 | 33 | 11 | 1 | 1 | 25.0 ± 0.10 |

*Incubation periods are the intervals between laying and hatching of the third egg of each species.

**Table 7**
Intervals between laying and hatching of successive eggs in clutches of California and ring-billed gulls, 1964

| | California gull eggs | | | | | | | | Ring-billed gull eggs | | | | | | | |
| | 1st-2nd | | | | 2nd-3rd | | | | 1st-2nd | | | | 2nd-3rd | | | |
| Intervals in days | 0 | 1 | 2 | 3 | 0 | 1 | 2 | 3 | 0 | 1 | 2 | 3 | 0 | 1 | 2 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. of laying intervals | | 2 | 14 | 1 | | 1 | 10 | 2 | | 4 | 15 | 2 | | 4 | 21 | 2 |
| No. of hatching intervals | 17 | 17 | | | 3 | 20 | 5 | | 39 | 29 | 1 | | 9 | 53 | 11 | 1 |
| Mean ± SE of laying intervals | 1.94 ± 0.10 | | | | 2.08 ± 0.14 | | | | 1.90 ± 0.12 | | | | 1.93 ± 0.09 | | | |
| Mean ± SE of hatching intervals | 0.50 ± 0.08 | | | | 1.07 ± 0.10 | | | | 0.53 ± 0.06 | | | | 1.05 ± 0.06 | | | |

**Table 8**
Comparison of effectiveness of incubation during laying in six species of gulls

| Gull species | Incubation effectiveness, % | | Source |
| | Interval between 1st and 2nd egg | Interval between 2nd and 3rd egg | |
|---|---|---|---|
| Herring | 30 | 53 | Paludan, '51 |
| Lesser black-backed | 18 | 60 | Paludan, '51 |
| Black-headed | 28 | 52 | Ytreberg, '56 |
| Glaucous-winged | 31 | 53 | Vermeer, '63 |
| California | 26 | 51 | This study |
| Ring-billed | 28 | 54 | This study |

**Table 9**
Incubation periods and adult weights in seven species of gulls

| Gull species | Incubation, days Mean ± SE | Sample | Source | Mean adult wt, g | Sample | Source |
|---|---|---|---|---|---|---|
| Herring | 27.2 ± 0.08 | 67 | Paludan, '51 | 1048 | 63 | Barth, '67 |
| Glaucous-winged | 26.9 ± 0.08 | 128 | Vermeer, '63 | 1051 | 31 | Vermeer, '63 |
| California | 26.6 ± 0.09 | 57 | This study | 769 | 39 | This study |
| Lesser black-backed | 26.1 ± 0.09 | 55 | Paludan, '51 | 736 | 19 | Barth, '67 |
| Mew | 25.8 ± 0.25 | 50 | Barth, '55 | 386 | 26 | Barth, '67 |
| Ring-billed | 25.0 ± 0.10 | 64 | This study | 497 | 39 | This study |
| Black-headed | 22.8 ± 0.07 | 156 | Ytreberg, '56 | 297 | 18 | Kruuk, '64 |

**Table 10**
Distribution of ages at first flight in California
and ring-billed gulls, 1964

| Gull species | Age in days at first flight | | | | | | | | | | | Age |
| | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | Mean ± SE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| California | 0 | 0 | 4 | 3 | 0 | 1 | 1 | 1 | 5 | 0 | 4 | 40.0 ± 0.72 |
| Ring-billed | 1 | 2 | 6 | 12 | 4 | 2 | 2 | 1 | 0 | 0 | 0 | 37.2 ± 0.28 |

**Table 11**
Decline in numbers of California and ring-billed
gulls on island A from July 26 to August 4, 1964

| Date | California gull | | | Ring-billed gull | | |
| | Adults | Fledglings | Adult/fledgling ratio | Adults | Fledglings | Adult/fledgling ratio |
|---|---|---|---|---|---|---|
| July 26 | 45 | 116 | 0.39 | 3 | 17 | 0.17 |
| July 28 | 26 | 71 | 0.37 | 0 | 2 | 0.0 |
| July 30 | 10 | 40 | 0.25 | 0 | 2 | 0.0 |
| July 31 | 12 | 35 | 0.29 | 0 | 2 | 0.0 |
| August 3 | 1 | 18 | 0.05 | 0 | 1 | 0.0 |
| August 4 | 0 | 1 | 0.0 | 0 | 1 | 0.0 |

## Nesting sites in the area

On May 7, 1964, egg-laying on island A
was already advanced, primarily in areas
where the dead herbaceous cover was short
and sparse. On April 25, 1965, when half
the island was free of snow, both species
settled on the snow-covered parts which had
least vegetation. On April 30, after the snow
had disappeared, I stripped the herbaceous
cover from one-and-a-half acres near the
ring-billed gulls' nesting locality. By the next
morning, many of them had established
territories in the clearing. This experiment
and observations of colonies of California
and ring-billed gulls in Alberta and Sas-
katchewan indicate that they prefer to nest
where vegetation is low and sparse.

The conspicuous plumage of nesting gulls
does not blend well with the surroundings,
and avoidance of dense herbaceous or shrub
cover may be an anti-predator mechanism.
By nesting in the open the gulls may more
easily protect themselves from approaching
predators – many birds can watch in all
directions, and an alarm call given by one
bird will alert all birds in the colony.

W. R. Salt (pers. comm.) has suggested
that gulls may require unobstructed sites so
they can fly away rapidly. On Mandarte
Island, many glaucous-winged gulls had
territories at the edge of dense shrubbery
under which they nested. Their nests were
connected with open meadows by vegetation-
covered tunnels, 3 to 10 feet long, from the
entrance of which the gulls would take flight
when I appproached. These gulls were not
forced by intraspecific competition for
nesting sites to choose such locations, for
areas of open meadow were still available.
Glaucous-winged gulls were probably sub-
ject to less predation than California and
ring-billed gulls.

California and ring-billed gulls avoided
nesting in dense herbaceous cover; however,
in some Albertan colonies where vegetation
was scarce they nested close to plants which,
in such conditions, may hide the nests from
predators.

California gulls nested chiefly on the
peripheries of islands A and B and on the

most elevated and boulder-strewn area on island A. Ring-billed gulls nested on flat, elevated terrain.

The choice of the nest-site is also partly determined by previous nest-location. In 1964, of six adults of each species colour-banded on island B, four (two California and two ring-billed gulls) returned the following year. Each occupied the same territory as in the previous year, and one ring-billed gull nested exactly where it did in 1964. One of the functions of nest-site faithfulness may be to ensure that the gulls return to grounds where successful breeding has occurred.

Although vegetation was scarce on some low-lying localities on the islands in Miquelon Lake, no (or few) gulls nested there. The low-lying areas had only recently emerged from the lake, and gulls may not yet have occupied them.

By mid-May 1965, 65 pairs of California gulls – 33 per cent of all California gulls breeding at Miquelon Lake that year – started to nest in region C (Fig. 2). This may have been caused by disturbance on islands A and B. One colour-banded California gull nested on island B in early May, but later moved to region C. Forty-seven clutches on peninsula $C_4$ were destroyed within 14 days of commencement of the first clutch. Tracks and large rectangular bites in the eggshells suggested that coyotes (Canis latrans) had destroyed the eggs. The remaining 18 clutches were located on island $C_1$ which, by May 30, had become connected to the mainland because of lowering of the lake. Within a week coyotes had destroyed all the clutches.

An inhabitant of the town of Lac la Biche told me that a coyote remained on one of the large islands in Lac la Biche after the spring thaw and as a result of its predation on a large colony of California gulls, no young were produced.

Murie (1940) showed that coyotes eat birds as well as eggs. He found that five per cent of 5,086 scats of coyotes in Yellowstone National Park contained birds, including ducks, geese, and grouse. The stomachs of

**Table 12**

The location of 206 California and 265 ring-billed gull nests on island A in relation to proximity to water, elevation above lake level, and type of topography, 1964

| | % of nests | |
| --- | --- | --- |
| Proximity to water, ft | California gull | Ring-billed gull |
| Within 75 | 68 | 27 |
| 75 - 150 | 32 | 63 |
| 150 - 225 | 0 | 10 |
| Elevation above lake level, ft | | |
| 0 - 2 | 60 | 16 |
| 2 - 4 | 14 | 78 |
| 4 - 6 | 26 | 6 |
| Topography | | |
| Boulder-strewn (rel. sloping) | 34 | 4 |
| Sloping | 61 | 6 |
| Flat | 5 | 90 |

30,000 coyotes examined over five years in western North America by the Bureau of Biological Survey, U.S. Fish and Wildlife Service, showed a six per cent frequency in remains of birds, other than poultry (Young, 1951). These observations suggest that gulls nest on islands because there they are relatively free of mammalian predation. Emlen et al. (1966) observed that raccoon predation on 1,000 ring-billed gull nests on a peninsula in Michigan caused parental neglect of eggs and young. Consequently, only a few chicks survived beyond the second day.

In temperate North America, colonial larids are confined chiefly to islands and marshes; in Europe, they nest successfully on coastal sand dunes (Goethe, 1956; Kruuk, 1964; Tinbergen, 1953). This may be a recent habit and may have become possible because of fewer terrestrial predators.

## Interspecific differences in the nesting habitat
Early in 1965 when the islands were still covered with snow, many California and ring-billed gulls appeared to have changing and very flexible territories. When the territories were being established, intraspecific clashes did occur, but no interspecific conflict was seen. California gulls encroaching on ring-billed territory were not evicted. From his studies on the interactions between

California and ring-billed gulls at Dog Lake, Manitoba, Moynihan (1956) observed that ring-billed gulls away from their territory usually retreated from California gulls; and on their territory only rarely made a brief and hesitant attack on an intruding California gull. At Miquelon Lake, ring-billed gulls behaved in the same way and their territories were thus limited by the presence of the California gulls.

Figure 8 shows the distribution of nests of both species on islands A and B in 1964. Figure 8 and Table 12 show that California gulls generally nested close to the water, in sloping areas. The ring-billed gulls nested farther from the water, and in flatter areas (Fig. 9). More California than ring-billed gulls nested in localities 4 to 6 feet above lake level, with large boulders which served as lookouts (Table 12, Fig. 10). A few California gulls nested among the ring-billed gulls, but only where large nearby boulders provided a viewpoint.

Comparison of Figures 8 and 11 shows that in 1965 ring-billed gulls on island A nested in an area occupied in 1964 solely by California gulls. On May 20, 1967, ring-billed gulls on island B nested in localities near the water (Fig. 12) occupied in 1964 and 1965 by California gulls. That ring-billed gulls were able to take over California gull territory was due to the absence of the latter species. Since California gulls nest among ring-billed gulls which, in turn, nest

**Figure 8**
**Island A**

Scale 1″ = 242′

**Island B**

Scale 1″ = 242′
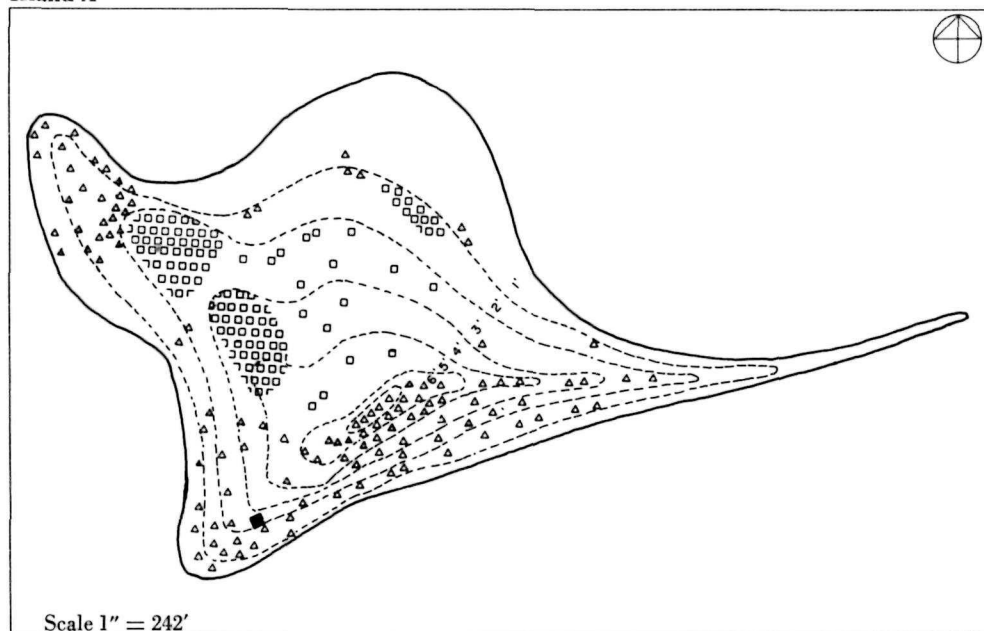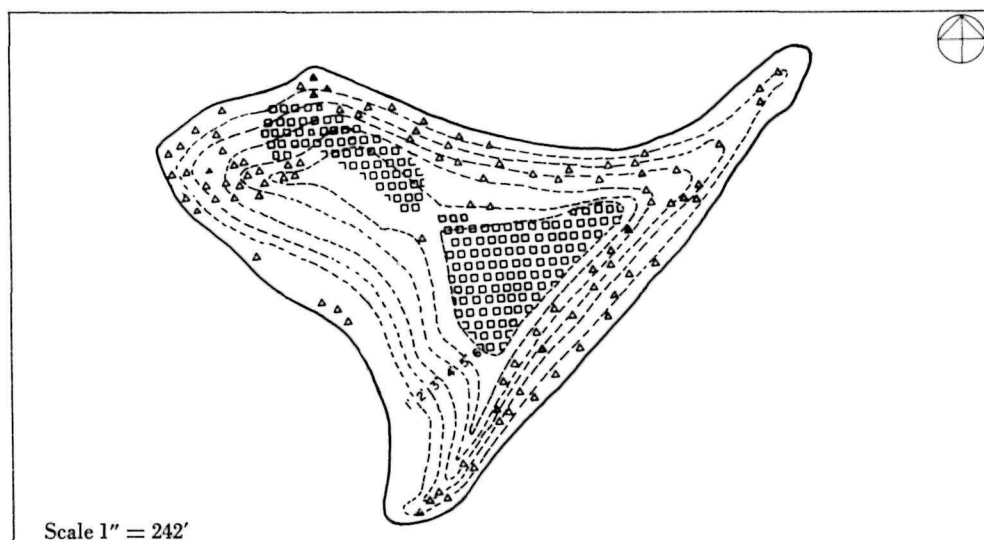
△ California gull
▢ Ring-billed gull
■ Observation cabin
--- Contour interval of one foot

in habitat previously occupied by the former, both species can nest in the same island habitat.

Table 13 shows the locations and degree of overlaps in the nesting habitat of California and ring-billed gulls on islands in Alberta and elsewhere. Either species may nest at the margins or in the centre, at low or elevated areas of the islands, but their colonies seldom overlap. At Honey Lake, California, gulls of both species nested together, probably because the island was small (Johnston and Foster, 1954).

Both species at Miquelon Lake nest on level ground. Black-headed gulls nest in dunes (Kruuk, 1964; Patterson, 1965), in marshes, or on islands (Ytreberg, 1956). Smith (1966) reports that glaucous gulls *(Larus hyperboreus)* nest on the ground or on cliff ledges, and Iceland *(L. glaucoides Kumlieni)* and Thayer's gulls *(L. thayeri)* nest almost exclusively on cliffs and occasionally on level ground. The mew gulls in North America nest in trees and on the ground. Compared to these intraspecific variations in nesting habitat, the interspecific differences in the California and ring-billed gulls' choice of nest site are not significant.

**Interspecific differences in the spatial distribution of nests**

Figure 13 depicts the distribution of distances from the nearest neighbour of 202 California and 230 ring-billed gull nests in a 30,000-square-foot area on island A, and of 193 glaucous-winged gull nests in a 30,000-square-foot area on Mandarte Island, British Columbia. The measurements were taken from the top of the rim of each nest to that of its nearest neighbour. The distribution of these distances is shown, with the distribution which would be expected if the nests were spaced entirely at random. The method of obtaining the random distribution curves is given in Appendix 2.

The Clark-Evans (1954) method was used to test whether the observed distributions in the three gull species departed from random. The distribution of nests of ring-

Figure 9. Ring-billed gulls nesting in flat and elevated area.

