THE BREEDING ECOLOGY OF THE GLAUCOUS-WINGED GULL (LARUS GLAUCESCENS) ON MANDARTE ISLAND, B.C.

by

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ABSTRACT

The breeding ecology and the behaviour of the Glaucous-winged Gull (Larus glaucescens) were studied at Mandarte Island, British Columbia, Canada, in the summers of 1961 and 1962.

Data were obtained on pair-bondage, pair formation, philopatry to nest site, egg-laying, clutch-size, incubation, egg and chick mortality, fledging rate, growth, age at first flight and colony departure, annual adult mortality and longevity. No support was found for:

1. The Fraser Darling Effect that there is a greater synchronisation of breeding at greater densities;
2. Lack's hypothesis that the clutch size of each species of bird has been adapted by natural selection to correspond with the largest number of young for which the parents can, on the average, provide enough food.

In the Glaucous-winged Gull the converse of these theories was established for the year 1962.

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SCOPE AND STUDY METHODS

The main object of this study was to obtain quantitative ecological data on the breeding of the Glaucous-winged Gull (Larus glaucescens). To a lesser extent the behaviour was studied.

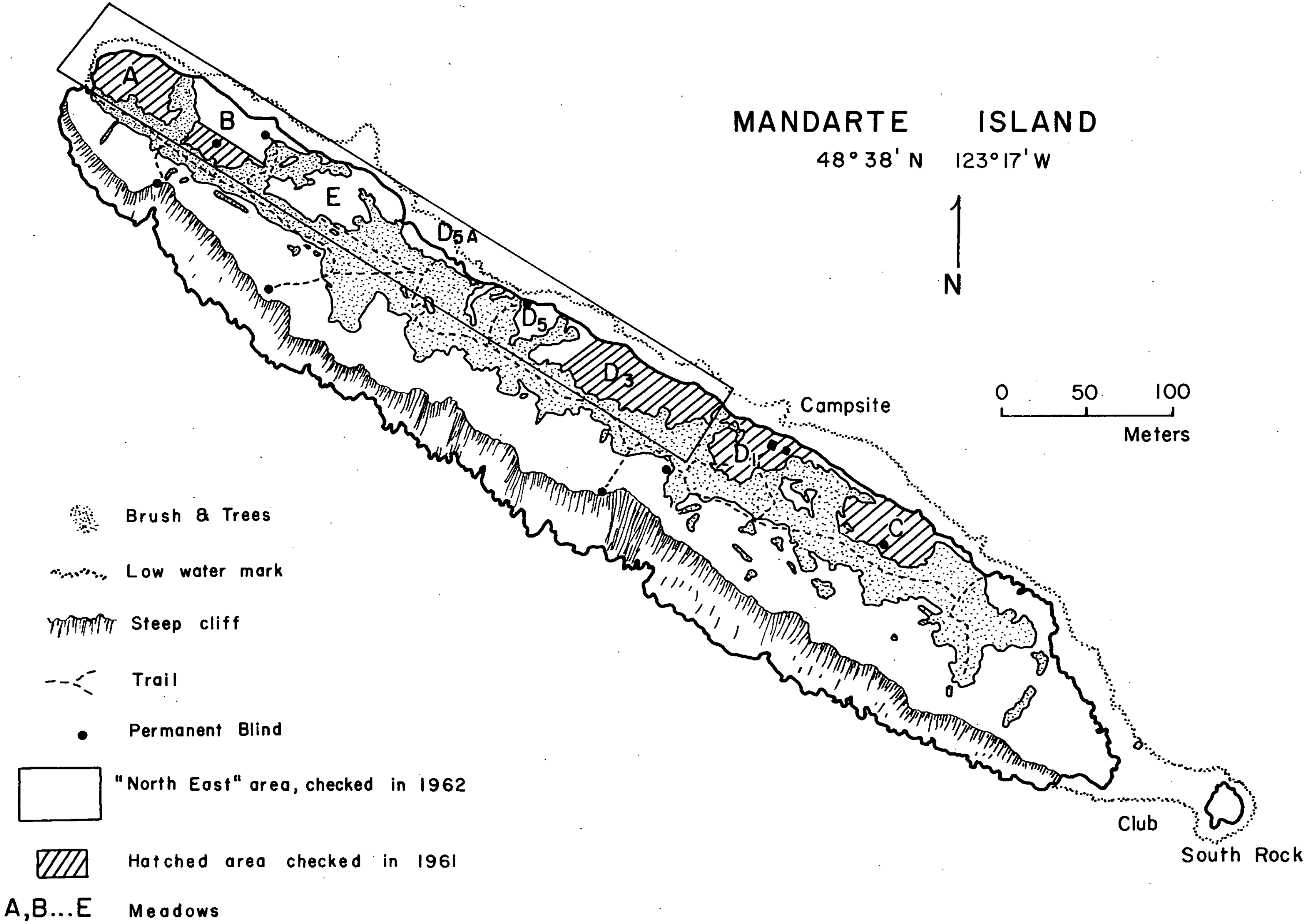
The study was done on Mandarte Island (48° 38'N, 123° 17'W), British Columbia, Canada. The island, made up of sedimentary rock, is about 100 meters broad and 700 meters long. Shrubbery is limited to a midway groove along the long axis and to tributary grooves between meadows along the northeast side. A small group of trees is present near the north end.

Field work was done in 1961 from May 1 to August 30. The areas checked daily in 1961, are indicated on Map I.

In the laying-hatching period, the a-, b-, and c- eggs (which were respectively the first, second and third eggs laid in a clutch) were marked, and the young were banded upon hatching with individual combinations of binders' tape; these were later replaced with individual colour combinations of plastic leg bands in addition to the standard aluminum rings.

Sixty-eight adults were caught on their nests by means of a trap. Due to egg collecting by Indians, visits by tourists, and extensive crow predation as a result of trapping on meadows A, B, C and D_1, only meadow D_3 remained in a natural condition for hatching and fledging data.

In 1962, I stayed on the island from May 2 until August 21.


MANDARTE ISLAND
48° 38' N 123° 17' W
N
0 50 100
Meters
A
B
E
D5A
D5
D3
D1
C
Campsite
Club
South Rock
Brush & Trees
Low water mark
Steep cliff
Trail
Permanent Blind
"North East" area, checked in 1962
Hatched area checked in 1961
A,B...E Meadows

The nests were provided with sturdy wooden sticks, with an average length of 30 cm. to which numbered metal game tags were attached. They proved to be more suitable than painted wooden stakes used in 1961 and could be placed in position quickly.

Meadow C was mainly used for behaviour study, while the meadows on the north-east side, indicated on map I by "North-East", were used for acquiring data on egg-laying, territory size, density of nests and chick production. As in 1961, the a-, b-, and c- eggs were marked, and the young were banded upon hatching as before.

In 1962 the whole "North-East" area could be kept in a natural state. The Indians did not visit the island for egg-collecting. Since the area checked in 1962 was larger than the one used in 1961, each meadow was searched on alternate days, from the beginning of the second week of June to the beginning of July. In July and for the first 12 days of August each meadow was checked thoroughly, every fourth or fifth day. After August 12, the area was visited less often, and only to look for chicks which had hatched late in the season and for dead ones.

The observations on the full grown chicks and these which had fledged in 1961 and 1962 were made mainly with binoculars and telescope.

Displays and calls (courtship feeding, head-tossing, copulation, choking, grass pulling, jabbing, alarm call, long call, and mew call) mentioned in this thesis do not differ qualitatively from the ones described by Tinbergen (1953, 1959) in the Herring Gull.

If the possibility of chance occurring was less than 5 per cent, when comparing observed and expected frequencies with values of chi-square, it was considered significant.

I PRE-EGG STAGE

A. Arrival

The exact date of the gull's first arrival on Mandarte Island is not known and may vary from year to year. From observations on week-end trips to the island during the winter and early spring of 1962, and 1963, and from spring arrival of banded breeding gulls of Mandarte Island in the proximity of their breeding grounds, it is concluded that they first settle on the meadows in the first half of February. From then on their numbers increase and by the latter half of April most of them have arrived.

From telescope observations on movements of banded adults from Mandarte Island by R. F. Oldaker over a four year period (1959-1962) it can be inferred that a large group of gulls winter away from their summer range. Their numbers increase rapidly from February to April in the Vancouver area as can be seen in Figure I. (Four winter months are not included due to fewer observations in that period).

The appearance of the Mandarte birds in the Vancouver area coincides with the end of the molt of the head, breast and neck feathers. The head, breast and neck region, which is dark during the fall and early winter, becomes white in the first few adults at the end of January. The majority are white-headed in March. In April all of the breeding birds observed had white heads. During the fall in the majority of the adults, black pigment advances from the base end of the bill over the