**Table 13**
Location and degree of overlap in the nesting habitat of California and ring-billed gulls at different geographical locations

| Geographical location | Species | Nesting location on island | | | | Degree of overlap in nesting habitat | | | Source |
|---|---|---|---|---|---|---|---|---|---|
| | | Periphery | Centre | Low | Elevated | None or little | Light | Moderate | |
| Big Stick Lake, Sask. | California gull | + | − | + | − | − | + | − | |
| | Ring-billed gull | − | + | − | + | − | + | − | Bent, 1921 |
| Columbia River, Wash. | California gull | − | + | − | + | + | − | − | |
| | Ring-billed gull | + | − | + | − | + | − | − | Hanson, 1963 |
| Honey Lake, Cal. | California gull | − | + | − | + | − | − | + | Johnston and |
| | Ring-billed gull | + | + | + | + | − | − | + | Foster, 1954 |
| Miquelon Lake, Alta. | California gull | + | − | + | + | + | − | − | |
| | Ring-billed gull | − | + | − | + | + | − | − | This study |
| Buffalo Lake, Alta. | California gull | + | + | + | + | + | − | − | |
| | Ring-billed gull | + | + | + | − | + | − | − | This study |
| Chip Lake, Alta. | California gull | + | + | + | − | + | − | − | |
| | Ring-billed gull | − | + | − | + | + | − | − | This study |
| Dowling Lake, Alta. | California gull | + | − | − | + | + | − | − | |
| | Ring-billed gull | − | + | − | + | + | − | − | This study |
| Frank Lake, Alta. | California gull | + | + | + | + | + | − | − | |
| | Ring-billed gull | + | + | + | + | + | − | − | This study |
| Keho Lake, Alta. | California gull | + | + | + | + | + | − | − | |
| | Ring-billed gull | + | + | + | + | + | − | − | This study |
| Lower Therien Lake, Alta. | California gull | + | + | + | + | + | − | − | |
| | Ring-billed gull | + | + | + | + | + | − | − | This study |
| St. Mary Reservoir, Alta. | California gull | − | + | + | + | + | − | − | |
| | Ring-billed gull | − | + | + | + | + | − | − | This study |

Figure 11. Distribution of California and ring-billed gull nests on island A, 1965.

Figure 12. Distribution of California and ring-billed gull nests on island B, 1967.



**Figure 11**
**Island A**
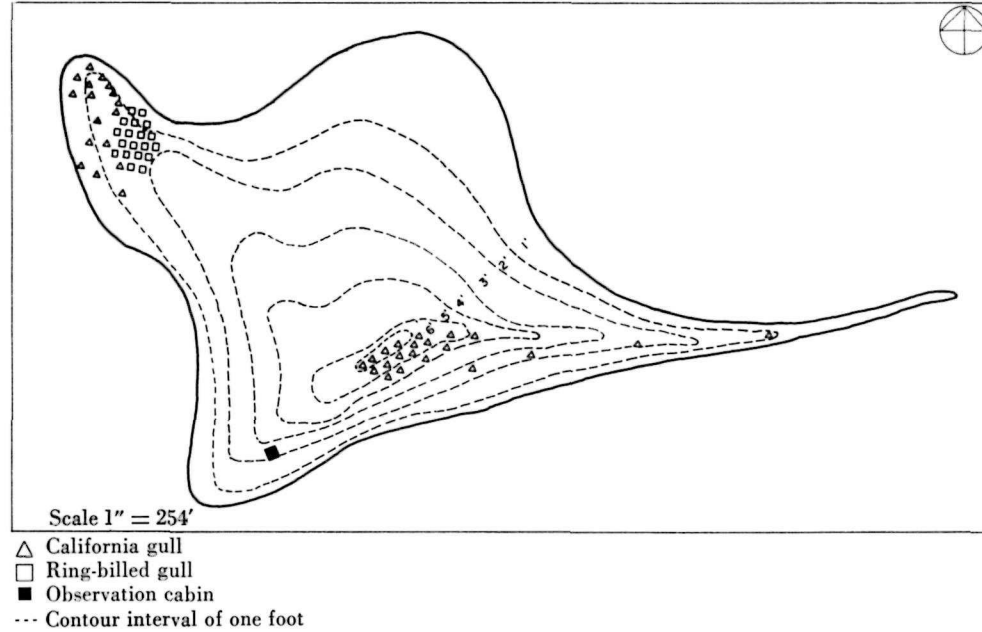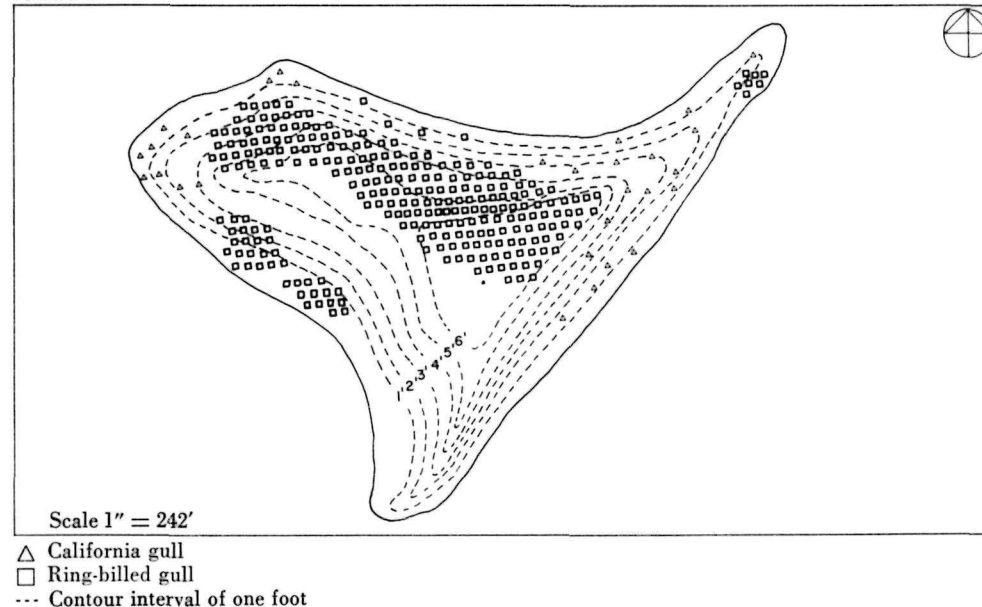
Scale 1″ = 254′

△ California gull
☐ Ring-billed gull
■ Observation cabin
--- Contour interval of one foot



**Figure 12**
**Island B**

Scale 1″ = 242′

△ California gull
☐ Ring-billed gull
--- Contour interval of one foot

billed gulls showed a significant deviation from randomness in the direction of aggregated spacing; that of California gulls, a non-significant deviation from randomness; that of glaucous-winged gulls, a significant deviation from randomness in the direction of uniform spacing.

The ring-billed gulls aggregated nesting pattern is similar to that of black-headed gulls breeding on dunes at Ravenglass (Cumberland) in the north of England (Patterson, 1965) and is therefore not a special adaptation to inland conditions. Kruuk (1964) suggested that this nesting pattern allowed a number of behavioural defence mechanisms such as the flight response to alarm calls and the mass attacks on a predator by a number of gulls. He showed experimentally that such attacks greatly reduced predation on eggs by crows and herring gulls. The ring-billed gulls' aggregated nesting pattern may protect them against such large predatory gulls as the California gulls which commonly prey upon very young ring-billed gull chicks.

The tendency toward uniform spacing of glaucous-winged gull nests may result from the strong territoriality observed in this species. A nest-moving experiment (Vermeer, 1963) showed that territorial aggression kept this species from nesting as densely as California and ring-billed gulls.

# Reproductive success

## Figure 13



Number of nests

Ring-billed gull
230 nests

• Observed distribution
x Random distribution
Areas: 30,000 sq. ft. for each species

California gull
202 nests

Glaucous-winged gull
193 nests

Distance in feet to nearest nest
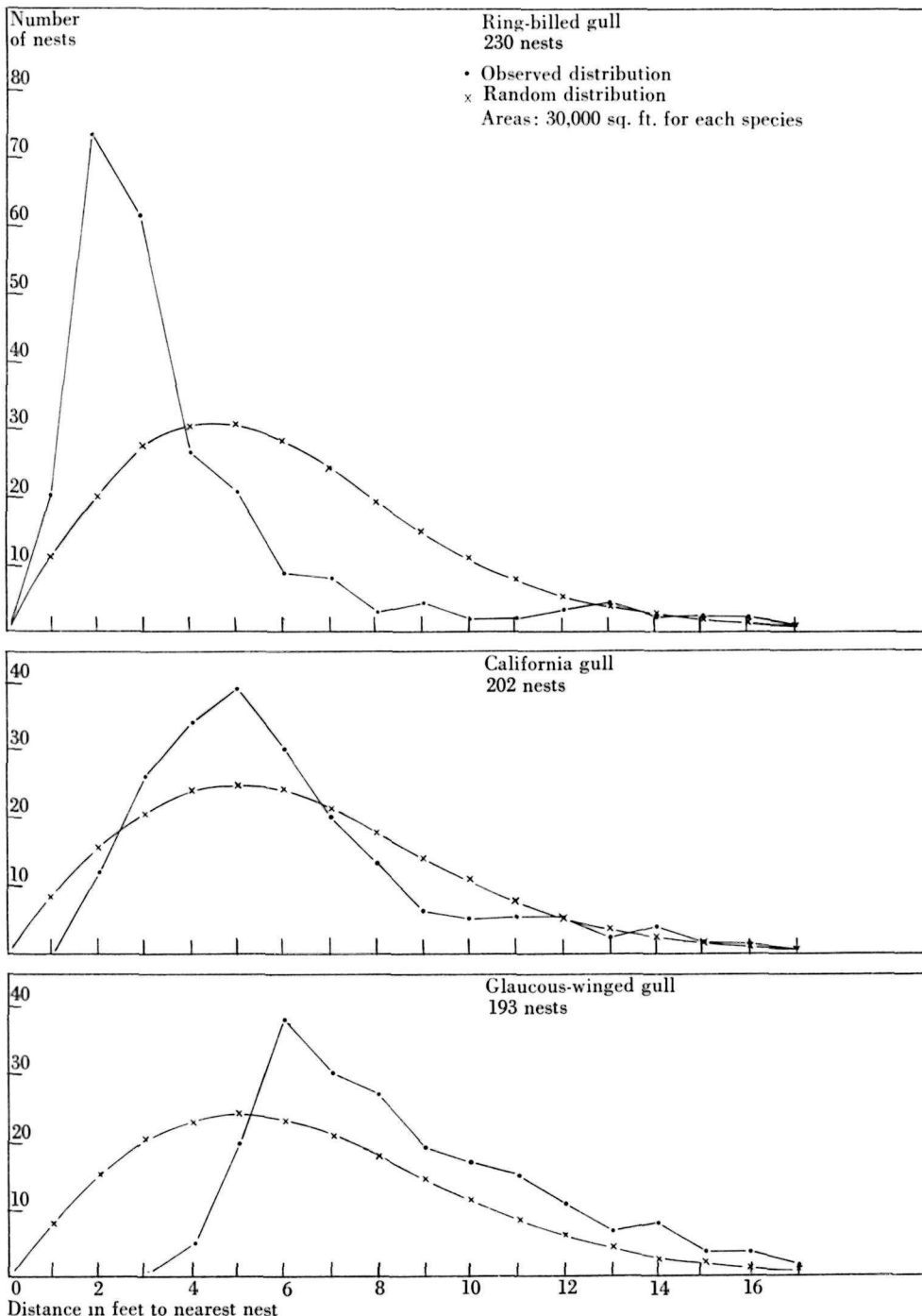
### Clutch size

The clutch sizes of California and ring-billed gulls for the years 1964 and 1965 are compared in Table 14. The average clutch size in 1965 was smaller than in the previous year. The 1965 data, however, may have been inaccurate, since more human and predatory disturbances that year may have led to greater loss of eggs. Table 14 also shows an interspecific difference in the mean clutch size in both 1964 and 1965. This significant difference may be related to the denser concentration of nests of the ring-billed gulls. Increased nest density may facilitate accidental laying by two females in one nest. The clutch with five eggs, listed in Table 14, may have been produced in this manner. One day there were three eggs in the nest; the next day, five. Since there are usually two days between the laying of successive eggs in a clutch, it is unlikely that one female produced two eggs within one day.

Other studies also show that clutches of more than three eggs occur more frequently in ring-billed gulls than in California gulls. Behle and Goates (1957) reported that of 400 California gull nests only one had more than three eggs. Johnston and Foster (1954) found that of 693 ring-billed gull clutches — many of them within three feet of each other – 20, 17, and 8 clutches contained 4, 5, and 6 eggs respectively. This also suggests accidental laying by two females in one nest.

Table 15 compares average sizes of clutches laid by California and ring-billed gulls with those of clutches laid by four other species of the genus *Larus* breeding along the coast. These studies of more than 200 clutches show that the mean clutch sizes of the California and ring-billed gulls are similar to those of the coastal-breeding gulls.

### Loss of eggs

Table 16 shows egg losses in California and ring-billed gulls in 1964 and 1965. On arrival at island A in the spring of 1964, I had to complete the observation tower.

**Table 14**
Clutch size of California and ring-billed gulls at
Miquelon Lake, 1964-65

| | No. of clutches | | | |
|---|---|---|---|---|
| | California gull | | | Ring-billed gull |
| Clutch size | 1964 | 1965 | 1964 | 1965 |
| 1 | 2 | 1 | | 2 |
| 2 | 35 | 33 | 30 | 76 |
| 3 | 168 | 97 | 227 | 345 |
| 4 | 1 | | 8 | 11 |
| 5 | | | | 1 |
| Total | 206 | 131 | 265 | 435 |
| Clutch size | 2.82 | 2.73 | 2.92 | 2.85 |
| Mean ± SE | ± 0.03 | ± 0.04 | ± 0.02 | ± 0.02 |

**Table 15**
Comparison of the mean clutch size in six species
of gulls

| Gull species | No. of clutches studied | Mean clutch size | Location | Source |
|---|---|---|---|---|
| California | 337 | 2.77 | Canada | This study |
| Ring-billed | 700 | 2.87 | Canada | This study |
| Ring-billed | 693 | 2.84 | U.S.A. | Johnston & Foster, 1954 |
| Glaucous-winged | 758 | 2.77 | Canada | Drent et al., 1964 |
| Herring | 1011 | 2.38 | Canada | Paynter, 1949 |
| Herring | 220 | 2.76 | England | Harris, 1964 |
| Herring | 217 | 2.91 | Denmark | Paludan, 1951 |
| Lesser black-backed | 242 | 2.75 | Denmark | Paludan, 1951 |
| Black-headed | 421 | 2.90 | Norway | Ytreberg, 1956 |

Because of my frequent activity in this area, California gulls deserted 264 (56 per cent) of 470 nests; and ring-billed gulls, 50 (16 per cent) of 315 nests. These egg losses are omitted from Table 16.

The percentage of eggs lost by California gulls was not much different in 1964 than in 1965, nor was there a significant difference in losses of eggs between the islands in 1965. On the other hand, ring-billed gulls lost significantly more eggs in 1965 and sustained a significantly greater loss on island B than on island A.

The egg losses for the California gulls in both years and the ring-billed gulls in 1964 were similar to those for other gulls studied (Harris, 1964; Drent et al., 1964). Table 17 shows a significant increase in ring-billed gull losses from "infertility or embryonic death" and "disappearance" in 1965. Many of the eggs which did not hatch

were cracked and, frequently, were eaten by the parents. Tinbergen et al. (1962) also observed that black-headed gulls, which usually do not attack an undamaged egg, devoured an egg once it had been broken. Since the ring-billed gulls ate many of their own decayed and cracked eggs, most of this species' egg loss in 1965 may have been the result of a higher rate of hatching failure. When the ring-billed gull eggs did not hatch at the expected time in 1965, 420 eggs on island B were opened and examined. Ninety-seven per cent of them had no embryo either because of infertility or early embryonic death.

Insecticide analysis of six decayed eggs of ring-billed gulls from island A disclosed the presence of 0.038 ppm DDT, 2.0 DDE, 0.029 DDD, and 0.028 dieldrin. The analysis was based on the wet weight of the composite sample.

On July 13, 1965, two ring-billed gull eggs from Beaverhill Lake, which were at the point of hatching, contained 5.18 ppm DDE and a trace of DDT, at least twice the total insecticide level of the eggs from island A. Lockie and Ratcliffe's (1964) study of insecticide residues in eggs of golden eagles (Aquila chrysaetos) in Scotland showed no evidence that concentrations of dieldrin below one ppm adversely affected reproductive success of this species. Therefore 0.028 ppm dieldrin in the analysed eggs from Miquelon Lake is unlikely to cause infertility or embryonic death.

Keith (1966) found that 30 to 35 per cent of eggs from 115 nests of herring gulls at Lake Michigan did not hatch. Nine eggs analysed for insecticides averaged 19 ± 3 ppm of DDT, 202 ± 34 of DDE, and 6.0 ± 0.9 of DDD (based on wet weight). The 84 per cent loss of ring-billed gull eggs at Miquelon Lake in 1965 was considerably greater than that of herring gulls in Keith's study. The insecticide contamination observed in the ring-billed gull eggs cannot be held responsible for hatching failure.

Data were sought on insecticide levels in the adult gulls, since contamination may have led to aberrations in incubation behaviour and subsequent parental neglect. Eight ring-billed and eight California gulls taken in June 1965 at Miquelon Lake, and eight ring-billed gulls taken in July 1965 from a Beaverhill Lake colony, were analysed for insecticides. I had the ring-billed gulls from Beaverhill Lake analysed, because I estimated that 1965 fledging success there was the same as, or better than, that at Miquelon Lake in 1964. The brains and uropygial glands were selected for analysis. The results of the analyses (Table 18) are difficult to interpret, but in both brain and uropygial tissue the descending order of DDE contamination was ring-billed gulls, Miquelon Lake; California gulls, Miquelon Lake; ring-billed gulls, Beaverhill Lake. These results may not be representative, since one highly contaminated gull may bias the mean contamination level in a small composite sample.

**Table 16**
Loss of eggs in two gull species at Miquelon Lake

| Year | Gull species | Island | No. of nests | No. of eggs laid | Loss of eggs No. | Loss of eggs % |
|------|--------------|--------|--------------|------------------|------------------|----------------|
| 1964 | California | A | 206 | 580 | 150 | 25.8 |
| 1964 | Ring-billed | A | 265 | 772 | 107 | 13.8 |
| 1965 | California | A | 87 | 233 | 53 | 22.7 |
| 1965 | California | B | 44 | 125 | 40 | 32.0 |
| 1965 | Ring-billed | A | 58 | 148 | 86 | 58.1 |
| 1965 | Ring-billed | B | 378 | 1093 | 955 | 87.4 |

**Table 17**
Analysis of failure to hatch in two gull species, 1964-65

| | No. of eggs California gull 1964 | California gull 1965 | Ring-billed gull 1964 | Ring-billed gull 1965 |
|------|------|------|------|------|
| Cause | | | | |
| Infertility or embryonic death | 76 (13.1) | 26 (7.3) | 62 (8.0) | 554 (44.7) |
| Disappearance — presumably eaten | 61 (10.5) | 60 (16.8) | 39 (5.0) | 465 (37.5) |
| Death in pipping | 6 (1.0) | 4 (1.1) | 6 (0.8) | 5 (0.4) |
| Incubation ceased* | 7 (1.2) | 3 (0.8) | | 17 (1.4) |
| Total egg loss | 150 (25.8) | 93 (26.0) | 107 (13.8) | 1041 (84.0) |

Note: The percentage of total number of eggs laid appears in parentheses.
*Eggs lost as a result of parents dying or eggs buried in the nest.

**Table 18**
Insecticide analysis of composite samples of brains and uropygial glands of gulls

| Tissue | Location | Date | No. in composite sample | Mean residue of content, ppm of wet wt California gull | Mean residue of content, ppm of wet wt Ring-billed gull |
|--------|----------|------|-------------------------|--------------------------------------------------------|---------------------------------------------------------|
| Brain | Miquelon L. | Mid-June | 8 | 2.6 DDE / 0.25 DDD / 0.07 DDT | 23.0 DDE / 0.12 DDD / 0.06 DDT |
| Brain | Beaverhill L. | Mid-July | 8 | | 0.37 DDE / 0.03 DDD / 0.01 DDT |
| Uropygial gland | Miquelon L. | Mid-June | 8 | 20.0 DDE / 0.38 DDD / 0.16 DDT | 30.0 DDE / 0.40 DDD / 0.14 DDT |
| Uropygial gland | Beaverhill L. | Mid-July | 8 | | 12.7 DDE / 0.36 DDD / 0.23 DDT |

In 1965, ring-billed gulls ate mainly waste grain left in the field throughout April and the first half of May; California gulls ate a more heterogeneous diet. Since the high level of insecticide residues in the ring-billed gulls at Miquelon Lake seemed to be a local phenomenon, a composite sample of 32 pellets of oats and barley was analysed. Analysis showed the presence of 3.0 ppm DDE, 0.5 DDT, 0.01 DDD, and a trace of dieldrin. These residues may have come from the digestive juices of the gulls. If the insecticide residues originated in the grain, the contaminated grain must have been locally distributed; otherwise the ring-billed gulls at Beaverhill Lake would have accumulated residues in similar amounts.

The greatest mortality occurred in eggs laid on island B (Table 16) early in the season. Ice conditions prevented me from visiting island B before May 7, when the egg-laying process was advanced. Ring-billed gull egg mortality was lower on island A, even though I occupied a cabin there, than on island B. Therefore, human disturbance may be disregarded as a cause of low fertility or early embryonic death.

In Table 19, the percentage of clutches started by ring-billed gulls on islands A and B has been calculated for different periods of the laying season in relation to a night-long snowstorm on May 17, 1965, when the temperature dropped to 32°F. The California gulls nesting close to the cabin on island A continued to incubate throughout the storm. I could not observe the ring-billed gulls at this time.

MacMullan and Eberhardt (1953) found that pheasant embryos were progressively more vulnerable to chilling as incubation progressed. Moreng and Bryant (1956) reported that chick embryos exposed to low temperatures after the fourth day of incubation showed a drastic reduction in ability to hatch. Table 19 shows that by May 17 the ring-billed gulls on island B were more advanced in laying than those on island A. If their eggs were exposed to the snowstorm, the more advanced embryos on island B would be more susceptible to chilling than

**Table 19**

Comparison of progress in clutch commencement between ring-billed gulls nesting on islands A and B in relation to a snowstorm on May 17, 1965

| | Clutches started in the ring-billed gull, % | |
|---|---|---|
| Time period | Island A | Island B |
| May 3 - 9 | 2.2 | 66.0 |
| May 10 - 16 | 88.9 | 28.1 |
| May 17 | — | 0.7 |
| After May 17 | 8.9 | 5.2 |

**Figure 14**



the less advanced on island A. It will be recalled that the loss of ring-billed gull eggs was significantly greater on island B than on island A (Table 16).

Chilling cannot be held solely responsible for the extensive egg mortality in the ring-billed gulls, otherwise the hatching success of the California gulls would probably have been similarly affected. As observed before, ring-billed gulls are much more excitable than California gulls. Extensive nocturnal predation occurred during the 1965 breeding season. If nocturnal predation occurred during the storm, the ring-billed gulls would probably be more easily disturbed and would leave their eggs exposed to chill longer than the California gulls. Emlen *et al.* (1966:679) reported that ring-billed gull eggs in Michigan became chilled when the parents fled in panic from a visiting nocturnal raccoon.

"The effects of these mass exoduses were apparent. The eggs and newly hatched young were cold; the cheeping heard shortly after a mass departure soon subsided as the chicks became chilled in the 5° to 15°C temperatures. A sampling of 87 eggs on June 5 revealed that 32 per cent of the embryos were dead. Daytime checks of nests on the days following the upflights showed a nightly mortality of between 30 and 80 per cent of one- to two-day-old chicks, and a check of the site in late June indicated that very few, if any, young had been produced."

Thus, nocturnal predation combined with bad weather may explain the hatching failure of ring-billed gulls at Miquelon Lake in 1965.
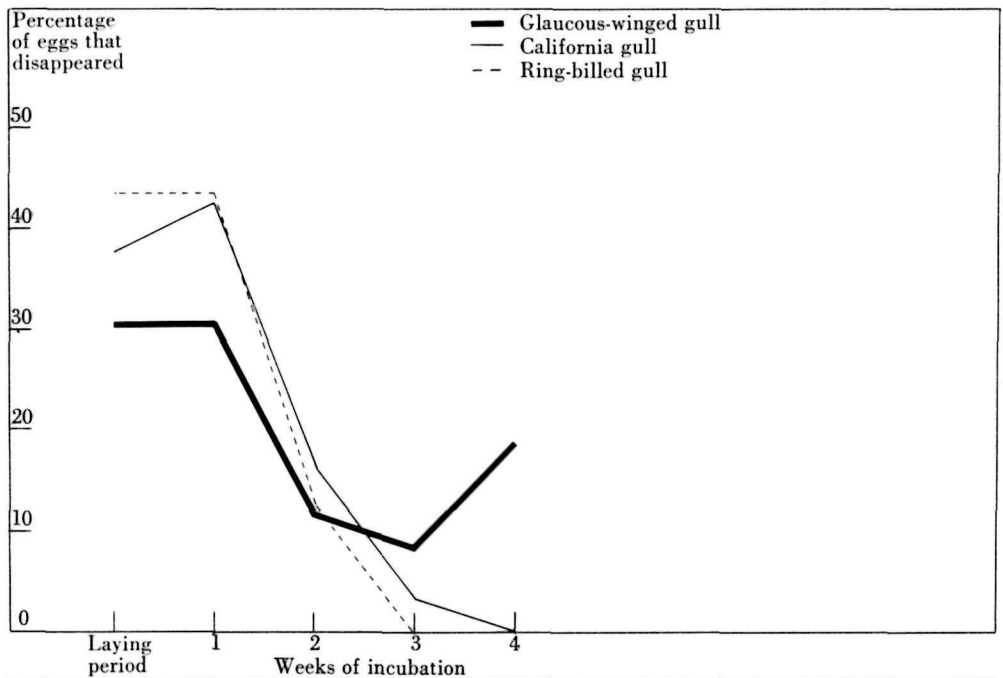
Table 20 shows the number of California and ring-billed gull eggs which disappeared or were eaten during the laying and incubation period. Only the 1964 data are used since conditions during laying and incubation were more natural in that year than in 1965. Similar data for glaucous-winged gulls on Mandarte Island in 1962 are shown for comparison.

Most eggs disappeared or were eaten, presumably by gulls, during laying and in the first week of incubation. Ytreberg (1956) reported that black-headed gulls lost four times as many eggs per time unit during laying, when gulls are more easily disturbed and more readily leave the nests, than during incubation. It appears that incubation provides warmth for the development of the embryo and also reduces egg predation. Figure 14 compares the number of eggs which had disappeared or were eaten during laying and the subsequent weeks of incubation with the total number of eggs disappeared or eaten in each species

(taken as 100 per cent). The rates of disappearance of California and ring-billed gull eggs were similar. The rate for eggs of glaucous-winged gulls differed, chiefly in the last week of incubation; but was, on the whole, similar to that of the inland-nesting species.

Three eggs of California gulls were lost in 1964 when the parents were decapitated. Three and 17 eggs of California and ring-billed gulls respectively were lost in 1965 for the same reason. One California gull was found dead on island A in 1964, and one California and six ring-billed gulls were found dead on island B in 1965. In all cases the dead birds were decapitated. Feathers in the area where the bodies were found in 1965 matched those of the great horned owl *(Bubo virginianus)*. In May 1963, I found ten decapitated adult gulls on island A, on or close to their nests.

No California and ring-billed adults were found dead as a result of predation after the eggs hatched. Kruuk (1964) also found

that predation on adults in a colony of black-headed gulls decreased sharply after hatching. After hatching, owls at Miquelon Lake probably preyed on chicks rather than on adults. Austin (1946) reported that one great horned owl at Cape Cod killed 15 to 20 adult common terns in a single night. Errington *et al.* (1940) examined pellets of great horned owls in Iowa and Wisconsin and showed that they prey considerably upon breeding and migrating coots, rails, grebes, and ducks. In summary, the great horned owl seemed to be the chief cause of mortality among breeding adults at Miquelon Lake. I did not observe predation on adults of the coastal glaucous-winged gulls on Mandarte Island in the summers of 1961 and 1962.

### Loss of chicks

Table 21 summarizes fledging success of California and ring-billed gulls on island A in 1964. No chicks fledged in 1965.

In July 1965, I investigated two gull colonies at the north end of Beaverhill Lake. About 200 pairs of California gulls occupied an island of approximately one acre. I estimated fledging success at 1.4 chicks per pair. A few miles away about 3,000 pairs of ring-billed gulls and less than 50 pairs of California gulls nested on an island of approximately 25 acres. I could not count the ring-billed gull chicks here, but I estimated success to be the same as, or better than, that of the same species at Miquelon Lake in 1964. Hence, the absence of fledglings at Miquelon Lake in 1965 appeared to be a local phenomenon.

Table 22 shows the loss of chicks of both species on island A in 1964 and 1965. Egg loss from 17 California gull nests on island A in 1965 was included in Table 16, but the loss of chicks from these nests was omitted from Table 22 since chicks were removed from them for an exchange experiment with chicks on island B. In most cases, I could not ascertain the cause of death for the chicks had disappeared between visits.

Gull chicks pecked to death by adults while wandering away from their parents

**Table 20**
Number of eggs disappeared or eaten during laying and incubation in three gull species

| | No. of eggs disappeared or eaten | | |
| | Ring-billed gull 1964 | California gull 1964 | Glaucous-winged gull 1962 |
|---|---|---|---|
| Laying* | 17 (2.2) | 23 (4.0) | 18 (1.3) |
| Incubation | | | |
| Week 1 | 17 (2.2) | 26 (4.5) | 18 (1.3) |
| Week 2 | 5 (0.6) | 10 (1.7) | 7 (0.5) |
| Week 3 | 0 | 2 (0.3) | 5 (0.4) |
| Week 4 | 0 | 0 | 11 (0.8) |
| Total no. of eggs disappeared or eaten | 39 (5.0) | 61 (10.5) | 59 (4.3) |

Note: The percentage of total number of eggs laid is shown in parentheses.
*Laying averaged 4 days for California and ring-billed gulls and 4½ days for the glaucous-winged gulls.

**Table 21**
Fledging success of two gull species at Miquelon Lake, 1964

| | | Young fledged | | |
| Gull species | Total | Per nest | % of egg | % of chicks |
|---|---|---|---|---|
| California | 210 | 1.0 | 36.2 | 48.8 |
| Ring-billed | 265 | 1.0 | 34.3 | 39.9 |

have been included in the category "pecked to death by gulls." Adult attack on strange chicks was the primary cause of chick mortality in glaucous-winged gulls on Mandarte Island. Aggressive adults also caused most of the chick mortality in ring-billed gulls in Michigan, U.S.A. (Emlen, 1956); and in herring gull colonies in Denmark (Paludan, 1951) and New Brunswick, Canada (Paynter, 1949).

Colour-bands of chicks were recovered in adult pellets and on legs left after the body had been devoured. California and ring-billed gulls were seen preying on chicks, mostly under one week old, of their own and the other species. But predation on chicks by California gulls was much more common.

Headless chicks were found on island A in 1964 and 1965. Feathers of great horned owls were found in the same area, and on several evenings I heard their calls near the island. I saw a great horned owl roosting during the day in willow bushes near a

ring-billed gull colony at Beaverhill Lake in July 1965, and found two decapitated gull chicks nearby.

Twelve three- and four-week-old headless chicks were also found on island B in 1965, and feathers at the site suggested that they were killed by the great horned owl. Newly hatched chicks, and some a few days old, were also found chilled and dead at that time. At least 10, and perhaps many more, died in this way, apparently from neglect during nocturnal predation.

I saw a red-tailed hawk *(Buteo jamaicensis)* kill a three-week-old California gull chick on island A in 1964 and located its nest containing two newly hatched young. Pellets below the nest contained colour-bands from two ring-billed gull chicks. Farther from the gull colony were two nests of red-tailed hawks. No remains of gull chicks were found in or below these nests, or in pellets of the hawk in 1964 or 1965. Red-tailed hawks were not seen preying on gull chicks in 1965.

**Table 22**
Causes of mortality among gull chicks on island
A, 1964-65

| Causes | California gull 1964 | | California gull 1965 | | Ring-billed gull 1964 | | Ring-billed gull 1965 | |
|---|---|---|---|---|---|---|---|---|
| Disappearance | 126 | (57.3%) | 85 | (63.0%) | 234 | (58.5%) | 39 | (62.9%) |
| Predation | | | | | | | | |
| Pecked to death by gulls | 31 | | 3 | | 34 | | 3 | |
| Eaten by gulls | 11 | | 4 | | 31 | | 2 | |
| Eaten by great horned owl (?)* | 0 | (19.5%) | 19 | (20.7%) | 3 | (17.5%) | 5 | (16.1%) |
| Eaten by red-tailed hawk | 1 | | 0 | | 2 | | 0 | |
| Eaten by weasel (?) | 0 | | 2 | | 0 | | 0 | |
| Other | | | | | | | | |
| Carcasses found, cause unknown | 37 | (16.8%) | 15 | (11.1%) | 84 | (21.0%) | 11 | (17.8%) |
| Exposure during rain | 7 | | 6 | | 0 | | 2 | |
| Disease | 2 | | 1 | | 6 | | 0 | |
| Crippling | 1 | (6.4%) | 0 | (5.2%) | 3 | (3.0%) | 0 | (3.2%) |
| Blindness | 1 | | 0 | | 0 | | 0 | |
| Suffocation on food | 3 | | 0 | | 1 | | 0 | |
| Crushed by observer | 0 | | 0 | | 2 | | 0 | |
| Total deaths | 220 | (100%) | 135 | (100%) | 400 | (100%) | 62 | (100%) |

*Gull chick mortality caused through predator-
induced exposure is included.