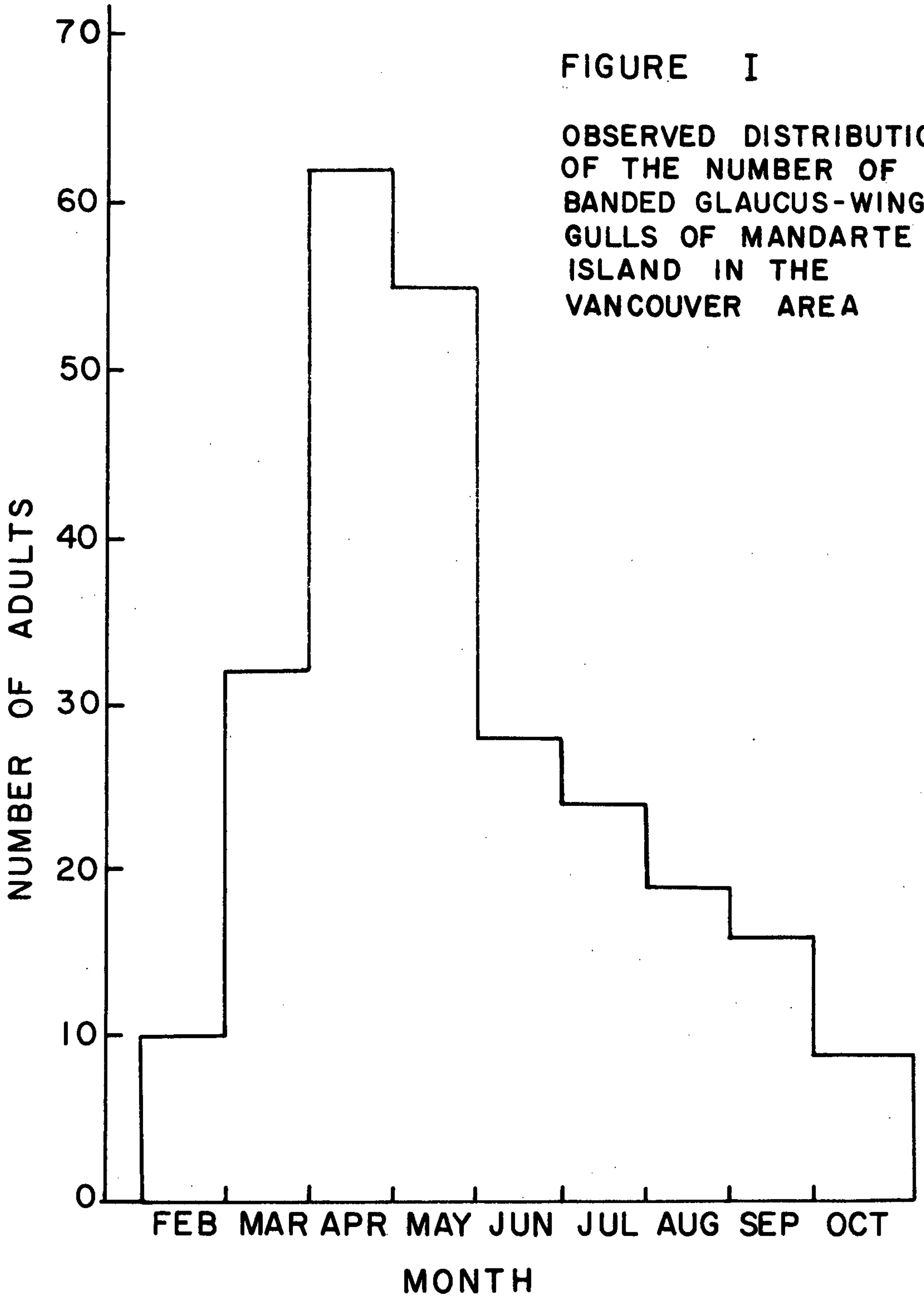


FIGURE I

OBSERVED DISTRIBUTION OF THE NUMBER OF BANDED GLAUCUS-WINGED GULLS OF MANDARTE ISLAND IN THE VANCOUVER AREA red gonydeal spot on the lower mandible. As spring approaches, the red gonydeal spot becomes clear again as the advancing and receding black pigment passes over it, while the latter disappears in front of the bill. In November and December approximately 90%, in March approximately 80% and in May approximately 30% of the adults have black pigment in their bills. In some of the banded young breeding birds a small amount of the black pigment was seen all summer.

During the pre-egg stage, adults travel between the island and feeding grounds in Vancouver (a distance of approximately 67 kilometers). Several of the colour-banded adults seen on early trips in the spring on the island were later observed in Vancouver. One banded gull was in Vancouver on March 30, 1962 and the day after it was seen on Mandarte. A colour-banded pair was observed on their breeding territory at 1500 on March 31 and was seen again at 1300 on April 1 on their winter territory at H.M.C.S. Discovery, in Stanley Park, Vancouver. Table I gives the sight records of this pair on the days when their winter territory was visited.

TABLE I

SIGHT HISTORY OF A COLOUR-BANDED PAIR ON THEIR WINTER TERRITORY IN VANCOUVER

Date Observed	Sex Present
November 26, 1961	♂ and ♀
December 3, 1961	♂ and ♀
December 31, 1961	♂
January 4, 27, 28, 1962	♂ and ♀
February 4, 9, 13, 18, 24, 1962	♂ and ♀
March 9, 16, 24, 1962	♂ and ♀
April 1, 14, 20, 23, 1962	♂ and ♀
April 8, 1962	♂
September 30, 1962	♂
October 10, 14, 27, 1962	♂
November 8, 1962	♀
November 11, 16, 1962	♂ and ♀
December 13, 1962	♂ and ♀
January 6, 9, 1963	♂
January 13, 1963	♂ and ♀
January 26, 1963	♂
January 27, 1963	♂ and ♀
February 7, 1963	♂
February 24, 1963	♂ and ♀

When both were present, they often were approximately 60 cm. apart. The male, as well as the female, defended this defined spot against other Glaucous-winged Gulls when the latter tried to land nearby. This is the first evidence that the mates of this species can maintain a strong pair-bond outside the breeding colony and can occupy a winter territory.

According to Tinbergen (1953) if two mates of the Herring Gull join the same winter flock, they never show any behaviour indicating personal attachment. Tinbergen thinks that they do not stay together all through the winter. Drost (1952), who observed banded Herring Gull pairs in the winter on the breeding territories, which are immediately adjacent to the winter feeding grounds at the harbour of Wilhelmshaven, Germany, found that gulls could be paired from October on, but the bond could be broken again by the coming in between of a new mate. As well as the pair in Table I, the mates of another coloured-banded pair were seen on May 7, 1962 together in Vancouver.

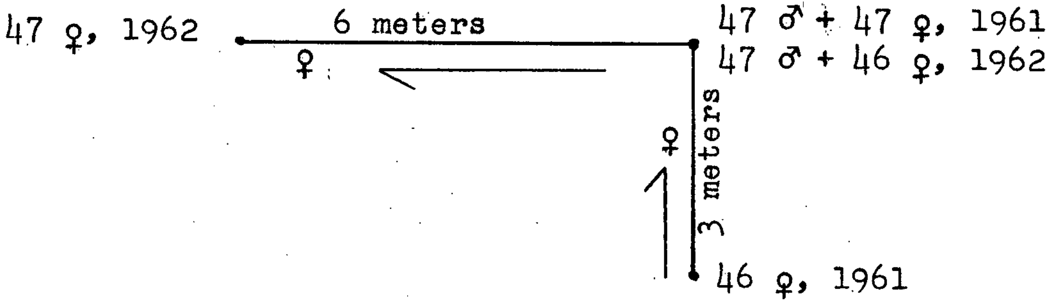
In early May most of the gulls are still too wary to stay on the island during the night and flock on the water. They return to the island as soon as it becomes light. During the first week of May the first gulls land on the meadows close to the campsite at about o315, and an hour later nest-building and copulation can be observed. Most of them leave between o800 and 1000 and come back in the late afternoon. Before and during twilight they are active again. They behave more warily on overcast than on clear evenings; during the former a little noise is sufficient to cause them to leave. The gulls become less fearful and stay longer on their territories as time in May passes on.

B. Pair-bond and Pair Formation

Pair-bondage -- In 1961, 26 of the 68 colour-banded Mandarte Gulls constituted pairs. From these 13 pairs, seven were still together in 1962. Of the six remaining pairs of 1961, only three males appeared next year, of which two acquired new mates, and for the third it was questionable whether he remained unmated or had a new partner. The six females all had new mates. Therefore the ratio of a one year long pair-bond to having acquired a new mate is for the females 7:6, for the males 7:2 (+1). Six gulls which constituted three colour-banded pairs in 1961, all returned in 1962, five of the six acquired new mates in the latter year, while for the sixth it was questionable whether he had acquired a new mate. The sample on pair-bondage is rather small compared with the one obtained over many years by Drost et al. (1961). Their figures for at least a three year period of pair-bondage show a ratio of 49:11 for females, and 49:13 for males, in favour of a pair-bond. This indicates that for both species a long period of pair-bondage occurs.

Pair Formation -- During two short periods in March and April 1962 spent on Mandarte, the gulls behaved warily and could not be observed easily. To what extent pair formation took place on the club (the term "club" is used here with the same interpretation as that for the Herring Gull by Tinbergen, 1953) is not known. I did obtain data on pair formation on the territories, as is shown below.

One pair, no. 47, and a neighbouring female, no. 46, were trapped on meadow C in 1961. In 1962 all three returned to meadow C, but the relations changed. On March 10, 1962, female no. 46 was by herself on meadow C and male no. 47 and female no. 47 were absent. On April 1, female no. 46 and male no. 47 were seen choking together, while female no. 47 was absent. In the first week of May it became clear, from their behaviour, that male no. 47 and female no. 46 were paired. In that week female no. 47 was observed with a new mate on the territory adjacent to that of male no. 47 and female no. 46. Male no. 47 and female no. 46 bred on the old no. 47 territory, while female no. 47 bred with her new mate on the adjacent territory. The change that took place is indicated by arrows in the sketch below:



It is very likely that the pairing between female no. 46 and male no. 47 took place on the territory, for female no. 46 had been observed there alone before the arrival of male no. 47, which in turn was seen later with female no. 46 before the arrival of female no. 47; the mating of female no. 47 with the neighbour makes it almost certain that pair formation took place there. Although very little agonistic behaviour was observed between these new pairs, boundary clashes did occur in 1962, where the female of a banded pair left her 1961 mate to mate with the neighbour. Clashes occurred between the old and new mate of this female. The pairing with neighbours probably happened because one of the 1961 partners arrived on the territory before the arrival of the former mate.

In the Herring Gull population Tinbergen (1953) studied, he claims that in mated pairs the members meet again outside their territory. This is also found in the Glaucous-winged Gull (see section A). The formation of new Herring Gull pairs takes place on the clubs, according to Tinbergen, but he does not mention that pair formation occurs on the territories.

Drost (1952), who had the opportunity to study a population of Herring Gulls whose breeding and wintering ground were almost identical, describes how pair formation takes place on this breeding-wintering ground, and how the ties between these pairs can be dissolved when one of the old pair takes a new mate.

C. Philopatry to Nest-site

From the 68 adults banded on their territories in 1961, 59 returned to the island in 1962. Forty-seven of these maintained their territory from one year to the next. They nested at the same site or, at most five meters away from it (average territory size: 16 m^2). Ten shifted territory. One gull (sex unknown) was seen only twice in 1962 on its 1961 territory. One male, separated from his 1961 mate, seemed unmated in 1962 and appeared on his original, as well as on a new territory 60 meters away. Of the 10 birds which shifted, eight were known to be females (in two the sex was unknown). Five of the latter occupied territories 30 to 100 meters away from their original ones and three mated with their previous neighbours. Two males, mated in 1961 to two of the eight shifting females, remained on their old territories and bred in 1962 with new mates. Of the females which did not shift territories, there was one whose mate did not return in 1962. This female returned to the old territory and bred there with a new mate. This then is an example of a male shifting to the territory of the female.

From the above it is inferred that usually the male establishes the territory. Drost et al. (1961), state that the male Herring Gull establishes the territory.

It is interesting that three gulls were seen in 1962 on their 1961 territory during the pre-egg stage, but nested between 30 and 100 meters away.

One of the females which shifted territories in 1962, changed her nest-site from within the shrubbery to the open meadow.

Sites for nests in the pre-egg stage may change from a position at the end of a tunnel several meters in the shrubbery to that of one just in the open at the edge of it (see section D, nesting).

One pair of Glaucous-winged Gulls started a nest on a roof at Vancouver harbour in 1962, and fledged two chicks successfully (pers. comm. R. F. Oldaker).