Two one-day-old California gull chicks
on island A, found blood-stained and with
puncture wounds on their neck and head,
subsequently died. They may have been
victims of a least weasel. Least weasels were
seen several times on island A. They were
probably preying on the abundant meadow
voles. Least weasels may have taken newly
hatched chicks, but since they are subject
to attack by the adults, they are not impor-
tant predators on gulls. The remains of one
least weasel were recovered from a gull
pellet, indicating that predator may be-
come prey.

In 1964, seven California gull chicks, dis-
turbed by me before a rainstorm, died. The
disturbance caused chicks to hide away
from the nest. They were not brooded by
the adults and thus became completely wet
and chilled. They seemed unable to return
to the nest-site in this condition and died
from exposure. Other chicks brooded by
their parents on the shore survived the
same storm. Very young gull chicks appear
to be vulnerable to persistent rain, even
without human disturbance. Six California
and two ring-billed gull chicks in their first
three days apparently died because of a
three-day rainfall in the last week of June
1965.

Two dead California gull chicks, found
with the hind limbs of a ground squirrel
protruding from their mouth, apparently
suffocated. One California and one ring-
billed gull chick died from ingesting a large
piece of bone.

The chick mortality in the different cate-
gories in Table 22 can be compared accord-
ing to species and years. The percentage of
missing chicks did not vary significantly
between the species. The slight increase in
the disappearance of chicks in 1965 may
have been the result of less frequent check-
ing of nests during the early chick stage in
1965 (once every three days) than in 1964
(once each day).

A higher proportion of gull chicks were
pecked to death by adults in 1964, when
denser nesting may have brought on more
aggressive encounters. A smaller propor-
tion of remains and colour-bands of chicks
eaten by gulls was found in 1965, because
the lush vegetation that year made it more
difficult to find the chick remains. Many
more headless gull chicks, presumably vic-
tims of the great horned owl, were found in
1965 than in 1964. Although predation by
owls varied seasonally, the total percentage
of chicks killed by all predators did not
vary significantly between species or years.

The total proportion of "carcasses found,
cause unknown" was significantly greater
in 1964 than in 1965. It may have been that
in 1965 no chicks reached their fifth week
of life when carcasses can readily be found.

Causes of mortality in chicks of Cali-
fornia and ring-billed gulls on island A, be-
tween 1964 and 1965, are compared with
total eggs hatched and with total mortality
in Figure 15. Deaths from all measured fac-
tors increased in 1965, so no factor can be
singled out as the cause of poor reproduc-
tive success in that year. Parental neglect
describes the situation without explaining.
Perhaps the increased activity of the great
horned owl contributed, as did a raccoon in
a colony of ring-billed gulls studied by
Emlen et al. (1966), to panic in the colony.

Several studies of colonial species, e.g.,
black-headed gulls (Kruuk, 1964; Patter-
son, 1965), have shown that small groups
have little success. In 1966, L. W. Dwerny-
chuk (pers. comm.) found 10 fledglings on
island A, but observed no great horned owl
predation. Hence the smaller size of the
group was not the cause, per se, of the
complete reproductive failure. Nocturnal
predation may, however, be much more
severe on a small colony of nesting gulls.
The predator-induced absence of parents

Figure 15. Comparison of mortality of California
and ring-billed gull chicks on island A to total
eggs hatched (absolute mortality) and total chick
deaths (relative mortality), 1964-65.

**Figure 15**
**Absolute mortality**
**(Eggs hatched = 100%)**

**Relative mortality**
**(Total deaths = 100%)**



☐ Rain, disease, accidents and other causes
▨ Predation
▪ Found, cause of death unknown
■ Disappeared
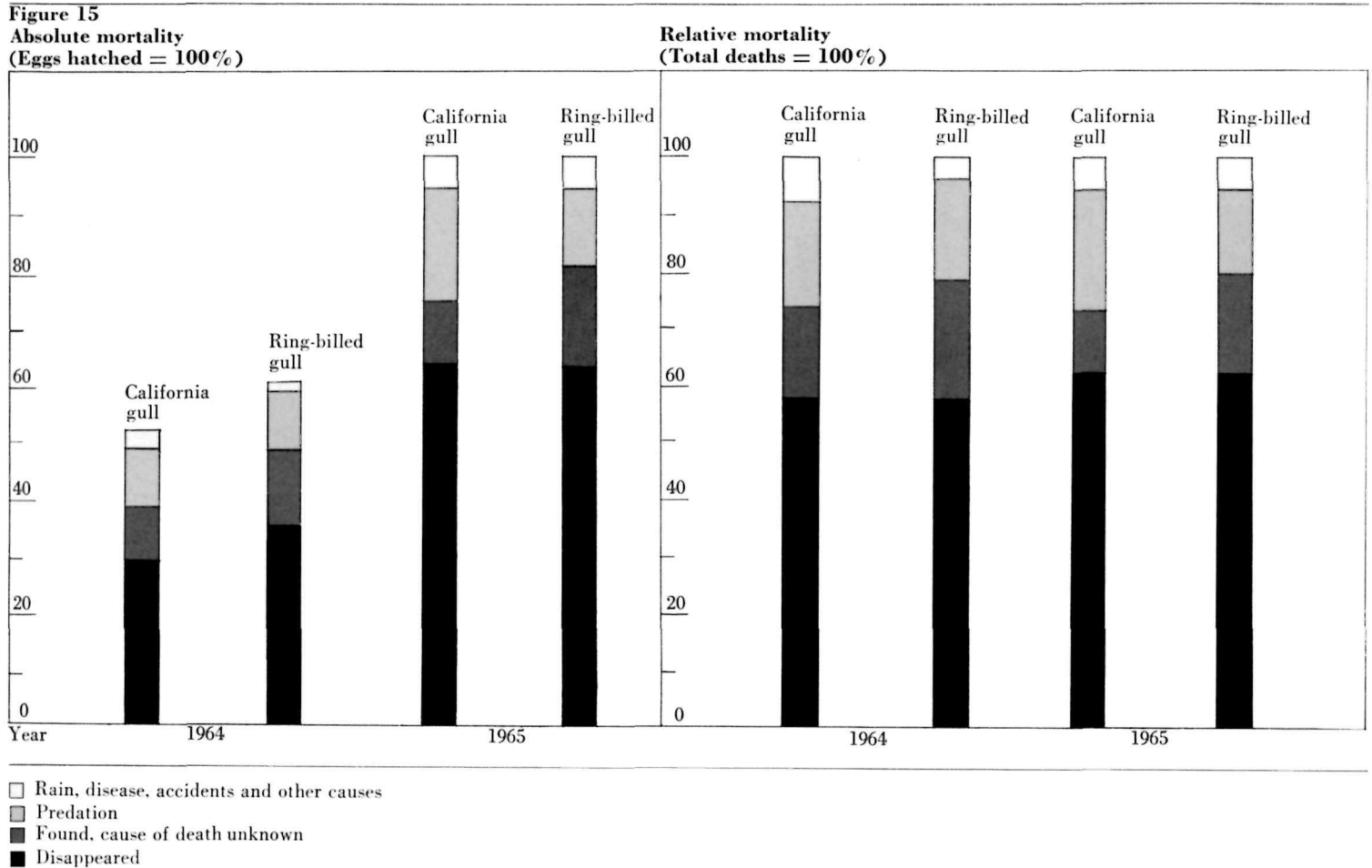
causes young chicks to die from exposure.
In addition, fewer warning calls by a
smaller number of adults may not provide
sufficient warning to the chicks to hide and
hence they are more vulnerable to predation.

Figure 16 relates fledging rates of Cali-
fornia and ring-billed gulls in 1964 and
those of the glaucous-winged gulls in 1962
on Mandarte Island to different times of
clutch commencement. The fledging rate per
egg laid, rather than the fledging rate per
clutch, is shown, since the average clutch
size in all three species declined with the
progress of the laying season. The mean
number of glaucous-winged gull fledglings
per egg was similar for clutches started in the

first six weeks, but declined significantly for
clutches initiated during the last two weeks of
the laying period. The combined California
and ring-billed gull fledging rate decreased
significantly for the second bi-weekly period
of laying. No chicks fledged from three
California and two ring-billed gull clutches
started after the first four weeks of clutch
commencement. Fledglings from late
clutches of California and ring-billed gulls
declined in number much earlier in the
season than those of glaucous-winged gulls.

The fledging rates per egg laid of the
three gull species of Figure 16 are sub-
divided into hatching and fledging rates per
egg hatched in Figure 17. The decreased

fledging rate of late clutches resulted chief-
ly from difficulties in raising chicks from
hatching to fledging, and not from a rise
in egg mortality caused by deterioration in
incubation behaviour of the parents towards
the end of incubation.

To test how growth and survival were
related to the time of hatching, California
gull chicks were raised in plots A and B
on an island in Joseph Lake in 1967. The
plots were fenced with wire mesh 2½ feet
high and were 50 feet by 30 feet each. Late
clutches in plot A and early clutches in plot
B were replaced by early and late clutches
respectively from other parts of the island.
The late clutches were obtained from an

Figure 16. Fledging rates of three gull species for clutches started during subsequent bi-weekly periods. Figures on top of bars show number of clutches started during each bi-weekly period; those in parentheses, the mean clutch size for each bi-weekly period.

**Figure 16**



Percentage of chicks fledged per egg laid

☐ Glaucous-winged gull
☐ California gull
■ Ring-billed gull

Time of clutch initiation in bi-weekly periods
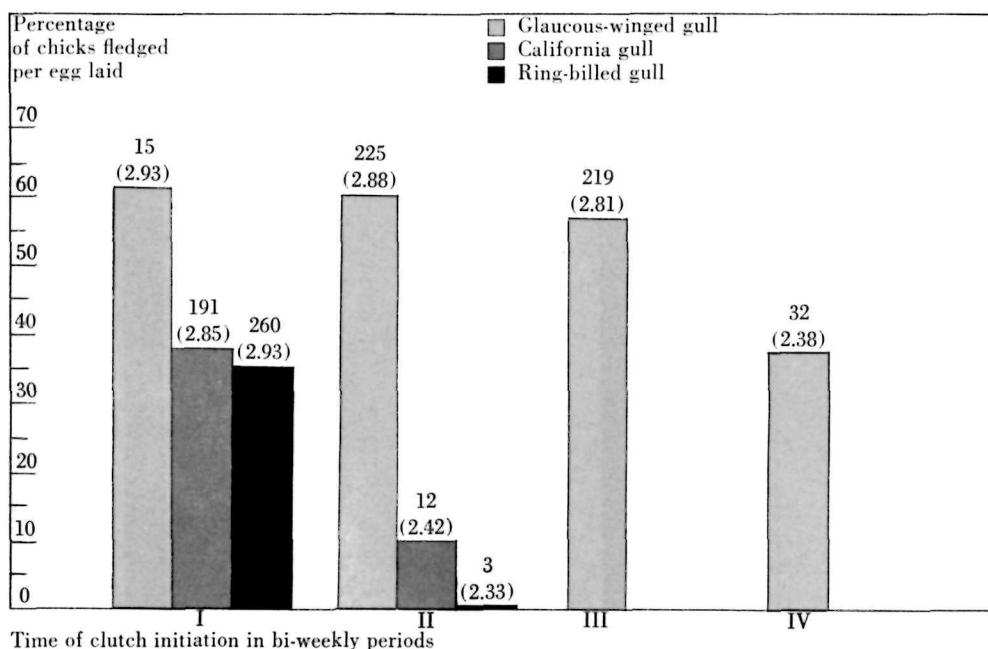
area where all clutches had been removed on May 20, and clutches started after that date were taken to replace early clutches in plot B. Chicks hatched late in the season survived as well and grew as rapidly as those hatched early in the season (Table 23).

Whether the lower chick survival for late clutches in 1964, compared with that in 1967, was caused by food shortage, predation, or other factors could not be ascertained. Predation on the gull chicks in 1967 may have been curtailed by the wire mesh fence which prevented them from straying into the open where they would be more subject to attack by adult gulls. In addition, herbaceous cover in the plots provided shelter from predation. Such predation was observed at Miquelon Lake in 1964 and 1965 on chicks, within their first two weeks of life, on the open beach and in the water. Paludan (1951) found that herring gull chicks which hatched late in the season had a considerably lower survival rate than early hatching chicks. This he ascribed to

**Table 23**

Comparative fledging success and body weights of early- and late-hatched chicks of California gulls, 1967

|  | Hatched | |
| --- | --- | --- |
|  | June 7-10 | June 23-27 |
| No. nests | 24 | 34 |
| No. chicks hatched | 72 | 60 |
| No. chicks fledged | 43 | 37 |
| Chicks fledged, % | 60 | 62 |
| No. chicks weighed* | 41 | 36 |
| Mean wt, g | 601 | 633 |
| Range in wt, g | 270-820 | 450-890 |

*Chicks in their sixth week.

the demand for food generated by rapid growth of the early chicks which increased predation by their parents upon the small later-hatching chicks. Like the herring gulls, the California gulls may have increased their predation on small gull chicks as the 1964 breeding season progressed.

The higher survival rate in late-hatching chicks in 1967 than in 1964 may be a result of these chicks being raised by gulls which initiated laying at normal times. Coulson

and White (1958) and Vermeer (1963) showed that late nesters are usually young, inexperienced birds, or repeat layers whose first clutches failed. Parental inexperience may also have contributed to the lower survival rate in the late chicks in 1964.

The 1967 experiment did not prove that a seasonally limited food supply governs the short breeding season of the inland-nesting California and ring-billed gulls, since both survival and growth were as good in the late-hatched California gull chicks as in those hatched earlier during the 1967 breeding season.

The mortality rate of the chicks varies with their age. Table 24 shows the weekly mortality rate of the California and ring-billed gull chicks in 1964 and glaucous-winged gull chicks on Mandarte Island in 1962. These rates were calculated from the number observed alive at the beginning of each week. Since 1965 was an abnormal year for chick production at Miquelon Lake, data for that year have not been included in the table.

The advanced state of vegetation in the first half of June 1964 made it difficult to gather data on the exact number of chicks still alive at the end of the first and second week of life. Therefore, since more chicks may have been alive at the onset of the second and third week, the figures may be slightly biased. Table 24 shows that in all three species most chicks died in the first week of life.

Figure 18 compares the relative weekly mortality rates of the chicks, taking total chick mortality per season in each species as 100 per cent. The rates of weekly mortality were similar in the California, ring-billed, and glaucous-winged gulls.