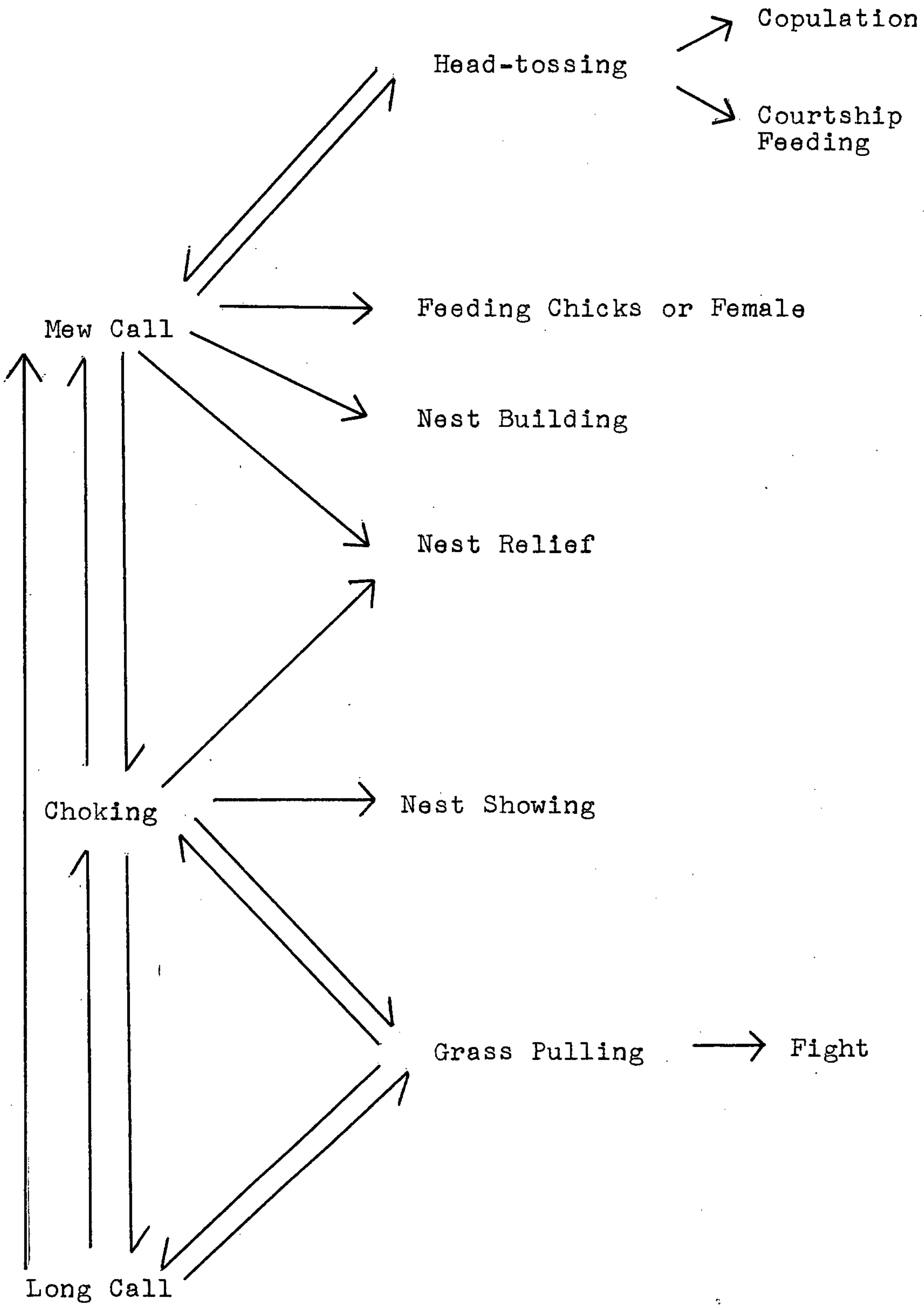
From the above it is concluded that the Glaucous-winged Gull is not restricted to any one nesting habitat.

The Herring Gull population at Wilhelmshaven harbour provides a good example of how flexible habitat selection may be (Drost et al., 1961). Another good example is the history and growth of a Kittiwake colony which became established on a warehouse at North Shields, Northumberland in 1949 (Coulson and White, 1958b).

With regard to nest-site faithfulness (philopatry) in the Glaucous-winged Gull, it seems to be the rule that most return to the same territory. Philopatry is also prominent in the European Herring Gull (Drost et al., 1961; Tinbergen, 1953). Tinbergen (1953) pointed out the importance of philopatry in relation to speciation and von Haartman (1949) demonstrated the role it plays in dispersion.

D. Displays, Nesting and Territorial Clashes

The displays mentioned in connection with the Glaucous-winged Gull do not differ qualitatively from the ones described by Tinbergen in the Herring Gull (1953, 1959). Therefore only few (mew call, long call, choking, head-tossing and forced matings) will be discussed since they may contribute most to understanding the behaviour of the gulls. The figure below shows some of the relationships between several displays which may precede one another in the Glaucous-winged Gull.


Head-tossing
Copulation
Courtship Feeding
Mew Call
Feeding Chicks or Female
Nest Building
Nest Relief
Choking
Nest Showing
Grass Pulling
Fight
Long Call

Mew Call - The mew call is often given in different situations. It is a sort of initial call which may pass into choking in a boundary dispute; it often precedes deposition of nest material, nest relief, courtship feeding and feeding of the young. Tinbergen (1959) thinks it is closely connected with attack and escape in the Herring Gull group. That it is in some way closely linked to feeding, was indicated by the observation of a mew-calling male regurgitating a fish without being provoked by the female; the female could not be seen to show any reaction. After regurgitating, the male went mew-calling to the still empty nest, holding the fish in his bill. Whether the fish was swallowed or dropped like nest material, I could not observe. This example indicates the close relationship between carrying nest material and feeding. Other evidence for this relationship comes from the observation that, during the chick stage, the parents presented nest material to the chicks away from the nest, and the chicks in turn took bits of this nest material from the parent's bill tip. After acceptance they dropped it.

Long Call - When a gull lands on its territory, it may give the mew call while landing, but the long call is often given also in the pre-egg and egg stage. Especially during these stages the meadows are filled with the reverberating sound of the long calls, when all the gulls return upon the appearance of an eagle or hawk. The mate already present on the territory will give the long call in return; often it is the one who is present on the territory which gives the call first.

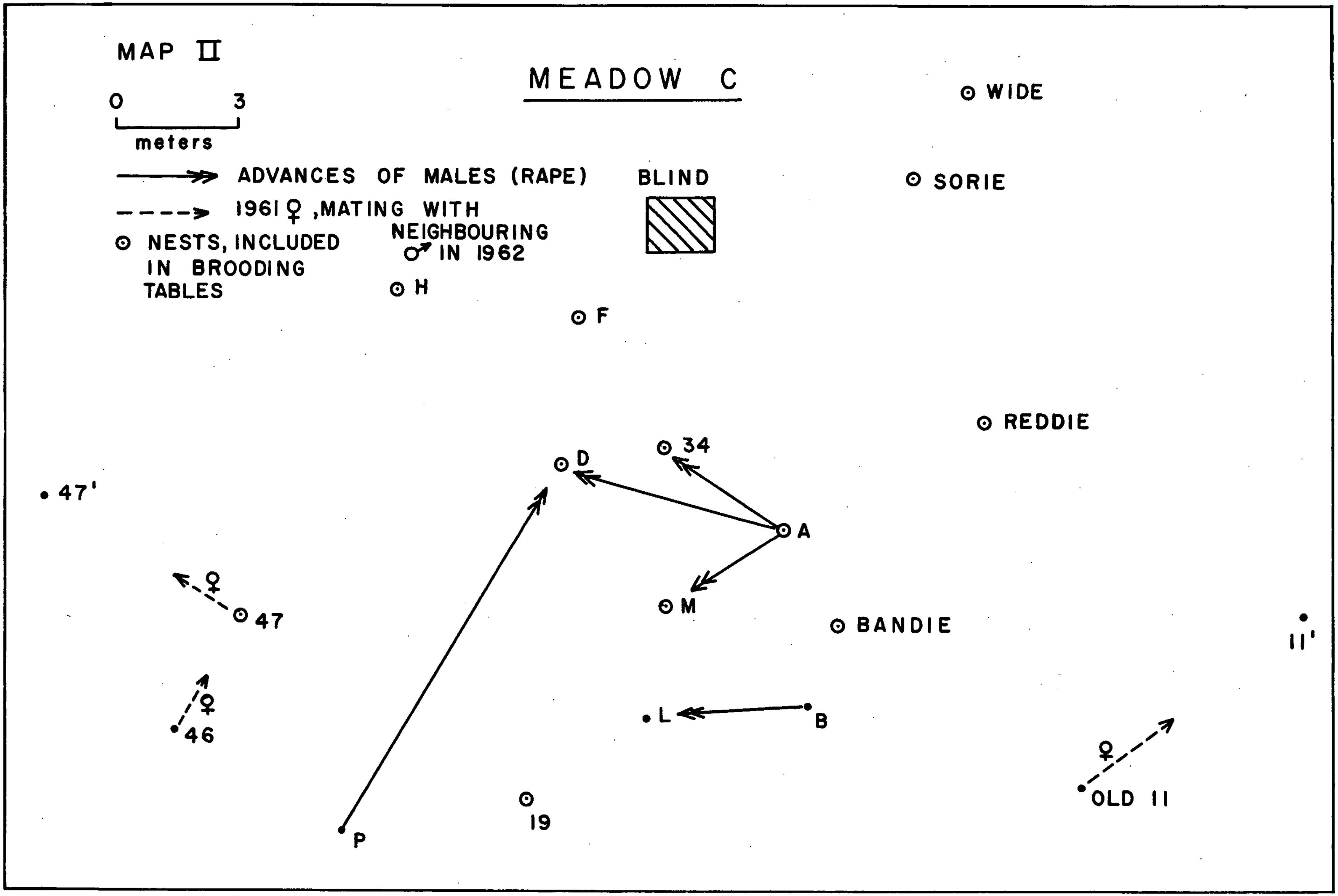
In many cases the surrounding territorial birds will give this call on another gull's return to its mate. The exchange of it between a pair is most frequent during the pre-egg and egg stage; during advanced incubation, when a gull returns to its mate on the territory the long call is less frequent, or even absent, and generally of shorter duration. The frequency of the long call also depends on how long the mate has been absent; it occurs less frequently when the time interval between departure and arrival of the mate is short. Later it becomes more frequent again at the time of hatching, and is often given when the chicks are moving. It is also given when a particular gull flying over the meadow is recognized. This call is given on almost every occasion of excitement. (Of course the alarm call will be given if predators or humans are present.) It seems that the frequency of the long call depends on the intensity of the excitement of the bird.

Choking - Choking as analyzed by Tinbergen (1959), can be either an aggressive display, or be concerned with nesting behaviour in the Herring Gull. In the Glaucous-winged Gull choking occurs mostly in the bending down movement and occasionally in the sitting position. In the latter position choking was very obvious in the female during forced matings and when a gull on the nest was approached by its mate it has been observed doing it, and would either stay on or let its mate take over the brooding. These observations seem to support Tinbergen's statement, that choking may have been derived from an incubation and nest-depositing movement.

Head-tossing - Head-tossing by the female can be followed either by copulation or regurgitation by the mate. I have seen one male that started head-tossing on the territory when the neighbouring male pulled the wing of the other. The latter observation may support Tinbergen's suggestion (Tinbergen's comments on Bateson and Plowright's article, 1959) that it is primarily an expression of fear, which has secondarily acquired an appeasement function in courtship. Head-tossing in hostile encounters has not been observed in European gull species, but it has been described by Moynihan (1958) in *Larus atricilla* and *Larus delawarensis*. Head-tossing was also obvious in hostile situations in *Pagophila eburnea*, where it is shown by the intimidated weaker bird (Bateson and Plowright, 1959).

Copulation - Between March 31 and April 2, 1962 only once was copulation observed. In the week before and during egg-laying copulation becomes frequent, but is absent after the last egg is laid. Copulation is preceded by head-tossing and occurs outside the breeding ground, on the club and on the breeding territory. In the Glaucous-winged Gull it is similar to that of the Herring Gull, described by Tinbergen (1953).

Rape - Attempted rape has not been observed by Tinbergen in the Herring Gull and he doubts that he would have missed them. Tinbergen (1959) observed male Black-headed Gulls trying to alight on females which were not their mates, but he does not mention if these males were neighbouring or remote ones. Because of the lack of such observations in the Herring Gull, a description of one follows. (For location of the individuals in the example below see map II: arrows indicate advances of males.):


MAP II
MEADOW C
0
3
meters
ADVANCES OF MALES (RAPE)
1961 ♀, MATING WITH NEIGHBOURING ♂ IN 1962
NESTS, INCLUDED IN BROODING TABLES
BLIND
WIDE
SORIE
H
F
REDDIE
34
D
47'
A
♀
47
M
BANDIE
11'
♀
46
L
B
♀
OLD 11
P
19

May 25, 1962, on meadow C. -- Rape.

0611: ♂ A starts head-tossing, ♀ A responds with faint head-tossing. ♂ A mounts, but ♀ walks away from beneath him.

0621: ♂ A walks in direction of neighbouring ♀ M and starts head-tossing. ♂ M is absent. ♂ A tries to mount ♀ M. ♀ M pulls grass and when he tries to mount again, ♀ M grasps and pulls his wing.

0625: ♂ A approaches neighbouring ♀ 34. ♂ 34 is absent. ♂ A starts head-tossing. ♀ 34 chokes (shows fear, head feathers flattened). ♀ 34 walks away. ♂ A goes on to neighbouring ♀ D. ♀ D chokes and walks away. ♂ A goes back to ♀ 34. ♀ 34 chokes and sits down. ♂ A starts head-tossing and mounts her. ♀ 34 pecks violently at chest of ♂ A; pecks at him, while ♂ A is still mounted on her. She tries to crawl from beneath him. ♂ A goes through act of copulation. ♀ 34 does not respond. ♀ 34 still tries to get away from him, while her wings are spread out and pressed against the ground. She tries to get rid of him, finally she succeeds. ♀ A who has been present all this time, approaches from A territory. ♀ A starts head-tossing. ♂ A flies away. One minute later, ♂ A arrives and starts preening.

0715: ♂ A starts head-tossing, ♀ A responds slightly. ♂ A goes to ♀ 34. ♀ 34 chokes and mews. ♂ A, silently and head-tossing slightly, approaches. ♀ 34 sits down and chokes. ♂ A starts head-tossing. ♂ A jumps over ♀ 34's head and lands on her back (he is back to front) and rearranges himself on ♀ 34's back. ♀ 34 pecks violently at his chest, while he is mounted. When he gets off (♀ 34 did not respond during copulatory act), ♀ 34 grasps and pulls his wing. ♂ A goes back to ♀ A. ♀ A mews slightly. ♀ 34 pulls grass when ♂ A leaves. ♀ 34 flies away.

0800: ♀ 34 arrives. ♂A (♀ A still present) gives long call at arrival of ♀ 34 and walks slowly and silently up to ♀ 34. She chokes, walks away and mews. ♂ A follows, utters slight alarm call when he sees me (♀ 34 came too close to the blind, and to observe how she reacted I moved in the blind). ♂ A returns to his territory, he head tosses and copulates with ♀ A.

0808: ♂ 34 arrives, ♀ 34 greets him with long call. ♂ 34 tries to mount her after exchange of head-tossing, but ♀ 34 is slightly fearful and copulation does not succeed.

May 27, 1962, on Meadow C. -- Rape.

Before
o815: ♂ A copulated successfully with ♀ A.

o815: ♂ A starts head-tossing, walks over to ♀ 34. (♂ 34 absent). ♀ 34 squats down. ♂ A walks to ♀ D (♂ D absent), ♀ D chokes, ♂ A head tosses, ♀ D sits down, ♂ A tries to mount and jumps over her head. She grasps and pecks him. She shakes him off. ♂ A flies away and soon arrives at his own territory. ♂ A starts head-tossing. ♀ A responds. Copulation between ♂ A and ♀ A is successful.

May 30, 1962, on Meadow C. -- Rape.

o715: ♂ A approaches ♀ 34 (♂ 34 just departed). ♂ A head tosses, jumps on back of ♀ 34. She is pressed down on nest, he stays long on her back and folds tail for fertilization. ♀ 34 grasps him at chest violently. ♂ 34 arrives during act of copulation. ♂ 34 gives long call. ♂ A gets off ♀ 34. ♀ 34 grasps and pulls wing of ♂ A. ♂ 34 looks on, then starts pulling grass, which is directed to ♂ A. ♀ A who has been present, goes in meantime to nest (containing one egg).

Rape was attempted by ♂ A and a few other males with neighbouring females. After ♀ A had completed her clutch, ♂ A stopped raping ♀ 34. Although the male in the process of rape went through the copulatory act, in no instance it was observed that the female responded.

Soliciting by females was also observed in several cases. One example follows below:

May 29, 1962, on Meadow C.

o915: ♂ Bandie present; mate absent. Strange ♀ lands close to ♂ Bandie. ♀ starts head-tossing. ♂ Bandie head tosses. Together they walk parallel to each other and go through mew call phase. Suddenly ♂ Bandie jabs at ♀ and grasps her wing. ♀ leaves.

The reason for rape is not known; one may speculate that it follows unsuccessful copulation (such as at o611 on May 25 in pair A). However at o815 on May 27 it followed successful copulation of pair A. Or, perhaps some males, endowed with a stronger concentration of sex hormones than others, are more active sexually.

Nesting - All the less precipitous open areas of the island are utilized. The majority nest in the meadows, and nests are regularly built in the brush fringe wherever the birds can penetrate by a sort of run-way. The nest, a rough saucer of grass, is located within the territory. In 1962, the average actual territory size on 7825 m^2 of meadow (all was utilized) for 477 pairs of gulls in the "North East" area was 16 m^2. The nest is similar in construction as that described for the Herring Gull (Paludan, 1951; Tinbergen, 1953).

Carrying of nest-building material and a few nests were observed in March and April, but it is not before the latter half of May that nests became numerous. As in the Herring Gull (Tinbergen, 1953), there is much variation of the nest-building drive before this period: several scrapes are made before a permanent site is taken up.

Nests, which are made at the end of tunnels, as much as three meters long, in the shrubbery may be abandoned for ones immediately at the edge of it, when foliage decreases light intensities, or the rain causes foliage to hang down in the tunnels.

Which one of a mated pair drops the first straw at a certain spot for a nest site is hard to distinguish, but the female as well as the male may initiate carrying of nest material. One example from my field notes reads: 1700-1915, May 19, 1962 on Meadow C.

> ♀ A while mew calling deposits nest material and chokes over it.
> ♂ A goes to "nest site" and they both choke over it.
> ♀ A deposits nest material again and hollows out "nest site" by swinging to and fro in it.
> ♂ A picks up nest material, deposits it at different site.
> Both choke over this new site.
> ♂ A leaves and the female hollows out a new "nest site".

From the above it is concluded that although it is mainly the male, which establishes the territory, both male and female may initiate nest-building. After initiation, both sexes have an equal share in building.

In _Larus argentatus_, both male and female collect material, but the male definitely does more of the collecting, according to Tinbergen (1953). Goethe (1956) also says, that the male collects the nest material.

Territorial Clashes - In boundary clashes, when both members of a pair are present, the male is usually the most aggressive and the most forward. The females are slightly behind the opposing males, and also pull grass and jab at the neighbouring territory owner, but less frequently and violently than their mates. The female, however, may take the initiative to defend the territory when a neighbouring male territory holder lands closer to her than to her mate. Some females even chase the intruder when it lands closer to her mate, but a female actually charging a neighbouring male while alone on her territory was not observed, although she may jab at him or pull grass. However, on several occasions a female attacked a neighbouring female. As in the male there is much variation among the individual females in respect to aggressiveness or fear. When there is a boundary clash, many neighbours become excited as well and give the long call.

Boundary clashes were also seen on the beach. In three neighbouring beach-territory holding pairs (one of these pairs started egg-laying later on the higher part of the beach) head-tossing, mew-calling and choking were often observed in water adjacent to the territories. During boundary clashes, grass pulling was substituted here by pulling kelp in the water; sometimes the heads of the males would go completely under as they pulled kelp. Grass pulling was not only seen in boundary clashes, but it was also observed to be directed at the trap, when the latter was placed over the nest in the process of catching adults.

Summary of Pre-Egg Stage

1. From the spring increase of banded Mandarte adult gulls in the Vancouver area, it is inferred that a large group of gulls winter away from their summer range.
2. The Glaucous-winged Gulls can maintain a strong pair-bond outside the breeding colony, while maintaining a winter territory.
3. Pair formation occurs on the breeding territory. It was usual for pair-bonds to last for at least a year.
4. Philopatry to the previous nest site was observed in the

majority of cases.

5. Territorial boundaries can be shifted during the pre-egg stage, but they become less flexible after the nest is built.
6. Although it is mainly the male which establishes the territory, both sexes may initiate nest-building.
7. Certain males are more prone in attempting to rape females on neighbouring territories than others.

II THE EGG STAGE

A. Start and Duration of Egg-laying

The mean of clutch commencement for 276 initial clutches in 1961 and the mean for 478 initial clutches in 1962 fall respectively on June 5, 1961 and June 3, 1962.

Clutch commencement as is shown in Figure IIA, started earlier in 1962 than in 1961, but this may be due to several factors. The area checked in 1962 was much larger than that of 1961. For instance, one area, meadow D_5, where most of the clutches before May 21, 1962 were started, was not included in the 1961 census. The exact dates of first occupation of the island in 1961 and 1962, which may affect clutch commencement are not known and may have been identical or different because of weather conditions (Monthly mean maximum and mean minimum temperatures in 1961 and 1962, at pre-egg and egg stage, did not deviate much). Paludan (1951) emphasizes from reliable data on the Herring and Lesser Black-backed Gull, the lack of correlation between definite temperatures and commencement of egg-laying. Richdale (1957) who has quantitative data over the years for egg-laying in Penguins could find no weather correlations. It will be seen that most of the eggs on Mandarte in 1961 and 1962 were laid in the last week of May and the first two weeks of June.

The clutch commencement of several of the colour-banded Glaucous-winged Gulls was known in 1961 as well as in 1962, as is shown in Tables IIA and IIB.