Studies of 37 dead ring-billed gull chicks in Michigan (Emlen, 1956) and 80 dead herring gull chicks in Wales (Harris, 1964) provided no evidence of greater mortality in the first week of life in these species. On the other hand, Paludan (1951) and Fordham (1964) found that death in gull chicks occurred most often in the first week of life. The samples of Emlen and Harris

**Figure 17**
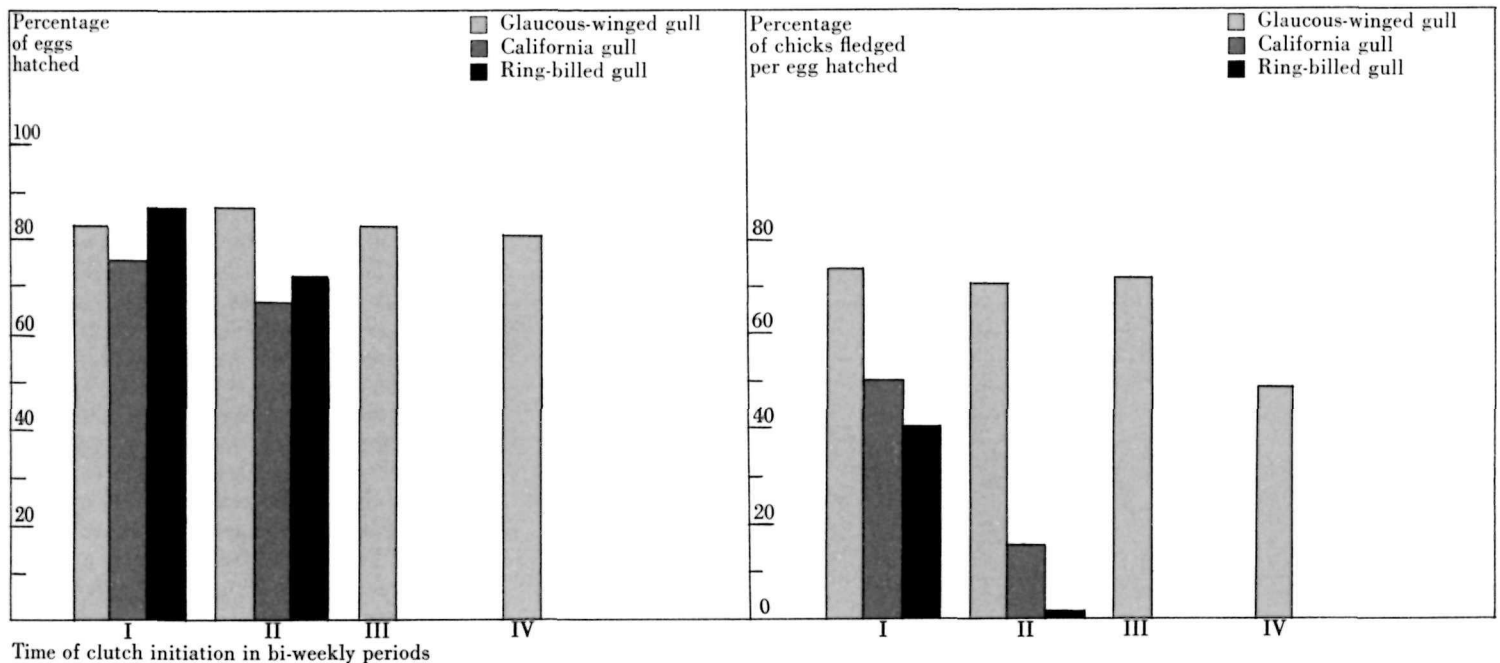


**Table 24**
Weekly mortality rates of chicks of three gull species

| | California gull (1964) | | | Ring-billed gull (1964) | | | Glaucous-winged gull (1962) | | |
|---|---|---|---|---|---|---|---|---|---|
| Age, wk | No. alive beginning of wk | No. dead | % dying | No. alive beginning of wk | No. dead | % dying | No. alive beginning of wk | No. dead | % dying |
| 1 | 430 | 135 | 31.4 | 665 | 220 | 33.1 | 1156 | 194 | 16.8 |
| 2 | 295 | 45 | 15.3 | 445 | 75 | 16.9 | 962 | 65 | 6.8 |
| 3 | 250 | 21 | 8.4 | 370 | 34 | 9.2 | 897 | 38 | 4.2 |
| 4 | 229 | 7 | 3.1 | 336 | 31 | 9.2 | 859 | 30 | 3.5 |
| 5 | 222 | 5 | 2.3 | 305 | 23 | 7.5 | 829 | 15 | 1.8 |
| >5 | 217 | 7 | 3.2 | 282 | 17 | 6.0 | 814 | 12 | 1.5 |
| No. fledged | 210 | | | 265 | | | 802 | | |

are biased for they did not take into account loss of chicks through disappearance. In addition, small chicks are more difficult to find than older and larger ones. On several occasions at Miquelon Lake, I observed adult California gulls swallowing chicks whole. Furthermore, gull pellets at Miquelon Lake contained many numbered colour-bands of chicks which had disappeared in their first week of life.

**Overall reproductive success**
The complete failure to produce fledglings in 1965 at Miquelon Lake is not completely understood. The hypothesis that insecticide residues caused embryonic death is un-proven. Firstly, the insecticide levels in the eggs of the ring-billed gulls at Miquelon Lake were 108 times lower than in the eggs of the herring gulls investigated by Keith (1966). Yet the former hatched 16

per cent of eggs laid; and the latter, 41 per cent. Secondly, the total level of DDT, DDE, and DDD in ring-billed gull eggs from Beaverhill Lake (normal success) was twice that in eggs from Miquelon Lake (poor success). Thirdly, insecticide contamination does not explain the differences in hatching success between ring-billed gulls on islands A and B. More likely, bad weather with nocturnal predation caused egg loss.

Figure 18. Relative weekly chick mortality in
three gull species.

# Food habits

**Figure 18**



| Percentage of chicks dying | Glaucous-winged gull — |
| | California gull — · — |
| | Ring-billed gull — — |
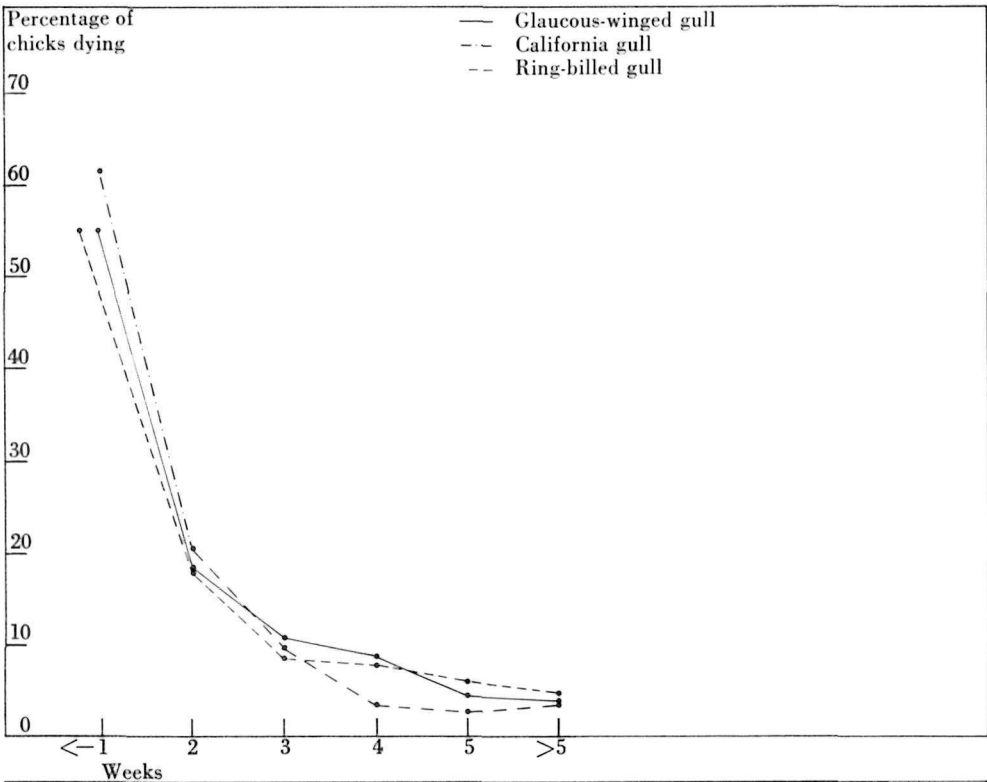
**Table 25**
Reproductive success of three gull species

| Gull species | Production per season per 100 nests | | | Study period | Source |
|---|---|---|---|---|---|
| | Eggs | Hatched | Fledged | | |
| California | 282 | 209 | 102 | 1964 | This study |
| Ring-billed | 291 | 251 | 100 | 1964 | This study |
| Glaucous-winged | 270 | 181 | 113 | 1958-62 | Drent et al., 1964; Vermeer 1963 |

Table 25 compares the reproductive success of the California and ring-billed gulls at Miquelon Lake in 1964 and the glaucous-winged gulls on Mandarte Island from 1958 to 1962. The glaucous-winged gull data were obtained from a large sample taken over a five-year period, with the same methods used in this study. Although the fledging rate of the glaucous-winged gulls fluctuated yearly from 0.5 to 1.7 fledglings per pair over a five-year period, the average reproductive success of this coastal species is remarkably similar to that of the two inland-breeding species at Miquelon Lake in 1964.

**Food habits during the breeding cycle**
Table 26 shows the percentage frequency and volume of identifiable food items collected from oesophagi and regurgitations of adults and chicks of both species during May, June, and July 1965. The diet of the ring-billed gull changed from plant foods in May, to insects in June, and to refuse in July. California gulls did not favour a particular food in May, but they ate mainly insects in June, and refuse in July. For both species, plant foods in May were mostly oats, barley, and wheat, but these may not make up the usual May diet, since the late spring season of 1965 may have limited other food sources. Chicks and adults ate the same foods in June and July. An analysis of adult gull pellets (Table 27) showed that both species ate large quantities of rodents throughout the breeding season. The pellets were relatively pure, 90 per cent of them containing only one food item.

In 1965, only 13 per cent of 39 ring-billed gull pellets collected from April 30 to May 19 contained meadow voles. Voles and mice must have become plentiful around May 20, for 56 per cent of 36 ring-billed gull pellets collected on that date contained mostly meadow vole and a few deer mice.

In 1966, four or five ring-billed gulls collected in mid-April contained the remains of meadow vole. That spring was probably exceptional, as the vole population level was extremely high and more than 90 per cent of gull pellets collected in the last week of April and the first week of May contained vole remains (Table 28).

The annual difference in appearance of rodents in the gull diet may reflect a yearly fluctuation in their numbers as well as their availability.

Plant foods, chiefly grains, were more important in the ring-billed gulls' diet than in the California gulls' in May 1965. Of the 39 ring-billed gull pellets collected from April 30 to May 19, 82 per cent were composed of grain. The decline of grain in the ring-billed gulls' diet was probably due to the sudden availability of meadow vole.

**Table 26**
Percentage frequency and volume of identifiable food items from oesophagi and regurgitations of adult and chick California and ring-billed gulls collected at Miquelon and Beaverhill Lakes, May-July 1965

| | | | Frequency and volume of food items, % | | | | | | | |
| | | | California gull | | | | Ring-billed gull | | | |
| | | | Adults | | Chicks | | Adults | | Chicks | |
| Location | Month | Food items | Freq. | Vol. | Freq. | Vol. | Freq. | Vol. | Freq. | Vol. |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **n** | **15** | | | | **12** | | | |
| Miquelon Lake | May | Plants | 33 | 28 | | | 75 | 68 | | |
| | | Arthropods | 7 | 0 | | | 25 | 6 | | |
| | | Amphibians | 0 | 0 | | | 0 | 0 | | |
| | | Bird remains | 20 | 18 | | | 0 | 0 | | |
| | | Rodents | 27 | 30 | | | 17 | 10 | | |
| | | Refuse | 27 | 24 | | | 17 | 16 | | |
| | | **n** | **60** | | **25** | | **21** | | **8** | |
| Miquelon Lake | June | Plants | 3 | 1 | 4 | 0 | 14 | 5 | 13 | 8 |
| | | Arthropods | 50 | 39 | 52 | 42 | 57 | 54 | 63 | 50 |
| | | Amphibians | 2 | 1 | 4 | 2 | 0 | 0 | 0 | 0 |
| | | Bird remains | 33 | 21 | 36 | 22 | 5 | 2 | 13 | 7 |
| | | Rodents | 18 | 23 | 20 | 24 | 19 | 29 | 25 | 21 |
| | | Refuse | 18 | 15 | 12 | 10 | 10 | 10 | 25 | 14 |
| | | **n** | **14** | | **18** | | **13** | | **16** | |
| Miquelon and Beaverhill Lakes | July | Plants | 14 | 6 | 0 | 0 | 0 | 0 | 13 | 10 |
| | | Arthropods | 14 | 4 | 12 | 2 | 15 | 4 | 13 | 1 |
| | | Amphibians | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | Bird remains | 0 | 0 | 12 | 11 | 0 | 0 | 6 | 8 |
| | | Rodents | 21 | 24 | 22 | 28 | 23 | 20 | 19 | 15 |
| | | Refuse | 71 | 66 | 61 | 59 | 85 | 76 | 69 | 66 |

The difference between the early spring diet of both species in 1965 (chiefly grain) and that in 1966 (chiefly rodents) suggests their opportunistic feeding habits.

Arthropods were the main food in June. Table 29 shows the relative importance of the different groups of arthropods in the diet of the two gull species. In both California and ring-billed gulls, ground beetles (Carabidae) and damsel fly (Coenagrionidae) naiads occurred most frequently. There were no apparent interspecific differences in the proportions of arthropods taken.

With the start of hatching of chicks, insects – ground beetles in the first week of June 1965, damsel fly naiads in mid-June – appeared in the gull diet. The appearance of damsel fly naiads was probably delayed by prolonged snow and ice, for in 1964 they appeared in the first week of June.

Refuse was the main food of both species in July (Table 26). Rodents may have been a more substantial part of the July diet before increasing human population made refuse available to the gulls. The August and September concentrations of adults and chicks on city garbage dumps indicate that they are an extensive source of food once gulls leave the breeding grounds.

In summer 1967, a survey was made to record the number of nesting California and ring-billed gulls in Alberta, and the location of their breeding grounds. At the same time, food pellets were collected in 14 different colonies to find out if the diet of the gulls at Miquelon Lake was typical of the province or reflected local conditions.

Figure 19 shows the distribution and size of gull colonies in Alberta. Colonies are larger and more numerous in the south than in the north. The short grass plains and the relatively open and cultivated aspen parkland make it possible for gulls to hunt rodents which make up a substantial part of their diet (Table 30). This may account for the larger colonies in the southern part of the province. As the gulls move northward, they start eating more fish. This change is apparent in pellets from Lower Therien Lake which contain both fish and rodents. In the relatively undeveloped and forested areas of northern Alberta, it is probably more difficult for gulls to obtain rodents. The yellow perch, which swims close to the water surface and spawns in shallow water in the summer (R. J. Paterson, pers. comm.), is the species of fish most frequently found in pellets.

The high percentage of carrion in pellets of California gulls at Lake Shanks and

St. Mary Reservoir (Table 30) indicates the scavenging habits of that species. The carrion was chiefly composed of cow hair and likely reflected the high mortality of cows resulting from an abnormally heavy snowfall in May 1967.

Tables 27 and 30 show that gulls at Miquelon Lake eat the same kind of food as those in the aspen parkland and short grass plains of Alberta.

**Interspecific differences in food habit**

The extensive grain diet of the ring-billed gulls (Tables 26, 27, and 30) shows that they prefer to feed in a terrestrial habitat. At Miquelon Lake, tiger salamanders (*Ambystoma tigrinum*) occurred three times in food samples of California gulls, but never in those of ring-billed gulls. Bird remains were more abundant in pellets of California gulls (Tables 26, 27, and 30). Table 31 shows the frequency of different bird and eggshell remains in oesophagi, regurgitations, and pellets of the gulls at Miquelon Lake in 1965. California gulls preyed more heavily on very young gulls and waterfowl than did ring-billed gulls. In the latter's diet, passerines were relatively more important.

California gulls ate many more duck eggs, whereas ring-billed gulls ate relatively more gull eggs. The fragments were too small for species identification, but ring-billed gulls were seen eating their own eggs in 1965.

Gadwall, lesser scaup and bufflehead (*Bucephala albeola*) ducklings were identified in California gull regurgitations. On seven occasions I saw California gulls consuming entire broods of ducklings at Miquelon Lake. The broods were those of a mallard, a pintail, a gadwall, and four lesser scaup. I also saw a coot chick taken by a California gull in a pond adjacent to Miquelon Lake.

In 1964 and 1965 the hatching success of early-nesting ducks, such as pintails and mallards, on islands A and B was low compared to that of the late-nesting lesser scaup and gadwall. This may have resulted

from the disturbance I caused while checking gull nests, and the consequent exposure of eggs left uncovered in the sparse vegetation by the departing duck. Hatching success of late-nesting ducks in 1964 was good. The nests were not exposed in the thicker vegetation and the ducks had become accustomed to my presence. Sixty-seven lesser scaup and 29 gadwall nests were found on islands A and B in 1964. The hatching success of the clutches of both duck species was 90 per cent. However, the fledging success of all ducks nesting on the islands was low, probably because of predation by California gulls. It is unlikely that any duckling survived its fourth day of life. As soon as a hen entered the water with her ducklings the gulls would pursue them, devouring the entire brood usually within ten minutes. If a gull did not swallow a duckling fast enough in the air, another gull would take the prey. On two occasions, when the brood of a scaup was reduced to

one, a second female scaup – without a brood – joined in its defence. Both hens tried to defend the duckling placed between them, but they were unsuccessful.

On July 30, 1964, when only 10 adult California gulls were on island A, a scaup took to the water with nine ducklings and lost them within a few minutes. It is obvious that a few gulls can kill substantial numbers of ducklings in a very short time. On two occasions I watched one pintail and one mallard brood move about in short herbaceous vegetation on the island for a few hours. Although the ducklings were conspicuous to me, they were not attacked by the gulls until they went into the water. The ducklings' colouration may have protected them in the vegetation but not in the water where they became more noticeable.