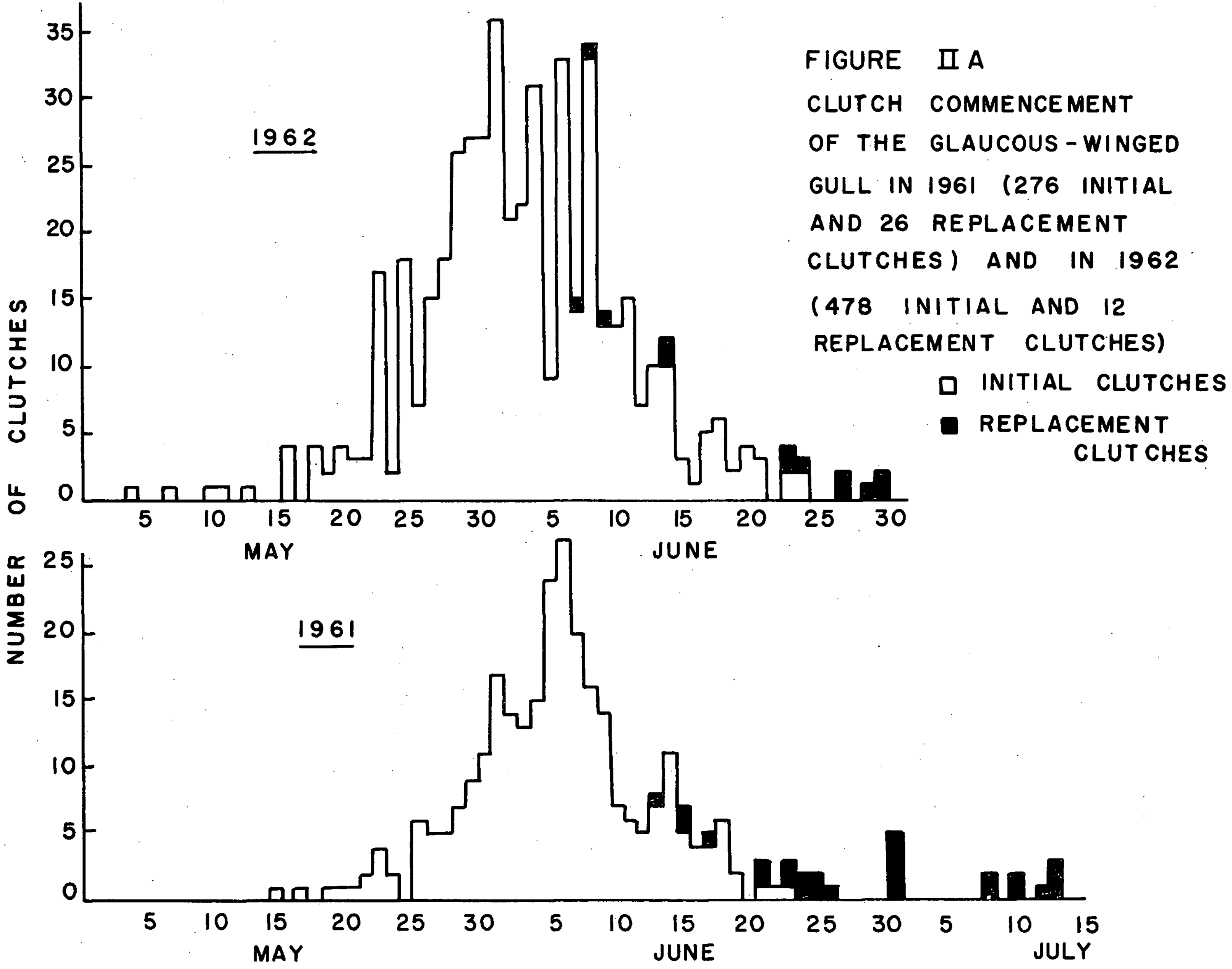


FIGURE II A
CLUTCH COMMENCEMENT OF THE GLAUCOUS-WINGED GULL IN 1961 (276 INITIAL AND 26 REPLACEMENT CLUTCHES) AND IN 1962 (478 INITIAL AND 12 REPLACEMENT CLUTCHES)

TABLE IIA

CLUTCH COMMENCEMENT IN COLOUR-BANDED FEMALES

Nest No.	1961	1962	Remarks
47	May 24	May 23	Different mate in 1962
51	May 17	May 18	Same mate in 1962 as in 1961. First clutch to be started on meadow B in 1961 and 1962.
76	May 15 (or earlier)	May 10	Same mate in 1962 as in 1961. First and second clutch respectively in 1961 and 1962, to be started on meadow A.
77	May 20	May 23	Same mate
39	May 31	May 28	Far from original territory in 1962.
48	June 3	June 7	Far from original territory, and different mate in 1962.
34	June 4	May 27	Different mate in 1962
13	May 28	June 2	
47	June 6	June 2	Different mate in 1962
71	June 5	June 8	Same mate in 1962 as in 1961

TABLE IIB

CLUTCH COMMENCEMENT IN PAIRS, WHERE ONE COLOUR-BANDED PARTNER WAS A MALE OR THE SEX UNKNOWN, AND WHERE 1961 AND 1962 TERRITORIES WERE IDENTICAL.

Nest No.	1961	1962	Remarks
110	May 25	May 22	Sex unknown
52	May 22	May 22	Sex unknown
B2	June 5	June 5	Male
B3	May 31	May 30	Male
V4	June 6	June 5	Sex unknown
E8	June 5	June 6	Sex unknown

The banded pair of nest no. 51 started the first clutch on meadow B in 1961 as well as in 1962, out of 93 pairs nesting on that meadow in 1962. The banded pair of nest no. 76 had completed their clutch on May 19, 1961, when this was the first clutch found on meadow A. Clutch commencement has been indicated in the 1961 histogram in Figure IIA as May 15, but this clutch may have been started before this date. This pair started its clutch on May 10 in 1962 and was then the second clutch started out of 100 pairs on meadow A.

From the data in the Tables IIA and IIB, it can be deducted that there is a close relation in the start of egg-laying by the same individuals in 1961 and 1962. Outside the passerines this has been shown for Yellow-eyed Penguins (Richdale, 1957), Velvet Scoters (Koskimies, 1957), and Greenshanks (Nethersole-Thompson, 1951). Richdale (l.c.) showed that the individual differences in laying dates in Yellow-eyed Penguins have a genetic basis.

B. Clutch Commencement in Relation to Density and Habitat

Darling's (1938) hypothesis of social stimulation suggests that stimulation received from other birds in a colony produced greater synchronisation of breeding within the colony and this in turn resulted in earlier breeding and a shorter spread of breeding in large colonies.

Coulson and White (1956) showed that the differences between colonies were not significant. Even the converse of Darling's hypothesis was shown by the latter authors in the Kittiwake, where the spread of breeding increased with the size of the colony. Coulson and White (1960) observed that the greater

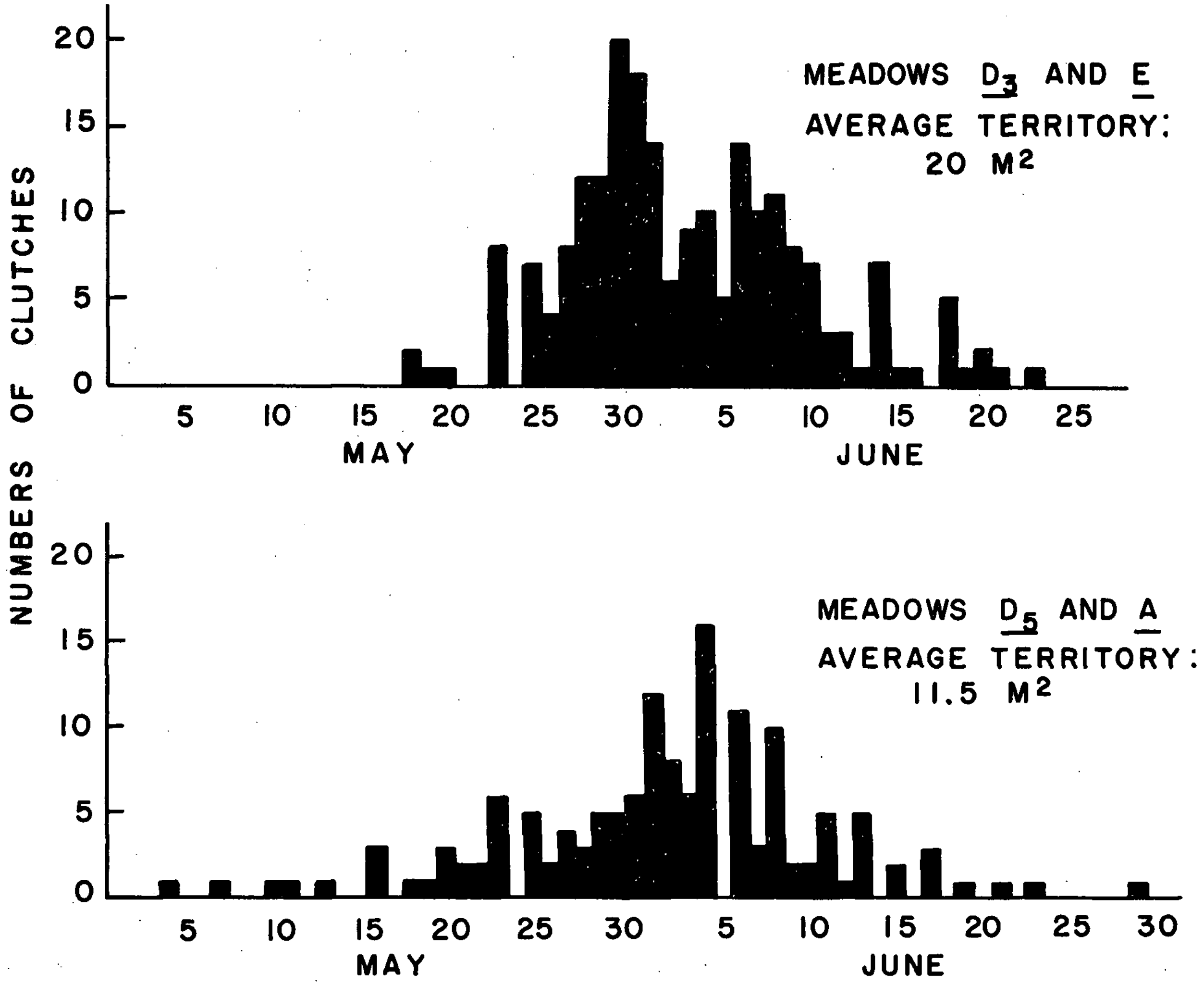


FIGURE II B CLUTCH COMMENCEMENT RELATED TO TERRITORY SIZE IN THE GLAUCCUS-WINGED GULL IN 1962.

part of the differences were correlated with density, presumably produced by the stimulation received from neighbouring birds. They found that the spread of breeding was greatest in dense colonies of Kittiwakes, which does not support Darling's contention. Moreover where the Kittiwakes nested more densely, they bred earlier.

Taking the two meadows D_3 and E (see map I) where the average territory size is largest and the two meadows D_5 and A, where the average territory size is smallest, and plotting the clutch commencements on these meadows in relation to territory size in Figure IIB, one can observe that the results support Coulson and White's data obtained in the Kittiwakes. In the Glaucous-winged Gulls the spread of breeding is greater and clutch commencement earlier on the meadows with the highest density of nests. Coulson and White (1958) found from a study of colour-banded Kittiwakes that birds breeding for at least a second time bred 7.5 days before birds breeding for the first time. They found in all colonies that the last few birds bred at the same time and according to them this is due to the fact that in all the colonies there are low-density areas and all have late breeding of young birds. It can be seen in Figure IIB that in the Glaucous-winged Gulls, the last few birds start clutch commencement at the same time on meadows with a low as well as a high density of nests.

The effect of age on breeding is not known (except in a few cases where the age of the individual breeding bird could be established) but the commencement of the last clutches may be due to the presence of young birds on all meadows. The last clutches started were mostly not in low density but rather in medium or high density areas, and therefore low density areas cannot account for last clutch commencements in the Glaucous-winged Gulls. On meadow D_5 there are many elevated rock outcrops interlaced with tall grass and, in meadow A there are many rounded rock ridges between grass valleys. Glaucous-winged Gulls prefer look-outs and the habitat on these meadows seems to be optimal for them. The reason the highest densities are found on these meadows is probably due to an optimal breeding habitat.