The frequency of different rodent species in gull pellets collected at Miquelon Lake in May and June 1965 is shown in Table 32. California gulls at Miquelon Lake

**Table 27**

Percentage frequency of different food items in 155 pellets of California and 250 pellets of ring-billed gulls collected, May-June 1965

| Food items | % pellets with food items | |
|---|---|---|
| | California gull | Ring-billed gull |
| Plants | 17 | 31 |
| Arthropods | 13 | 20 |
| Bird remains | 37 | 7 |
| Rodents | 48 | 61 |
| Refuse | 5 | 3 |
| Other: fish, amphibians, weasel | 7 | 3 |

**Table 28**

Percentage frequency of food items in 25 California and 55 ring-billed gull pellets collected respectively on April 29 and May 7, 1966

| Food items | % pellets with food items | |
|---|---|---|
| | California gull | Ring-billed gull |
| Grain | 0 | 5 |
| Arthropods | 4 | 5 |
| Meadow vole | 100 | 91 |
| Deer mice | 8 | 3 |
| Richardson's ground squirrel (*Citellus richardsonii*) | 0 | 3 |

Figure 19. California and ring-billed gull colonies in Alberta.

| Colony location | Latitude | Longitude |
|---|---|---|
| **Censused populations** | | |
| 1. Beaverhill Lake | 53° 30′ N | 112° 30′ W |
| 2. Buffalo Lake | 52° 28′ N | 112° 52′ W |
| 3. Burntwood Island | 58° 58′ N | 110° 33′ W |
| 4. Chip Lake | 53° 40′ N | 115° 25′ W |
| 5. Craigdhu Reservoir | 51° 18′ N | 113° 33′ W |
| 6. Dowling Lake | 51° 43′ N | 111° 59′ W |
| 7. Eagle Lake | 50° 59′ N | 113° 20′ W |
| 8. Frank Lake | 50° 35′ N | 113° 43′ W |
| 9. Frog Lake | 53° 54′ N | 110° 19′ W |
| 10. Joseph Lake | 53° 18′ N | 113° 05′ W |
| 11. Keho Lake | 49° 58′ N | 113° 01′ W |
| 12. Lac La Biche | 49° 50′ N | 112° 00′ W |
| 13. Lake Shanks | 49° 04′ N | 112° 43′ W |
| 14. Lower Therien Lake | 53° 57′ N | 111° 23′ W |
| 15. Miquelon Lake | 53° 15′ N | 112° 55′ W |
| 16. Murray Lake | 49° 47′ N | 110° 58′ W |
| 17. Namur Lake | 57° 27′ N | 112° 37′ W |

| Colony location | Latitude | Longitude |
|---|---|---|
| 18. Newell Reservoir | 50° 24′ N | 111° 58′ W |
| 19. Pelican Lake | 55° 47′ N | 113° 17′ W |
| 20. St. Mary Reservoir | 49° 18′ N | 113° 13′ W |
| 21. Stirling Lake | 49° 31′ N | 112° 34′ W |
| 22. Utikuma Lake | 55° 53′ N | 115° 20′ W |
| 23. Winefred Lake | 55° 28′ N | 110° 31′ W |
| **Uncensused populations** | | |
| 1. Cowoki Lake | 50° 35′ N | 111° 43′ W |
| 2. Jay Reservoir | 50° 28′ N | 111° 44′ W |
| 3. Johnson Lake | 50° 20′ N | 111° 48′ W |
| 4. Louisiana Lake | 50° 34′ N | 111° 38′ W |
| 5. Milk River Ridge Reservoir | 49° 22′ N | 112° 35′ W |
| 6. Rolling Hills Reservoir | 50° 22′ N | 111° 54′ W |
| 7. Scope Reservoir | 50° 05′ N | 111° 58′ W |
| 8. Taber Lake | 49° 48′ N | 112° 05′ W |

**Figure 19**



[:] Aspen parkland
[/] Short grass plains
▲ California gull
● Ring-billed gull
▴ · 100 nests
▲ ● 100 – 500 nests
▲ ● 500 – 1000 nests
▲ ● 1000 – 3000 nests
● 3000 nests
■ California & ring-billed gull Populations of undetermined size
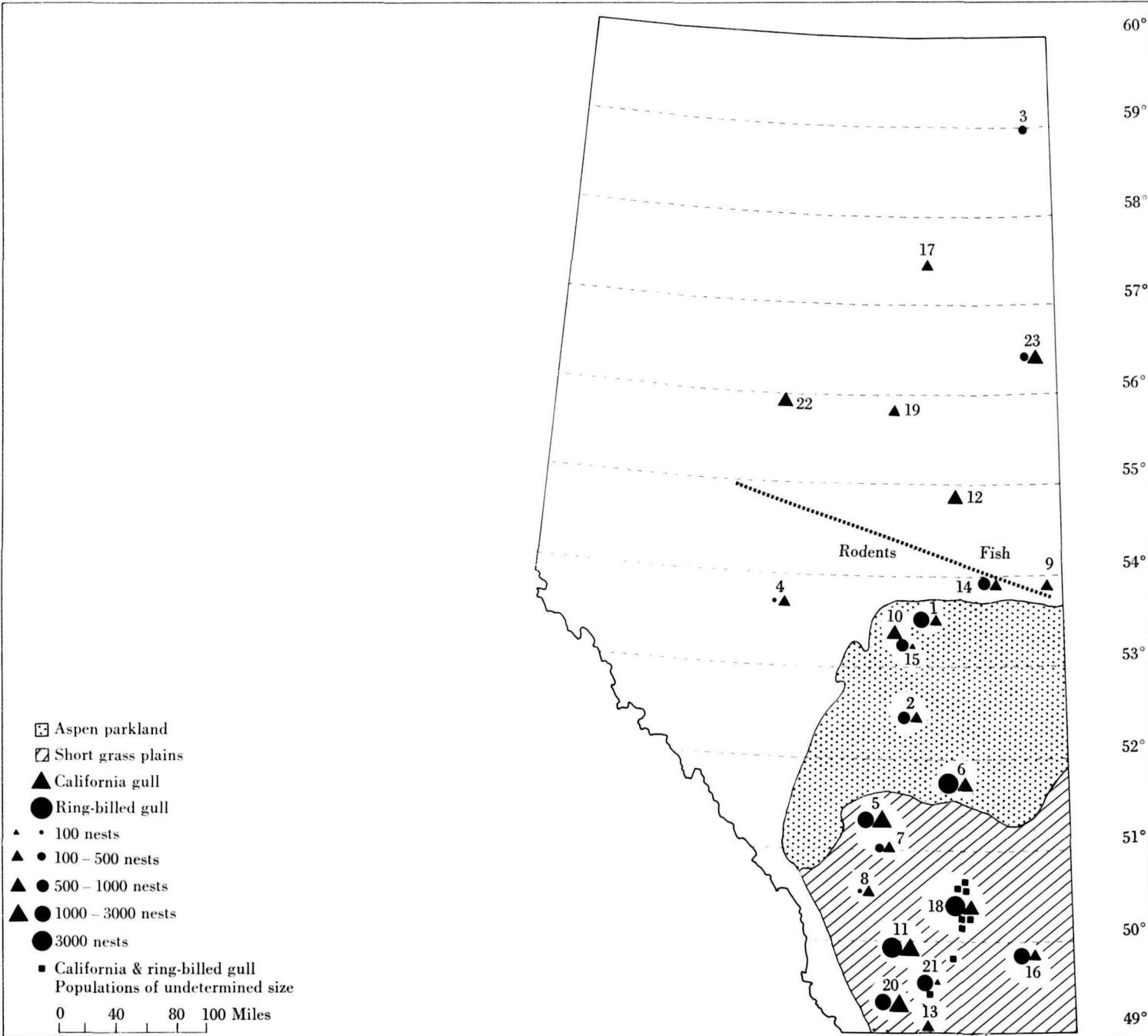
0    40    80   100 Miles

**Table 29**

The relative importance of specific arthropods in
oesophagi and regurgitations of 40 California and
25 ring-billed gulls, 1965

| Arthropods | % oesophagi and regurgitations in which items occurred | |
|---|---|---|
| | California gull | Ring-billed gull |
| Arachnida | | |
| Lycosidae (adults) | 2.5 | 0 |
| Crustacea | | |
| Anostraca (adults) | 0 | 12 |
| Malacostraca *(Gammarus lacustris)* | 2.5 | 0 |
| Insecta | | |
| Siphonaptera | 0 | 4 |
| Hemiptera | | |
| Corixidae (adults) | 4 | 0 |
| Reduviidae (adults) | 2.5 | 0 |
| Coleoptera | | |
| Carabidae (adults) | 60 | 48 |
| Scarabaeidae (adults) | 10 | 4 |
| Curculionidae (adults) | 5 | 4 |
| Dytiscidae (adults) | 2.5 | 0 |
| Hysteridae (adults) | 2.5 | 0 |
| Elateridae (adults) | 2.5 | 0 |
| Trichoptera | 0 | 8 |
| Plecoptera | 2.5 | 0 |
| Lepidoptera | | |
| Noctuidae (larvae) | 2.5 | 4 |
| Pieridae (adult and pupae) | 0 | 4 |
| Diptera | | |
| Tipulidae (larvae) | 2.5 | 0 |
| Therevidae (pupae) | 0 | 4 |
| Tabanidae (larvae) | 2.5 | 0 |
| Tachinidae (pupae) | 0 | 4 |
| Sarcophagidae (larvae) | 5 | 0 |
| Chironomidae (larvae) | 2.5 | 12 |
| Hymenoptera | | |
| Ichneumonidae (pupae) | 0 | 4 |
| Sphecidae (adult) | 0 | 4 |
| Odonata | | |
| Coenagrionidae (naiads) | 22.5 | 32 |
| Ephemoptera (adults) | 2.5 | 4 |
| Orthoptera | | |
| Acrididae (nymphs) | 2.5 | 4 |

concentrated on the larger rodents and
ring-billed gulls on mice.

Table 33 shows that this difference in
rodent diet is typical of both species in the
southern half of Alberta. The California
gull is a greater scavenger than the ring-
billed gull (Table 30). The large number
of Richardson's ground squirrels in the diet
of the California gull at Dowling Lake and
Newell Reservoir (Table 33) may also re-
flect its scavenging nature. After the crow,
it appeared to be the most frequent scav-
enger of ground squirrels killed by vehicles
in southeastern Alberta during May, June,
July, and August 1967 (Table 34).

The literature on the food and feeding
habits of the California and ring-billed
gulls in the spring and summer supports
the interspecific dietary differences re-
ported in this study. Munro (1936) also
found that grain predominated in ring-
billed gull pellets collected in May 1934, at
Bittern Lake, 15 miles from Miquelon
Lake. Rothweiler (1960) identified various
insect families in stomach samples collected
in Montana, and also showed that both
species ate many ground beetles. He found
no tiger salamanders in ring-billed gulls,
but found them in 10 per cent of the Cali-
fornia gull stomachs.

Predation on eggs by California gulls
at Miquelon Lake was primarily on duck
eggs. Other studies have shown similar pre-
dation. Wunder (1949) showed that they
destroyed 11 per cent of 834 waterfowl eggs
at Farmington Bay, Utah. Wingfield (1951)
calculated that they destroyed eight per
cent of all waterfowl eggs in his study in
Utah. Odin (1957) reported that Cali-
fornia gulls at Farmington Bay destroyed
18 per cent of 2,997 duck and coot eggs
within a two-mile radius of their colonies.
In the studies by Wingfield and Odin, pre-
dation was heaviest on poorly concealed
nests. At Miquelon Lake, 35 of 287 oeso-
phagi, regurgitations, and pellets contained
duck eggshells. This is a 12 per cent occur-
rence, compared with a 13 per cent occur-
rence of duck eggshells in the California
gull samples collected by Odin. According

# Table 30

Percentage frequency of food items in California
and ring-billed gull pellets collected at different
locations[a] in Alberta, May and June 1967

| | 13.* Lake Shanks | 20.* St. Mary Reservoir | 21.* Stirling Lake | 18.* Newell Reservoir | 8.* Frank Lake | 7.* Eagle Lake | 6.* Dowling Lake | 2.* Buffalo Lake | 10. and 15.* Joseph and† Miquelon Lakes | 14.* Lower Therien Lake | 12.* Lac la Biche | 22.* Utikuma Lake | 19.* Pelican Lake |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | % pellets with food items | | | | | | | |
| **California gull** | | | | | | | | | | | | | |
| No. of pellets | 257 | 128 | | 132 | 132 | 188 | 135 | 104 | 248 | 59 | 200‡ | 150‡ | 23 |
| Plants § | 34 | 15 | | 6 | 5 | 2 | 8 | 1 | 4 | 15 | 10 | 0 | 0 |
| Arthropods ‖ | TR | 1 | | 4 | 2 | 2 | 3 | 6 | 11 | 25 | 0 | 4 | 0 |
| Fishes ¶ | 2 | 2 | | 2 | 0 | 0 | 0 | 2 | 1 | 14 | 90 | 93 | 100 |
| Birds ** | 5 | 2 | | 16 | 10 | 11 | 2 | 6 | 9 | 34 | 0 | 1 | 0 |
| Rodents †† | 5 | 16 | | 61 | 80 | 84 | 80 | 87 | 80 | 10 | 0 | 2 | 0 |
| Carrion ‡‡ | 53 | 61 | | 8 | 2 | 2 | 6 | 0 | 0 | 2 | 0 | 0 | 0 |
| Refuse | 1 | 2 | | 1 | 3 | 0 | 1 | 1 | 4 | 0 | 0 | 0 | 0 |
| Other §§ | 0 | 2 | | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| **Ring-billed gull** | | | | | | | | | | | | | |
| No. of pellets | 29 | 75 | 89 | 66 | 67 | 148 | 166 | 620 | 74 | | | | |
| Plants | 52 | 66 | 76 | 17 | 9 | 22 | 4 | 11 | 59 | | | | |
| Arthropods | 3 | 3 | 0 | 0 | 2 | 47 | 2 | 11 | 27 | | | | |
| Fishes | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | | | | |
| Birds | 0 | 1 | 2 | 3 | 0 | 1 | 1 | 1 | 1 | | | | |
| Rodents | 31 | 28 | 22 | 82 | 90 | 30 | 94 | 76 | 8 | | | | |
| Carrion | 17 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | | | | |
| Refuse | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | |
| Other | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | | |

\* See Figure 19 for locations.
† Grouped because of proximity to one another.
‡ Disintegrated pellets could not be counted
  precisely.

§ Mostly grain.
‖ Mostly beetles.
¶ Mostly yellow perch.
** Includes eggshells.

†† Rodent species shown in Table 33.
‡‡ Cows, sheep, and chickens.
§§ Long-tailed weasels *(Mustela frenata)*, least
  weasels, and hares *(Lepus* Spp.).

# Table 31

Frequency of different bird and eggshell remains
in oesophagi, regurgitations and pellets of
California and ring-billed gulls at Miquelon Lake,
May-June 1965

| | Frequency of bird remains | | Frequency of eggshell remains | |
|---|---|---|---|---|
| Species | California gull | Ring-billed gull | California gull | Ring-billed gull |
| Gull | 25 | 3 | 6 | 5 |
| Duck | 5 | 0 | 35 | 2 |
| Coot | 3 | 0 | 4 | 0 |
| Grebe | 2 | 0 | 2 | 0 |
| Passerine | 1 | 5 | 0 | 0 |
| Unidentified | 9 | 4 | 3 | 2 |
| Total | 45 | 12 | 50 | 9 |

# Table 32

Percentage frequency of different rodent species,
in order of decreasing size, in 74 California and
152 ring-billed gull pellets containing rodents
collected at Miquelon Lake, May-June 1965

| | % pellets with rodent species | |
|---|---|---|
| Rodent species | California gull | Ring-billed gull |
| Muskrat *(Ondatra zibethicus)* | 3 | 0 |
| Richardson's ground squirrel | 53 | 17 |
| Pocket gopher *(Thomomys talpoides)* | 13 | 18 |
| Meadow vole | 27 | 52 |
| Deer mouse | 4 | 13 |

**Table 33**
Number of rodent species, in order of decreasing size, found in California and ring-billed gull pellets collected at different locations in Alberta

| | Lake Shanks | St. Mary Reservoir | Stirling Lake | Newell Reservoir | Frank Lake | Eagle Lake | Dowling Lake | Buffalo Lake | Joseph & Miquelon Lakes | Lower Therien Lake | Total No. | Total % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **California gull** | | | | | | | | | | | | |
| No. of pellets | 13 | 20 | | 81 | 106 | 159 | 107 | 90 | 195 | 6 | 777 | |
| Muskrat | 0 | 0 | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | TR |
| Richardson's ground squirrel | 4 | 9 | | 81 | 11 | 29 | 105 | 8 | 13 | 4 | 264 | 34 |
| Thirteen-lined ground squirrel (Citellus tridecemlineatus) | 1 | 0 | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | TR |
| Pocket gopher | 0 | 0 | | 0 | 0 | 9 | 0 | 0 | 1 | 2 | 12 | 2 |
| Meadow vole | 7 | 9 | | 0 | 92 | 116 | 2 | 76 | 179 | 0 | 481 | 62 |
| Deer mouse | 2 | 2 | | 0 | 10 | 5 | 0 | 15 | 6 | 0 | 40 | 5 |
| **Ring-billed gull** | | | | | | | | | | | | |
| No. of pellets | | 9 | 21 | 20 | 54 | 60 | 43 | 156 | 469 | 6 | 838 | |
| Muskrat | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | TR |
| Richardson's ground squirrel | 2 | 0 | 1 | 0 | 0 | 0 | 8 | 1 | 2 | 1 | 15 | 2 |
| Thirteen-lined ground squirrel | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Pocket gopher | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 4 | TR |
| Meadow vole | | 6 | 20 | 17 | 46 | 57 | 30 | 139 | 442 | 2 | 759 | 91 |
| Deer mouse | | 0 | 2 | 2 | 14 | 11 | 9 | 53 | 46 | 2 | 139 | 17 |

**Table 34**
Numbers of observations of bird species scavenging upon vertebrates killed by vehicles on paved roads in southeastern Alberta (between latitudes 49° N. and 54° 30' N. and longitudes 110° W. and 114° W.), May-August 1967

| | Scavengers | | | | |
|---|---|---|---|---|---|
| Carrion | Common crow | Black-billed magpie (Pica pica) | California gull | Ring-billed gull | Franklin's gull (Larus pipixcan) |
| Richardson's ground squirrel | 45 | 10 | 19 | 2 | |
| Muskrat | | | | | 1 |
| Porcupine (Erethizon dorsatum) | 1 | | | | |
| White-tailed jack rabbit (Lepus townsendii) | 1 | 1 | | | |
| Common crow | | 1 | | | |
| Ring-necked pheasant (Phasianus colchicus) | 1 | 1 | | | |
| Domestic chicken (Gallus gallus) | | 1 | | | |
| American widgeon | 1 | | | | |
| Pintail duck | 1 | | 1 | | |
| Sandpiper (Erolia sp.) | | | 1 | | |
| Western meadow lark (Sturnella neglecta) | | | | 1 | |
| Total | 50 | 14 | 21 | 3 | 1 |

to this, California gulls at Miquelon Lake and at Farmington Bay prey on duck eggs to the same extent.

Anderson (1965) in California, Rothweiler (1960) in Montana, and Williams and Marshall (1938) in Utah showed that California gull predation on waterfowl nests was less than five per cent. Thus, California gull predation varies from region to region, and probably depends on such factors as the amount of cover in which duck nests are located, proximity of gull colonies, availability and abundance of other food sources, location of feeding area where the gulls were collected for food analysis, and extent of human disturbance.

Several sources have reported California gull predation on young waterfowl. Cottam (1945) and Greenhalgh (1952) reported California gulls preying upon ducks, of unspecified age, incapacitated by botulism. Greenhalgh (1952) also found seven ducklings in 184 California gull stomachs collected at two locations in Great Salt Lake, Utah. Odin (1957) saw California gulls taking a week-old pintail and a 10-day-old redhead and found a seven-day-old avocet, a young coot, and duck down in California gull stomachs. Odin considered that once they had reached three-quarters of their growth, young waterfowl were safe from California gull predation. Behle (1958) mentions taking of crippled and sick ducks, young pelicans, and cormorants. Chura (1962) saw a California gull swallow a mallard duckling held in an enclosure. The duckling was 23 days old, and weighed 260 g. Anderson (1965) observed the capture of a young eared grebe and a newly hatched coot. J. Guay (pers. comm.) and Wolford (1966) observed respectively that eggs of Franklin's gulls and black-crowned night herons *(Nycticorax nycticorax)* were taken by ring-billed gulls in Alberta. Ring-billed gulls at Miquelon Lake were not observed eating young waterfowl, but they ate relatively more passerine birds than the California gulls (Table 31).

Anderson's (1965) analysis of mammalian remains in gull stomachs in California showed that ring-billed gulls ate more mice, while the California gulls took larger mammals. Interspecific differences in size may account in part for the size of mammals taken (Appendix 3). Larger species of shorebirds tend to prey upon larger organisms (Recher, 1966).

From the above observations it can be concluded that the two gull species have slightly different food niches.

I do not know of any quantitative food study of California and ring-billed gulls on coastal wintering grounds. However, fish (Bartholomew, 1942; Norris-Elye, 1945) and marine invertebrates (Meyerriecks, 1965; Wales, 1926) appear to form a substantial part of their diet. Quantitative food studies on the herring gull show that inland-nesting populations can feed chiefly on rodents (in Kalmytskaya, Russia – Minoranskii, 1963), while coastal populations feed mainly on fish and marine invertebrates (Barents Sea, Russia – Belopolskii, 1957; coastal western Europe – Harris, 1965; coastal eastern North America – Mendall, 1935 and Pimlott, 1952). Ishunin (1964) found that inland-nesting black-headed gulls at Lake Sivash, Russia, fed chiefly on rodents. Although food studies of inland-nesting gulls are few, a rodent diet may be common among such gulls.

Figure 20 and Table 35 summarize the weight records of 28 California and 31 ring-billed gull broods. The average weights at fledging for 18 California and 30 ring-billed gull juveniles respectively were 573 g (435-675) and 377 g (260-503). The average weights of 39 adult California and 39 adult ring-billed gulls collected during the breeding season were respectively 771 g (610-964) and 497 g (390-670). These figures show that the average California and ring-billed gull juvenile reaches respectively 74 per cent and 76 per cent of the weight of the average adult.

Figure 21 summarizes the weight of chicks over 10 days old from 20 broods of one and 8 broods of two California gull chicks; and 18 broods of one, 10 broods of two, and 3 broods of three ring-billed gull chicks. In the latter species the broods of two and three are lumped together. The weight records of 29 broods of one, 25 broods of two, and 11 broods of three glaucous-winged gull chicks from Mandarte Island are shown for comparison. It can be seen that in all three gull species single chicks grew faster, on the average, than did chicks from broods of two or three.

Figure 22 shows the growth rates of California, ring-billed, and glaucous-winged gull chicks. This figure was constructed after Drent's (1965) composite graph method. The weight increase is plotted on a semi-logarithmic scale with the weight of the newly hatched chicks as a fixed starting point. It can be seen that the three species are very similar up to the twentieth day. On the average all three species doubled their weight by 4½ days; trebled by 10 days; and quadrupled by 20 days. The time for a 100 per cent increase in weight is longer each time, i.e., 4 days, 6 days and 10 days, an indication of the declining growth rate.

Although the breeding period in California and ring-billed gulls is much shorter than in coastal-nesting gulls, the growth period is not shorter. Nelson (1966) has shown adaptation of a shorter growth period by the family Sulidae. The growth

period of the gannet *(Sula bassana)* in Scotland is compressed when compared with their tropical-breeding counterparts. Nelson suggested that gannet chicks could best use the available food by compressing growth to suit the period when there is most fish. Thus, chicks could build up a substantial fat reserve.

**Table 35**
Growth of California and ring-billed gulls

| California gull | | | Ring-billed gull | | |
|---|---|---|---|---|---|
| Days after hatching | Sample size | Mean ± SE, g | Days after hatching | Sample size | Mean ± SE, g |
| 0 | 24 | 50.9 ± 0.8 | 0 | 39 | 38.5 ± 0.7 |
| 1 | 26 | 59.5 1.2 | 1 | 34 | 45.5 0.9 |
| 2 | 17 | 70.8 1.6 | 2 | 37 | 55.6 1.1 |
| 3 | 23 | 79.9 3.1 | 3 | 37 | 65.1 1.1 |
| 4 | 18 | 92.2 2.3 | 4 | 29 | 76.9 1.4 |
| 5 | 13 | 114.9 6.2 | 5 | 27 | 91.8 2.3 |
| 6 | 16 | 111.4 3.5 | 6 | 21 | 106.3 2.5 |
| 7 | 12 | 145.4 8.6 | 7 | 23 | 125.6 4.1 |
| 8 | 14 | 164.8 9.2 | 8 | 23 | 135.5 4.7 |
| 9 | 12 | 192.8 12.5 | 9 | 19 | 156.1 5.9 |
| 10 | 14 | 209.7 7.8 | 10 | 22 | 168.9 5.6 |
| 11 | 9 | 219.8 10.7 | 11 | 13 | 176.4 5.0 |
| 12 | 12 | 268.6 9.7 | 12 | 19 | 196.1 5.9 |
| 13 | 11 | 247.4 16.1 | 13 | 14 | 212.2 8.7 |
| 14 | 16 | 299.9 15.5 | 14 | 20 | 241.3 9.5 |
| 15 | 14 | 320.4 16.3 | 15 | 18 | 238.9 10.0 |
| 16 | 14 | 340.8 17.1 | 16 | 20 | 254.2 9.6 |
| 17 | 18 | 357.8 16.1 | 17 | 20 | 253.6 10.3 |
| 18 | 11 | 395.5 19.7 | 18 | 18 | 284.5 10.5 |
| 19 | 17 | 381.4 17.0 | 19 | 22 | 272.8 8.5 |
| 20 | 12 | 422.4 20.1 | 20 | 19 | 302.1 11.4 |
| 21 | 15 | 428.5 18.6 | 21 | 20 | 287.3 10.9 |
| 22 | 13 | 452.4 26.2 | 22 | 20 | 307.1 13.5 |
| 23 | 19 | 451.2 14.6 | 23 | 20 | 308.2 12.3 |
| 24 | 10 | 460.4 30.5 | 24 | 12 | 311.5 17.1 |
| 25 | 15 | 498.5 22.2 | 25 | 18 | 325.8 11.0 |
| 26 | 16 | 496.8 19.8 | 26 | 20 | 322.2 12.4 |
| 27 | 14 | 505.4 26.4 | 27 | 18 | 316.3 14.2 |
| 28 | 14 | 508.4 25.0 | 28 | 19 | 340.0 13.9 |
| 29 | 14 | 531.4 25.2 | 29 | 21 | 365.2 12.8 |
| 30 | 21 | 528.2 18.3 | 30 | 20 | 359.5 10.1 |
| 31 | 10 | 554.5 35.7 | 31 | 20 | 377.2 16.4 |
| 32 | 15 | 531.8 19.1 | 32 | 20 | 358.3 12.4 |
| 33 | 9 | 536.7 28.3 | 33 | 18 | 374.2 14.5 |
| 34 | 13 | 546.4 26.2 | 34 | 16 | 370.1 12.5 |
| 35 | 8 | 585.6 34.3 | 35 | 13 | 400.5 18.3 |
| 36 | 13 | 520.6 27.2 | 36 | 11 | 365.2 11.9 |
| 37 | 4 | 539.9 | 37 | 14 | 382.3 19.0 |
| 38 | 8 | 501.3 | | | |
| 39 | 2 | 508.7 | | | |
| 40 | 6 | 527.4 | | | |

Figure 20. Growth of California and ring-billed gull chicks, 1964.

Figure 21. Growth in broods of one, two, and three chicks of A. glaucous-winged, B. California, and C. ring-billed gulls. Mean weights given in broods of one, two, and three chicks.

Figure 22. Growth in three gull species: A. glaucous-winged gull, B. California gull, and C. ring-billed gull. Weight increase is shown in relation to the average weight of newly hatched chicks.



**Figure 20**

Weight in grams

California gull

Ring-billed gull

Age in days

**Figure 21**

Weight in grams

A
— Broods with 1 chick
···· Broods with 2 chicks
-- Broods with 3 chicks

B
— Broods with 1 chick
···· Broods with 2 chicks

C
— Broods with 1 chick
···· Broods with 2 and 3 chicks

Age in days

**Figure 22**

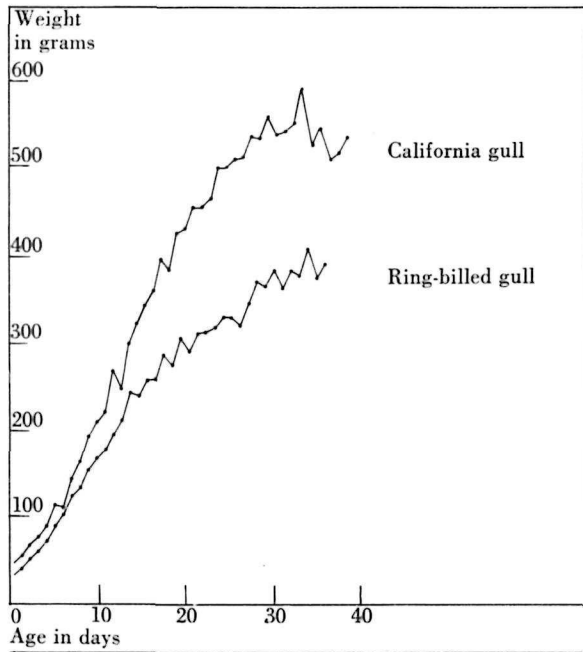Per cent increase in body weight
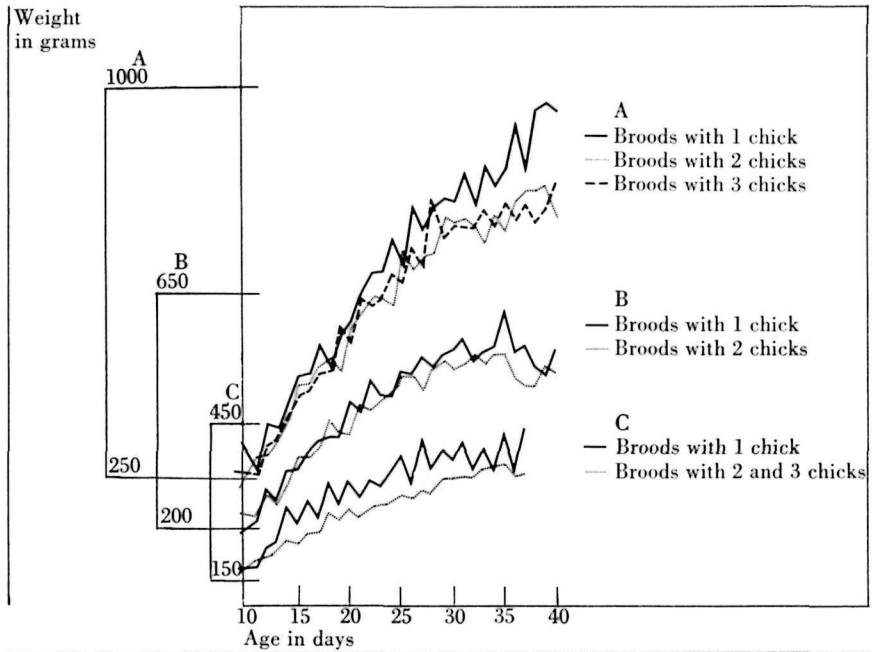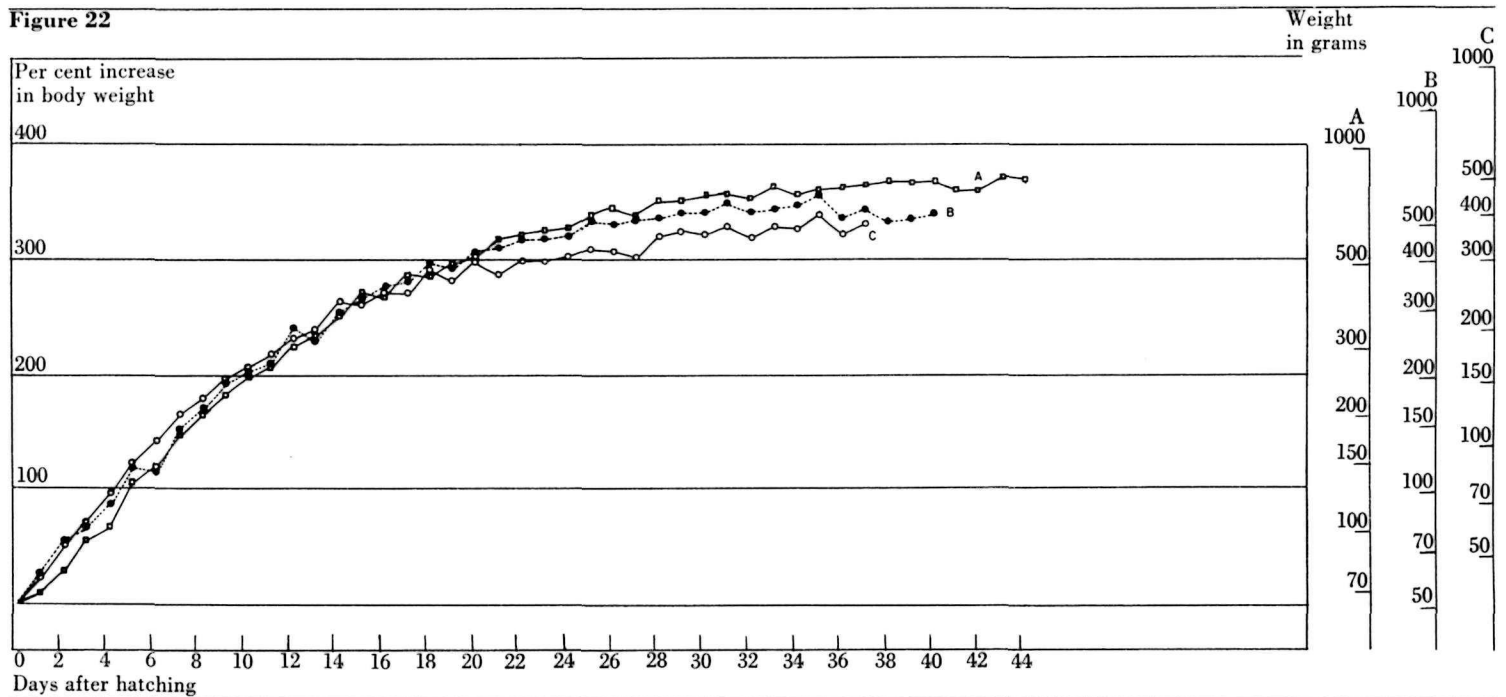
Weight in grams

Days after hatching

# Discussion

There are not many basic differences between inland-breeding and marine gull species. Growth and reproductive rates of the California and ring-billed gulls appeared to be similar to those of glaucous-winged gulls. Although predation on gulls at Miquelon Lake was greater than on the glaucous-winged gulls on Mandarte Island, all are ground-nesters. In the inland habitat, mew gulls occasionally nest in trees and Bonaparte gulls *(Larus philadelphia)* regularly do so (Godfrey, 1966), presumably to counteract predation. However, the presence of many colonies of California and ring-billed gulls on islands in the interior of North America shows that they can maintain themselves well in this type of nesting habitat.