C. Laying Pattern

The Larus species may lay eggs at any time of the day or night (Goethe 1937, Paludan 1951, Barth 1955, Goodbody 1955, Weidmann 1956, Ytreberg 1956). Ytreberg (1960) thinks that it is probably an insufficiency of data which has led to the belief that eggs are laid during certain times of the diurnal period.

In 1962, meadows D_3, D_5, D_{5A} and E were checked three times daily from May 25 till the night of June 6. The empty nests were marked with numbered metal game tags attached to pieces of wood, about 30 cm. long, which could easily be distributed and moved to new scrapes as old ones often were disregarded by the gulls. The meadows were searched slowly and thoroughly so as not to disturb the gulls. Each inspection took two hours: in the morning, from 0330 to 0530, at noon from 1130 to 1330, and at night from 1830 to 2030. The same route was always followed and since the time interval at inspection was two hours, the area was divided up in two parts. The first part included all the nests, which were checked from o330 to o430, 1130 to 1230, and 1830 to 1930 with respectively o400, 1200 and 1900 as the mean of the time intervals. The second part included all the nests checked from o430 to o530, 1230 to 1330 and 1930 to 2030 with respectively o500, 1300 and 2000 as the mean of the time intervals. The time interval between the laying of the individual eggs in a clutch was determined to plus or minus nine hours maximally, if the means of the time intervals in both areas are taken. The time at which eggs were laid was determined for 390 eggs with an average maximum error of measurement of ± 4.0 hours.

Table IIIA indicates almost an exact fit of the expected in relation to the observed frequency of egg-laying and therefore a uniform laying in these three periods. Table IIIB deviates more, but still the difference is not significant ($.50 > p > .30$). The greatest deviation between observed and expected frequencies is found in the 2000 - o500 interval.

TABLE IIIA

COMPARISON OF EGGS LAID DURING THE PERIODS 1900 - 0400, 0400 - 1200, and 1200 - 1900

Period	Observed No. of Eggs	Expected No. of Eggs If Uniform Laying
1900 - 0400	86	86.2
0400 - 1200	77	76.7
1200 - 1900	67	67.1

TABLE IIIB

COMPARISON OF EGGS LAID DURING THE PERIODS 2000 - 0500, 0500 - 1300, and 1300 - 2000

Period	Observed No. of Eggs	Expected No. of Eggs If Uniform Laying
2000 - 0500	69	60
0500 - 1300	49	53.3
1300 - 2000	42	46.7

Both Tables IIIA and IIIB indicate uniform laying during any part of the day with a possible exception of a higher frequency of egg-laying in the first hour after sunrise. The time of sunrise during the checking period ranged from 0422 on May 25 to 0413 on June 6.

Table IV A shows a uniform distribution for the a-, b- and c- eggs, Table IV B indicates more deviation for the a-, b- and c- eggs, but the differences are not significant. (For the a-, b-, and c- eggs respectively $.20 > p > .10$, $.30 > p > .20$, $.70 > p > .50$). Figures in brackets indicate the number of eggs from nests in which only one or two eggs were laid.

TABLE IV A

COMPARISON OF a-, b-, AND c-EGGS LAID DURING THE PERIODS 1900 - 0400, 0400 - 1200, AND 1200 - 1900

Egg No.	Period	Observed No. of Eggs	Expected No. of Eggs if Uniform Laying	Total
a	1900 - 0400	30 + (2)	31.1	83
	0400 - 1200	24 + (2)	27.7	
	1200 - 1900	20 + (5)	24.2	
b	1900 - 0400	28 + (2)	31.1	83
	0400 - 1200	27 + (1)	27.7	
	1200 - 1900	22 + (3)	24.2	
c	1900 - 0400	24	24	64
	0400 - 1200	23	21.3	
	1200 - 1900	17	18.7	

TABLE IV B

COMPARISON OF a-, b-, AND c- EGGS LAID DURING PERIODS 2000 - 0500, 0500 - 1300, AND 1300 - 2000

Egg No.	Period	Observed No. of Eggs	Expected No. of Eggs if Uniform Laying	Total
a	2000 - 0500	23 + (4)	21.7	58
	0500 - 1300	13 + (3)	19.3	
	1300 - 2000	13 + (2)	17	
b	2000 - 0500	23 + (2)	21.4	57
	0500 - 1300	19 + (2)	19	
	1300 - 2000	11	16.6	
c	2000 - 0500	17	16.9	45
	0500 - 1300	12	15	
	1300 - 2000	16	13.1	

Table V contains the egg-laying pattern of 91 clutches, for which the laying time for all three eggs in the clutch was determined with an average maximum error of measurement of ± 4.0 hours.

TABLE V

DISTRIBUTION OF EGG LAYING PATTERN BASED ON THREE INSPECTIONS PER DAY

Pattern No.	Laying Pattern Days After Laying of a- Eggs								Number of Clutches
	0	1	2	3	4	5	6	7	
1	a - -	b - -	- - -	c					1
2	a - -	- b -	- - -	c					1
3	a - -	- b -	- - -	- - c					2
4	a - -	- - b	- - -	- - c					3
5	a - -	- - b	- - -	- - -	- c				1
6	a - -	- - -	b - -	- - -	c				8
7	a - -	- - -	b - -	- - -	- c				11
8	a - -	- - -	b - -	- - -	- - c				3
9	a - -	- - -	b - -	- - -	- - -	c			1
10	a - -	- - -	- b -	- - -	- c				18
11	a - -	- - -	- b -	- - -	- - c				13
12	a - -	- - -	- b -	- - -	- - -	c			11
13	a - -	- - -	- - b	- - -	- - c				5
14	a - -	- - -	- - b	- - -	- - -	c			2
15	a - -	- - -	- - b	- - -	- - -	- c			3
16	a - -	- - -	- - -	b - -	- - -	c			1
17	a - -	- - -	- - -	b - -	- - -	- - c			2
18	a - -	- - -	- - -	b - -	- - -	- - -	c		1
19	a - -	- - -	- - -	- b -	- - -	- - -	c		1
20	a - -	- - -	- - -	- - b	- - -	- - c			1
21	a - -	- - -	- - -	- - b	- - -	- - -	c		1
22	a - -	- - -	- - -	- - -	- - b	- - -	- - -	c - -	1

The egg-laying pattern groups itself around pattern no. 10 with a laying time of 4.5 days. Taking into account the possible average maximum error of measurement of ± 8 hours when comparing the laying time for two eggs, patterns no. 6, 7, 8, 11 and 13 can belong to the same egg-laying pattern. These six patterns cover 64% of all patterns. Pattern no. 22 deviates much and protracted laying may have occurred here (see section D).

Table VI shows the distribution of the time intervals between a- and b- eggs, b- and c- eggs, and between a- and c- eggs. All intervals were determined with an average maximum error of measurement of ± 8 hours. In 18 clutches only the a-b, and in another 18 clutches only the b-c intervals were known. No clutches with two eggs are included. The average time between the a- and b- egg is 54.83 hours, between the b- and c- eggs 54.90 hours and between the a- and c- eggs 110.15 hours. The average time lapse for both the a-b and b-c intervals is 54.86 ± .63 hours.

TABLE VI

EGG-LAYING INTERVALS OF a-b, b-c, AND a-c IN EACH CLUTCH

Interval In Hours	No. of Cases a-b	b-c	Total	a-c
24	1		1	
32	3		3	
40	6		6	
48	31	44	75	
56	47	39	86	
64	12	23	35	
72	5	3	8	1
80	1		1	1
88	2		2	5
96				8
104				30
112	1		1	21
120				15
128				3
136				3
144				3
152				
160				
168				1
	109	109	218	91

Table VII shows the time intervals of laying between the individual eggs of a clutch in relation to length of adults, egg sizes, and length of incubation in three different species. In these members of the Laridae it can be seen that egg-laying and incubation take longer in larger birds with larger eggs. Whether this is the case for all gull species, can only be established by more knowledge about their breeding biology.

TABLE VII

A. AVERAGE TIME INTERVAL BETWEEN LAYING OF a- AND b-, b- AND c-, AND a- AND c- EGG IN A CLUTCH

Species	Average Time Interval Sample Number of Eggs in Brackets			Source
	a-b	b-c	a-c	
Larus ridibundus	42.26 hrs. (53)	41.81 hrs. (62)	83.13 hrs. (46)	Ytreberg, 1960
Larus canus	45.42 hrs. (59)	45.45 hrs. (69)	89.02 hrs. (47)	Ytreberg, 1960
Larus glaucescens	54.83 hrs. (109)	54.90 hrs. (109)	110.15 hrs. (91)	This Paper

B. AVERAGE LENGTH OF SPECIES

Species	Average Length in cm.	Source
Larus ridibundus	36 - 38	Witherby et al., 1941
Larus canus	41 - 46	Peterson, 1961
Larus glaucescens	61 - 69	Peterson, 1961

C. AVERAGE EGG SIZE OF SPECIES

Species	Average Egg Size in mm. Sample Number of Eggs in Brackets			Source
Larus ridibundus	Length: Breadth:	51.40 36.31	(624)	Ytreberg, 1956
Larus canus	Length: Breadth:	57.64 41.83	(100)	Witherby et al., 1941
Larus glaucescens	Length: Breadth:	70.05 49.8	(30)	Veitch and Booth, 1954
	Length: Breadth:	70.6 48.8	(43)	Schultz, 1951

D. AVERAGE LENGTH OF INCUBATION

Species	Incubation period in Days	Sample	Source
Larus ridibundus	22.8	156	Ytreberg, 1956
Larus canus	25.9	56	Barth, 1955
Larus glaucescens	26.9	128	This Paper

D. Clutch Size

The Glaucous-winged Gull normally lays three eggs; not one undisturbed nest with four eggs was observed. The eggs varied in size, colour and shape, but the ones of the same clutch usually resembled each other in these aspects. With regard to clutch size, the 1961 sample was small (average clutch size: 2.74) and some replacements may have been included among the initial clutches. The 1962 data are more accurate with respect to distinguishing between initial and replacement sets, due to the mapping of the inspected area. Therefore only the 1962 data are used for the calculation of the clutch size. In 1962, 479 pairs of gulls in the "North East" area produced 1386 eggs (of which 1351 in initial - 31 in repeat - and 4 eggs in protracted laying). The initial clutches consisted of:

Initial Clutch Size	Number of Cases	Mean Clutch Size
three	401	
two	70	2.82 ± .02
one	8	

Of 479 initial clutches started in the "North East" area in 1962, 237 began before June 3 with a mean clutch size of 2.90 ± .02 and another 241, with a mean clutch size of 2.74 ± .03 were initiated from June 3 on. (Of one clutch the egg-laying date was unknown). The difference between the means of the clutch size in the first and latter half of the season was statistically insignificant ($.30 > p > .20$). The lower mean clutch size in the latter half of the season was mainly due to the larger number of c/2 and c/1 (clutches of two and one eggs) clutches laid in that period. There were 19 c/2 and 2 c/1 initial clutches laid in the first half and 51 c/2 and 6 c/1 clutches in the second half of the laying season. The higher number of c/2 clutches found in the latter half of the laying season may be partly due to the higher percentage of young birds breeding late. Not enough data are available on the clutch size of Glaucous-winged Gulls breeding for the first time. Coulson and White demonstrated that Kittiwakes breeding for the first time bred much later than older ones (1958) and no female breeding for the first time had been observed to lay three eggs (1961). However, the difference in clutch size in the Kittiwakes was not solely the result of older birds breeding earlier, but the clutch size was also influenced by the time of laying. Coulson and White (1961) also found that another unknown factor or factors (which may have a genetic basis) operate(s) to cause certain individuals to lay a consistently larger or smaller clutch than might be expected by chance.

Comparison of the mean clutch and average territory size between 213 pairs of gulls on meadows D_3 and E (mean clutch: 2.86; average territory: 20 m^2) and 144 pairs of gulls on meadows D_5 and A (mean clutch: 2.80; average territory: 11.5 m^2) did not show a significant difference ($.80 > p > .70$) at the prevailing densities in egg production.

There is evidence for Larus argentatus and Larus fuscus (Paludan, 1951) and Larus ridibundus (Weidmann, 1956) that loss of eggs as they are laid causes protracted laying, i.e., the birds are indeterminate layers. Two cases with several records on protracted laying in the Glaucous-winged Gulls showed that the egg-laying interval between the third and fourth egg laid was similar to the interval between eggs in undisturbed clutches. The records are:

Nest No. 243

May 26	0500	1 egg	
May 26	2000	egg gone	(eaten by crows)
May 28	0500	1 egg	
May 30	1200	2 eggs	
May 30	2000	1 egg	(1 egg eaten by crows)
June 1	2000	2 eggs	

Nest No. 777

May 28	1200	1 egg
May 29	1200	egg pecked
May 29	2000	egg gone
June 1	0400	1 egg
June 3	2000	2 eggs
June 6	0400	3 eggs

Loss of the entire clutch after sufficient brooding to suppress the fourth follicle results in a replacement clutch, in L. *argentatus* and *fuscus* in 11 - 12 days (Paludan, 1951); in L. *ridibundus* in about the same period (Weidmann, 1956). In 1961, three records were obtained on colour-banded Glaucous-winged Gull pairs, when they lost their clutches due to crow predation after trapping. The egg shells remained for several days in the nest. Records for the interval between loss of the initial clutch of three and the appearance of the first egg of the replacement clutch of these three pairs are 13, 15 and 16 days. Probably the birds were disturbed due to trapping, because from 1962, there are six records of an 11- and five of a 12-day interval between loss of the initial clutch and the appearance of the replacement clutch. In the latter case, the birds were not banded, but the replacement clutches were found close or at the same spots as the initial clutches. Replacement clutches were also found after chicks of the original clutch were lost.

All replacement clutches in 1961, after June 26, were found in meadow C. Although trapping of the last bird occurred on June 26 on this meadow, the gulls were extremely fearful due to past experience and the constant alarm of crows, which were numerous there. From the point of view of population dynamics, replacement seems to be only important when large disturbances occur. The incidence of numerous replacements occurring after a snowstorm in the Herring Gull is well-known from Paludan's (1951) study.

E. Share of Sexes in Brooding

Broodiness in the empty nest could be observed in some cases many days before the first egg was laid. Pair B and pair Bandie in Table VIII are examples of this.

TABLE VIII

TIME SPENT BY PAIR B AND PAIR BANDIE ON NEST DURING OBSERVATION PERIOD BEFORE THE FIRST EGG WAS LAID

PAIR B:

	Time of Observation		Time on Nest in Minutes		
Date	Period	No. of Minutes	Total	♂	♀
8/6/62	0645-0915	150	39	28	11
13/6/62	0630-0915	165	4	1	3
18/6/62	0615-0840	145	.5	.5	0
22/6/62	First egg laid				

PAIR BANDIE:

	Time of Observation		Time on Nest in Minutes		
Date	Period	No. of Minutes	Total	♂	♀
2/6/62	0730-0930	120	25	0	25
8/6/62	0550-0630	40	30	29	1
10/6/62	0645-0845	120	79	79	0
12/6/62	First egg laid				

The female of pair Bandie, was a banded four year-old and it is unlikely that she had bred before (she was not present on meadow C the preceding year and her plumage seemed to indicate recent maturation). After the eggs were laid she took an even share in the observed incubation (see brooding tables in the Appendix). More pronounced brooding starts on the day the first egg is laid and it increases in frequency till the clutch has been completed, as can be observed from the brooding tables in the appendix. The share of the sexes in incubation is indicated in Table IX. There is much variation in the share taken by the individual pairs, but from the average brooding times it can be observed that the sexes share equally in diurnal incubation. (For time of day see brooding tables in the Appendix). Ytreberg (1956) found similar results in the Black-headed Gulls, but his data do not show the extreme differences in the amount of incubation done by the individuals of a pair.

TABLE IX

ANALYSIS OF BROODING TABLES (SEE BROODING TABLES, APPENDIX)

Nest No.	Observation Period in Minutes	Incubation Times in Minutes Total	♂	♀	Per Cent ♂	♀
Wide	1775	1607	1162	445	72.3	27.7
47	4122	4020	2168	1852	53.9	46.1
19	3762	3666	1447	2219	39.5	60.5
Sorie	3575	3527	1600	1927	45.4	54.6
34	1485	1444	777	667	53.8	46.2
D	1647	1611	763	848	47.4	52.6
A	3582	3447	838	2609	24.3	75.7
Reddie	3290	3011	2530	481	84.0	16.0
M	2905	2883	1081	1802	37.5	62.5
Bandie	1955	1932	981	951	50.8	49.2
F	2290	2137	986	1151	46.1	53.9
H	2030	1757	398	1359	22.7	77.3
Total	32418	31042	14731	16311	47.5	52.5

Although one of the sexes may be dominant respecting a certain aspect in the breeding cycle, there is no rule for the Glaucous-winged Gull that either male or female plays a dominant role in all the breeding activities. It is usually the male who establishes the territory and which often is the most aggressive during the pre-egg stage, but either sex may defend the territory, initiate nest-building and take a major share in incubation.

F. Brooding Intensity and Nest Relief Behaviour

Brooding on the empty nest is very superficial; this can be observed in pair B below: 0645-0915 -- June 8, 1962

(22/6/62 - First egg laid)

Observation on Pair B

0645: ♀ on nest.
0650: ♂ gives mew call, ♀ gets off.
0655: ♀ on again.
0657: ♀ off.
0706: ♂ goes on nest.
0720: ♀ mews and goes to nest, she head tosses, ♂ gets off nest. ♂ head tosses and copulation follows.
0726: ♂ on nest.
0730: ♂ stands up for several seconds due to the activity of the neighbours.
0740: ♂ off nest, pulls grass, directed to neighbouring male, ♀ goes on nest.
0742: ♀ off.
0756: ♀ on.
0758: ♀ off.
0800: ♂ utters mew call, while going to nest, but he does not go on.
0815: ♀ goes to nest, mews and deposits nest material, but she does not go on.
0915: ♀ and ♂ present.

Brooding is still liable to be interrupted frequently after the first egg is laid, but the intensity comes close to maximum value after the clutch has been completed. To assess brooding intensity one has to observe the birds in both undisturbed and disturbed circumstances. When the clutch has not, or has just been completed, and the bird on the nest comes into a conflict situation, eg., when a neighbour or stranger comes close to the nest site, the urge for aggressive behaviour is often stronger than the brooding urge. Later in advanced incubation, more provocation or disturbance is needed to dislodge the bird from the nest.

The strength of the brooding urge also depends on how far the bird has advanced in the shift. At the end of a shift, less provocation is needed for getting off the nest. The brooding urge also varies much from one individual to the next. Even when different birds are advanced to approximately the same extent in incubation, certain types of alarm may cause one to fly from the nest, while another one may stay on or just stand up for a few seconds. The main alarms among the gulls were due to frequent appearances of Bald Eagles, (Haliaeetus leucocephalus) and crow alarms. The latter in turn were often the result of human activity on the island. These alarms were good indicators of the brooding intensity. The ones which had started steady incubation proved to be least disturbed by it. Although females are generally more fearful in territorial clashes, in some cases when there were several alarms during the observation period, the female would stay on during an alarm, while her partner would leave the nest in a succeeding one.

Some of the frequent incubation shifts during the observation periods were due to these alarms, when the bird which happened to brood at the time would leave the nest, while its partner would make use of the occasion to get on. The females often had a chance to go on the nest when their mate's arousal over the intrusion of a neighbour or stranger became stronger than the brooding urge.

The birds showed different types of behaviour at nest relief. A male may give the mew call at a certain distance from the nest, the female would respond to it by leaving the nest and, while head-tossing she would approach the male. The male in turn may (or may not) feed her (or copulation could follow when the clutch was not complete) and he would go on the nest.

A gull (male or female) may go to its partner on the nest while mew-calling and also may deposit nest material, while the bird on the nest would (or would not) choke in response and the arriving bird may be let on. An incubating bird may leave the nest without calling and walk away from it, while its partner would go on the nest also without calling, or with the mew call. There are several other variations of nest relief, but they did not seem to differ very much from the three types mentioned above.

The variations in nest relief are mainly due to the degree of brooding intensity. For instance, when a bird gets off the nest and walks away without calling, this is due to a low brooding intensity caused by a long shift. In other instances a bird may walk several times to the nest site and the partner might not want to leave. Sometimes force was used to push the partner from the nest.

Incubation continues unabated during hatching and even when the chicks are present, brooding will continue for the first few days, but it reduces rapidly. At the arrival of the chicks, the parents show more excitement than during incubation. The frequency of long calls increases and parents are more aggressive when chasing crows, juvenile or adult gulls from the territory.

G. Nest-moving Experiment

In the "North East" area, nests within one meter of one another were observed on the meadows. Little was known about the distance and means necessary for peaceful coexistence for these close neighbours. In 1962, an experiment was set up for two pairs, pair D and pair 34, which had nests three meters apart in front of the blind on meadow C. Over a three day period the nests were moved so that they were approximately 75 cm. apart on June 18 (The clutches of pair 34 and pair D had been completed respectively on June 1 and June 8). At that distance the boundary clashes between the two pairs became as frequent as during the territory establishment in the pre-egg stage. There were no boundary clashes as long as both ♂♂ or ♂ 34 and ♀ D were incubating, but when the belligerent ♂ 34 was present and did not incubate, trouble arose. Within the next three days the nests were moved and on June 21, the nest edges were approximately 50 cm. apart. Because of the state of excitement in the boundary clashes at this distance ♂ D and ♀ D delivered pecks at each other. On June 24, the nests were 45 cm. apart, again there were no boundary clashes when both ♂♂, or ♂ 34 and ♀ D were on the nest. On the eve of June 25, the nests were placed 35-40 cm. from one another and this proved to be too close as can be seen from field notes on June 26:

0630 - 0930 -- June 26, 1962

> One egg had rolled halfway between the two nests, since I had placed them on June 25, 35-40 cm. apart. The egg probably rolled out of nest 34 during a fight.

0630: At my arrival in the blind, the gulls depart and when they return within 40 seconds, both ♂ 34 and ♂ D go on the nest. At first ♂ 34 is sitting perpendicular in respect to the position of ♂ D on the nest (♂ 34 has one eye almost closed and is squinting it, probably as a result of a recent fight).

0632: ♂ 34 turns and faces ♂ D (the tips of their bills are about 20 cm. apart in normal sitting position). ♂ 34 jabs at ♂ D on the nest. ♀ D and ♀ 34 are present as well and the pairs choke. ♂ D grasps the neck of his mate in the excitement. ♀ D pecks back at her mate.

0636: ♂ D reaches for no. 34 egg, which is halfway between nests, but does not dare to go all the way.