Ability to exploit a seasonal abundance of rodents and a short breeding season are apparent adaptations to inland breeding. The short breeding season is marked by a compressed pre-egg period, a short laying period, and little repeat laying. Lack (1954) suggested that natural selection governs the time of production in such a way that it takes place when the food supply for the young is most plentiful. The 1967 experiment did not provide evidence that food supply governs the short breeding season. However, this does not mean that the time of breeding is not actually controlled, in the first place, by the need to time hatching to coincide with availability of food. An alternative is that post-fledgling survival of late-hatched chicks may be lower than that of chicks hatched earlier in the breeding season.

The laying periods of the California and ring-billed gulls are synchronized to the extent that the large majority of clutches are started at the beginning of the laying season. Kruuk (1964) and Patterson (1965) suggested that the synchronized egg-laying at the start of the laying period in the black-headed gulls nesting on dunes at Ravenglass, England, had an anti-predator function. Patterson recorded the proportion of black-headed gull broods reaching the fledging stage, and found that the broods hatched during the peak of the hatching curve had a much higher success than the late broods. The higher losses of the later broods were mainly the result of predation by foxes. As Kruuk and Patterson suggested for the black-headed gulls, the synchronized clutch initiation at the start of egg-laying in the inland-nesting California and ring-billed gulls may also be influenced by predation. Predation can lead to the evolution of synchrony in laying to the extent that food resources which would be available to raise young after the peak of the rearing season remain unexploited.

# Summary

1. The juveniles of the California and ring-billed gulls raised at Miquelon Lake winter chiefly along the coast of California and the west coast of Mexico.
2. The first ring-billed gulls arrived in the Edmonton region and on the nesting grounds simultaneously, in the last days of March. The first California gulls were observed a week later. Snow depth did not seem to influence the time of the birds' arrival. Air temperature may be important as a threshold factor in that the birds may not arrive unless a certain temperature has been surpassed. In the autumn, the ring-billed gulls remained in the Edmonton region longer than the California gulls.
3. In contrast to gulls breeding in coastal Europe, whose arrival in the spring depends on the melting of the ice, the two species at Miquelon Lake occupied the breeding grounds before snow and ice disappeared. The pre-egg periods of the California and ring-billed gulls were shorter than that of the marine-nesting glaucous-winged gulls.
4. Two daily peaks of activity by the gulls occurred during the pre-egg period on the breeding grounds. During this period the gulls did not spend the night on the island, a factor which may reduce predation.
5. In 1964, the date of mean clutch commencement was May 8 for both species; in 1965, May 10 for the ring-billed gulls and May 11 for the California gulls. The date of mean clutch commencement seemed to be influenced by air temperature and disturbance. Food was not a primary factor in determining the time of reproduction.
6. The egg-laying periods of the inland-breeding California and ring-billed gulls are much shorter than those in gull species nesting in a coastal climate. The extent of repeat-laying in the two species was much less than in the marine-nesting gulls.
7. The average dates of commencement of hatching of the California gulls were June 6, 1964, and June 13, 1965; those of the ring-billed gulls were June 4, 1964, and June 14, 1965. The later hatching of both species in 1965 was linked to a later com-

mencement of laying and possibly increased human and predatory disturbance.

8. In California gulls only 26 and 51 per cent of the full incubation effectiveness was achieved after the laying of the first and second eggs respectively. The corresponding figures for the ring-billed gulls were 28 and 54 per cent. Effectiveness of incubation during laying in both species was similar to that of gulls nesting in a marine habitat.

9. The average incubation periods of the California and ring-billed gulls were 26.6 $\pm$ 0.09 and 25.0 $\pm$ 0.10 days, respectively. Compared with incubation in coastal-nesting gulls, these periods were not shorter.

10. The California and ring-billed gulls fledged at the average age of 40 and 37.2 days, respectively. Considering their weights, the fledging period of these species is similar to that of the coastal glaucous-winged and herring gulls. California and ring-billed gulls remained on the breeding grounds an average of 11 days after fledging, a period similar to that in the glaucous-winged gulls.

11. Most families of California and ring-billed gulls appear to break up at the colony, as the counts show that the parents left just before the juveniles. The earlier departure of the adults at the end of July may indicate that the food supply near the breeding grounds was limited. Once the juveniles leave the islands, they do not return to Miquelon Lake.

12. California and ring-billed gulls' avoidance of areas with dense vegetative cover at the time of territorial establishment may be an anti-predator mechanism.

13. Clutches of California gulls on a peninsula at Miquelon Lake were all destroyed by coyote predation. The nesting of gulls on islands is thought to be an adaptation to counteract mammalian predation.

14. California gulls nested along the peripheries of both islands and on the most elevated boulder-strewn area on island A. The ring-billed gulls nested farther from the water and in relatively flatter areas. Both species could nest in the same habitat. The interspecific differences in the choice of nest-site were not very significant when compared with intraspecific variation in nesting habitat of other gull species.

15. The nests of the California gulls were randomly distributed. Those of the ring-billed gulls showed a significant deviation from randomness in the direction of aggregated spacing, while those of the glaucous-winged gulls showed a significant deviation from randomness in the direction of uniform spacing. The aggregated nesting pattern of the ring-billed gulls may be an anti-predator mechanism rather than a special adaptation to inland conditions.

16. The average clutch sizes of the California gulls were 2.82 $\pm$ 0.03 in 1964 and 2.73 $\pm$ 0.04 in 1965. The corresponding figures for the ring-billed gulls were 2.92 $\pm$ 0.02 in 1964 and 2.85 $\pm$ 0.02 in 1965. The clutch sizes of the California and ring-billed gulls were similar to those of coastal-breeding gulls.

17. Total egg losses for the California gulls were similar in 1964 and 1965, but increased significantly for the ring-billed gulls in 1965. The egg losses for the California gulls in both years and the ring-billed gulls in 1964 were similar to those for gull studies in marine habitats.

18. Most of the egg losses of both species occurred in the categories "infertility or embryonic death" and "disappearance – presumably eaten." The greatest loss of eggs of the ring-billed gulls in 1965 occurred in early layers of this species and was either the result of infertility or early cessation of embryonic development. The extensive egg loss of the ring-billed gulls in 1965 may have been caused by a combination of bad weather and nocturnal predators.

19. Eggs were also lost as a result of parents being killed by a nocturnal predator. Feathers from the areas where the decapitated adult gulls were found matched those of the great horned owl. No adults were found dead as a result of predation after the eggs hatched. No predation was observed on adults of the coastal glaucous-winged gulls nesting on Mandarte Island.

20. Most of the California and ring-billed gull eggs, like those of the glaucous-winged gulls that disappeared or were eaten, did so during laying and the first week of incubation. Besides providing the warmth necessary for the development of the gull embryo, incubation also appears to reduce egg predation.

21. In 1964 each species raised, on the average, one juvenile per nest, showing that they can produce offspring successfully when nesting together. No chicks of either species fledged at Miquelon Lake in 1965. This was a local phenomenon, since California and ring-billed gulls 22 miles away fledged at a normal rate.

22. In most cases, the cause of chick death could not be ascertained because the chicks disappeared between my visits. The greatest known cause of chick mortality was predation. The California gulls in both years and a great horned owl (?) in 1965 were the greatest predators on gull chicks.

23. The number of fledglings raised from late clutches of California and ring-billed gulls in 1964 and from glaucous-winged gulls in 1962 were significantly less than those from early clutches. The decreased fledging rate of late clutches in the three species resulted chiefly from difficulties in raising chicks from hatching to fledging and not from a rise in egg mortality toward the end of incubation. The decline in the number of chicks which fledged from late clutches in the California and ring-billed gulls came much earlier than for glaucous-winged gulls.

24. In an experiment to test the relationship of growth and survival to the time of hatching of California gull chicks raised in two fenced plots in 1967, it was found that chicks hatched late in the season survived as well and grew as rapidly as those hatched early in the season. The results of the 1967 experiment do not provide evidence that a seasonally limited food supply governs the short breeding season in the island-nesting gulls.

25. Weekly mortality rates of chicks were similar in California, ring-billed, and glaucous-winged gulls. In all three species, chick mortality was greatest in the first week of life.

26. The reproductive success of the California and ring-billed gulls in 1964 was similar to the average reproductive success, over a five-year period, of the glaucous-winged gulls. No single factor was responsible for the poor reproduction of California and ring-billed gulls in 1965. Parental neglect describes the state of affairs without explaining it.

27. The main discernible change in the diet of the ring-billed gulls at Miquelon Lake was from grain in May to insects in June to organic refuse in July. California gulls did not favour any particular food in May but, as in the ring-billed gull, they ate more insects in June, and more refuse in July. The adults and chicks ate the same foods in June and July. Rodents were an important food source for both species throughout the breeding season. In spring 1966, when meadow voles became abundant, they appeared in more than 90 per cent of the pellets in both species, thus showing the opportunistic feeding habits of the gulls. A 1967 survey of nesting gulls in Alberta showed that the gulls' diet at Miquelon Lake is typical for the aspen parkland and short grass plains of Alberta.

28. It appears that California and ring-billed gulls have slightly different food niches. Both species feed on grain, insects, rodents, birds, and bird eggs; but ring-billed gulls eat more grain and mice and less birds and waterfowl eggs. The California gull diet consists of more amphibians, waterfowl eggs, young waterfowl, and larger rodents; and it is a greater scavenger than the ring-billed gull.

29. The California and ring-billed gulls' breeding seasons are much shorter than the coastal glaucous-winged gulls', but their growth periods are similar. All three species doubled their weight by 4½ days, trebled by 10 days, and quadrupled by 20 days. At the time of fledging, California and ring-billed chicks respectively reached 74 and 76 per cent of the weight of the average adult. In all species, single chicks grew faster than those in broods of two or three.

30. There are few basic differences between inland-breeding gull species and marine forms. The apparent adaptation to breeding in an inland habitat is a shortened breeding season, marked by a compressed pre-egg period, a short laying period, and little repeat laying.

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# Appendices

## Appendix 1
Distribution in length and width of California and ring-billed gull eggs at Miquelon Lake in 1965

| Length, mm | No. of eggs California gull | No. of eggs Ring-billed gull |
|---|---|---|
| 71.9-70.0 | 6 | |
| 69.9-68.0 | 26 | |
| 67.9-66.0 | 51 | |
| 65.9-64.0 | 101 | 6 |
| 63.9-62.0 | 82 | 21 |
| 61.9-60.0 | 31 | 44 |
| 59.9-58.0 | 8 | 82 |
| 57.9-56.0 | 1 | 65 |
| 55.9-54.0 | | 26 |
| 53.9-52.0 | | 7 |
| 51.9-50.0 | | 1 |
| Total | 306 | 252 |
| Mean ± SE | 64.60 ± 0.13 | 58.53 ± 0.16 |

| Width, mm | No. of eggs California gull | No. of eggs Ring-billed gull |
|---|---|---|
| 49.9-48.0 | 39 | |
| 47.9-46.0 | 150 | |
| 45.9-44.0 | 99 | 10 |
| 43.9-42.0 | 16 | 110 |
| 41.9-40.0 | 2 | 113 |
| 39.9-38.0 | | 18 |
| 37.9-36.0 | | 1 |
| Total | 306 | 252 |
| Mean ± SE | 46.23 ± 0.09 | 41.78 ± 0.09 |

## Appendix 2
Calculation of the random distribution of inter-nest distances

The formula: $n \left( \exp. \left[ (-\pi n/A)(x - \tfrac{1}{2}a)^2 \right] - \exp. \left[ (-\pi n/A (x + \tfrac{1}{2}a)^2 \right] \right)$

for the calculation of the random distribution of inter-nest distances was acquired from Dr. J. M. Cullen (by correspondence). The letters in the formula denote:

A = Area with nests, which was 30,000 square feet for each of the three gull species.

n = Number of nests in the area A, which was 193, 202, and 220 for the glaucous-winged, California, and ring-billed gulls respectively.

a = Unit of measurement used for measuring distances between nests. The unit of measurement was one foot for each of the three gull species.

x = Distance to nearest neighbouring nest.

### Example
Assignment: To calculate the number of California gull nests which would be 10 feet from the nearest neighbouring nest, if randomly distributed.

### Solution

$N(x) = n \left( \exp. \left[ (-\pi n/A)(x - \tfrac{1}{2}a)^2 \right] - \exp. \left[ (-\pi n/A)(x + \tfrac{1}{2}a)^2 \right] \right)$

$N(10) =$
$202 \left( \exp. \left[ (-\pi 202/30000)(10 - \tfrac{1}{2}.1)^2 \right] - \exp. \left[ (-\pi 202/30000)(10 + \tfrac{1}{2}.1)^2 \right] \right)$

$N(10) = 202 \,(\text{antilog} - 1.8952 - \text{antilog} - 2.3153$

$N(10) = 202 \,(0.150 - 0.099)$

$N(10) = 10.4 \text{ nests.}$

## Appendix 3
Adult body weights and culmen lengths of California and ring-billed gulls

| Body wt, g | No. of cases California gull male | No. of cases California gull female | No. of cases Ring-billed gull male | No. of cases Ring-billed gull female | Culmen l., mm | No. of cases California gull male | No. of cases California gull female | No. of cases Ring-billed gull male | No. of cases Ring-billed gull female |
|---|---|---|---|---|---|---|---|---|---|
| 999 - 900 | 3 | | | | 57.9-56.0 | 6 | | | |
| 899 - 800 | 16 | 2 | | | 55.9-54.0 | 3 | | | |
| 799 - 700 | 4 | 4 | | | 53.9-52.0 | 5 | | | |
| 699 - 600 | | 10 | 2 | | 51.9-50.0 | 1 | 3 | | |
| 599 - 500 | | | 13 | 4 | 49.9-48.0 | | 4 | | |
| 499 - 400 | | | 4 | 15 | 47.9-46.0 | | 3 | 4 | |
| 399 - 300 | | | | 1 | 45.9-44.0 | | 6 | | |
| | | | | | 43.9-42.0 | | | 4 | 1 |
| | | | | | 41.9-40.0 | | | 1 | 3 |
| | | | | | 39.9-38.0 | | | | 3 |
| | | | | | 37.9-36.0 | | | | 4 |
| Total | 23 | 16 | 19 | 20 | | 15 | 10 | 15 | 11 |
| Mean ± SE | 826 ± 5.83 | 688 ± 8.81 | 533 ± 5.75 | 463 ± 2.53 | | 54.6 ± 0.49 | 48.8 ± 0.49 | 44.5 ± 0.45 | 39.2 ± 0.60 |

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