0637: Quiet.

0648: ♀ 34 chases intruder away from territory, both ♂ 34 and ♂ D give long call on nest and choke faintly afterward.

0652: ♀ 34 deposits nest material while mewing. Pair 34 chokes.

0709: ♂♂ jab at each other.

0712: ♀ D deposits nest material, pecks gently at neck of ♂ D, ♂ D head tosses.

0717: ♀ 34 deposits nest material (2x), pair 34 choke, so does ♂ D. ♂♂ jab at each other.

0719: Quiet.

0722: ♂♂ jab.

0724: ♀ 34 deposits nest material (2x). Pair 34 chokes. ♂ 34 stands and pulls grass. ♂ D pulls grass. Long calls by both pairs. ♂ 34 grasps ♀ D by her bill and pulls her. ♂ D grasps then the bills of ♂ 34 and ♀ D in a triangular hold. They release - long calls and pulling grass alternately. ♀ D goes on nest. ♂ ♂ pull grass and give long calls alternately.

o730: ♀ 34 goes on nest. Choking, grass pulling, long calls by all four.

o735: ♂ 34 stands behind ♀ 34, which is on nest and reaches over her, while jabbing at ♂ D. ♀ 34 gets up. ♂ D grasps ♂ 34's bill and drags him over the 34 nest. One 34 egg is also dragged out of the nest and rolls down slope. While ♂ ♂ are fighting at a distance from the nests, the ♀ ♀ try to go on the nests. ♀ 34 tries to settle on the egg, which is halfway between the nests, but doing so the ♀ ♀ touch and grasp each other by the bills. It is a double fight. The nest of pair 34 is destroyed. One egg of nest D is dragged one third of the way to nest 34 during the struggle between the ♀ ♀.

o740: Since it seems that the experiment has reached the limit, the eggs are placed back in the nests, the latter are moved approximately one meter apart. The ♂ ♂ go on the nest, as soon as this is done, and peace dominates till o930, the end of the observation period.

From the above one can observe that the minimal distance for coexisting incubation in these two neighbouring nests was approximately 40 cm. The bills of the males could touch at this distance when they stretched their necks while being on the nest. When the nests were further than 45 cm. apart and the males were incubating at the same time, there did not seem to be much trouble. It also depends on the degree of aggressiveness of the individuals of two close neighbouring nests, for incubation to be successful.

A few days after hatching, the two pairs with their chicks were back at their original nest sites (three meters apart). This indicates that more space is needed when there are chicks, than during incubation, due to the mobility of the latter and the habit of adults to attack strange chicks.

H. Hatching and Effectiveness of Incubation

The time interval from the appearance of the first crack to the emergence of the chick is called the breaking period of the egg. In Table X the breaking periods for the a-, b-, and c- eggs are shown. The average breaking period is almost the same for the a-, b- and c- eggs.

TABLE X

BREAKING PERIOD OF a-, b- AND c- EGGS IN 1961

Period in Days	Number of Eggs a	b	c	Total
1		1	1	2
2	4	7	4	15
3	14	16	15	45
4	7	9	5	21
5	1	2	3	6
Total	26	35	28	89
Mean	3.19	3.11	3.18	3.16

Hatching takes time and the process can be followed. It does not happen as rapidly as the laying of an egg and when knowing the breaking period, the occurrence can approximately be estimated in case the hatching was not observed. The dates of hatching can be observed in Table XI. The incubation period is calculated from the laying of the last egg till the hatching of that egg. These data show the average incubation period to be 26.9 ± .077 days.

TABLE XI

HATCHING OF CHICKS CORRELATED WITH TIME OF LAYING OF THE c- EGG OF THE CLUTCH

Days After c- Egg Laid	Number of Cases		
	Young		
	A	B	C
22	2		
23	11	1	
24	21	14	
25	37	36	6
26	24	54	33
27	10	19	64
28	3	6	21
29			3
30			1
Total	108	130	128
Average Days	25.0	25.7	26.9 ± .077

Although the average time interval between laying of the a- and c- egg is slightly more than 4.5 days, the average hatching interval is 1.9 days. From Table XI it can be deduced that the "full effectiveness" of incubation is reached only after the c- egg has been laid (The term "full effectiveness" is used to denote the application of the definitive brood-patch temperature to the eggs). Only 31% and 53% of its full value are obtained after respectively the a- and b- egg are laid, which results in synchronous hatching. From the brooding tables in the Appendix it can be seen that after the laying of the b- egg and before production of the c- egg, the gulls incubate 92% of the diurnal observation periods. Working out

Ytreberg's data (1956, 1960), I found his results corresponded to my figures. In the Black-headed Gull only 28% and 52% of the full incubation effectiveness is obtained after the a- and b- egg are respectively laid. The Black-headed Gulls sit for 95% of the diurnal observation periods on the clutch after the laying of the b- egg and before the c- egg is produced. The discrepancy between the % attentiveness during diurnal incubation and % of incubation effectiveness after the b- egg has been laid and before the c- egg is produced is large in the Glaucous-winged and Black-headed Gull (Respectively: 92% - 53% and 95% - 52%). This must be mainly due to a lag in the capability to warm the eggs sufficiently in the laying period. That the eggs are not warmed appreciably when the bird sits during laying, may be due to insufficient development of the brood-patches and/or to a failure to bring the three brood-patches in close contact with the eggs. Ryves (1943) and Swanberg (1950) found that a number of birds have been found to sit on the eggs during the laying period, without warming them to the touch. That in Black-headed Gulls the brood-patch temperature is not continuously applied to the eggs until the clutch is complete, was shown by Beer (1962), by recording the % of eggs warm to the touch on successive days. Elliot and Moreau (1947) for the Herring Gull, Barth (1955) for the Common Gull, Holstein (1944) for the Goshawk and Baldwin and Kendeigh (1932) for the House Wren have given evidence of a similar pattern in these species. Beer (l.c.) also measured brood-patches and found the area to increase from the 2- egg to the

3- egg stage. It seems therefore that the increasing effectiveness of incubation is due to more regular brooding, which in turn forms the external tactile stimulus for the development of the cutaneous and subcutaneous tissue of the brood-patches when these come into contact with the eggs.

Paludan (1951) showed in the Herring Gull, that incubation effectiveness is not directly due to changes in the ovaries, since it was possible to produce effective incubation prior to egg-laying.

Paludan also carried out an egg-shifting experiment on Larus argentatus and Larus fuscus and came to the conclusion that the effectiveness of incubation immediately following completion of the clutch cannot differ markedly from that of the remainder of the incubation period. Barth (1955) showed in Larus canus that definitive incubation temperatures were reached by the end of egg-laying or shortly thereafter.

At what time incubation reaches its full extent after the c- egg has been laid in the Glaucous-winged Gull, is not known (Thermocouples were not available in 1962) but it presumably does not differ much from Larus canus, Larus argentatus and Larus fuscus. The length of incubation in the gulls seems therefore to be similar to the period of full incubation effectiveness.

Table XII shows that the eggs normally hatched in the same sequence as they were laid. From 1962, two cases are known of the b- egg hatching before the a- egg, probably due to the fact that incubation was not very effective before the b- egg was laid. The letters A, B and C in Table XII indicate the chicks hatched from respectively the a-, b-, and c- eggs.

TABLE XII

HATCHING PATTERN FOR 42 CLUTCHES IN 1961

Hatching of Young

Days Before Hatching of C Young					Number of Cases
4	3	2	1	0	
A	-	B	-	C	1
	A	-	B	C	2
	A	B	-	C	5
	AB	-	-	C	1
		A	B	C	14
		AB	-	C	2
			AB	C	12
			A	BC	3
				ABC	2
Total					42

Decreasing Effectiveness of Incubation in the Laying Period.

I. Resistance of Embryos

From Baldwin and Kendeigh's (1932) work on the House Wren, Matthews (1954) study on the Manx Shearwater and Romanoff's (1960) chicken data it appears that so long as proper incubation has not set in (i.e., the embryo has not been brought up to a certain temperature) eggs can withstand prolonged periods of heating and chilling; and that periods of extreme cold can be survived.

In 1961, several incidents happened, which gave the impression that it was more vital to cover the eggs during the hot part of the day, than at any other time, and also that absence from the eggs for certain periods during the night did not seem to influence the embryonic development to great extent. In 1962, initial experiments were set up to test the resistance of embryos to nocturnal temperatures after clutch completion of respectively one and two weeks. Twenty different nests were covered with screened wooden frames, 15 cm. high, which kept the parents from incubating the eggs and at the same time the nests were susceptible to direct air temperatures. Ten nests were covered for three 8-hour periods during the night at least one week after completion of the clutch, and the same was repeated for ten other nests which were covered for one 8-hour period during the night at least two weeks after clutch completion. The results indicated in Tables XIII and XIV show no adverse effect on the average hatching and fledging rate (The average hatching and fledging rate in the "North East" area in 1962 were respectively 83% and 1.7 per/pair). Moreover the length of incubation does not seem to deviate much from the normal (26.9 days) as can be seen from Tables XIII and XIV. (The exact deviation could not be calculated since the checking at the time of hatching was spaced several days apart).

TABLE XIII

EMBRYONIC RESISTANCE TO NOCTURNAL TEMPERATURES
COVERING OF TEN NESTS, EACH NIGHT FROM 2040 TO 0440 ON JUNE 11, 12 AND 13 (TO 0440 ON JUNE 14) IN 1962.

AIR TEMPERATURES: AVERAGE TEMPERATURE 2040: 11.7°C, AVERAGE TEMPERATURE 0440: 11.1°C AND AVERAGE MINIMUM TEMPERATURE: 9.4°C

Nest No.	Clutch Started	Clutch Completed	Clutch Size	Information on Day of Hatching	No. Hatched	No. Fledged
785	May 31	June 2	2	June 30 A chick B addled	1	0
240	May 30	June 4	3	June 30 2 chicks C shows bill through shell	3	2
161	May 29	June 3	3	June 30 2 chicks A addled	2	2
169	May 28	June 2	3	June 30 3 chicks	3	1
167	May 30	June 3	3	June 30 2 chicks C shows bill through shell	3	2
157	May 30	June 4	3	June 30 A addled B chick C pipped	2	1
153	May 26	May 31	2	June 27 A chick B shows bill through shell	2	2
236	May 30	June 3	3	June 30 C shows bill through shell	3	3
217	May 30	June 2	2	July 1 2 chicks	2	2
186	May 30	June 4	3	June 30 A and B show bill through shell-C pipped	3	2
	TOTAL		27		24	17
	HATCHING RATE				89%	
	FLEDGING RATE					1.7 per pair

TABLE XIV

EMBRYONIC RESISTANCE TO NOCTURNAL TEMPERATURES

COVERING OF TEN NESTS FROM 2040 ON JUNE 25 TO 0440 ON JUNE 26.

AIR TEMPERATURES: TEMPERATURE 2040: 17.8°C, TEMPERATURE 0440: 12.2°C AND MINIMUM TEMPERATURE: 9.2°C

Nest No.	Clutch Started	Clutch Completed	Clutch Size	Information on Days of Hatching	No. Hatched	No. Fledged
170	June 6	June 10	3	July 9 A addled 2 Chicks	2	2
165	June 5	June 9	3	July 4 2 chicks C shows bill through shell	3	0
238	June 6	June 11	3	July 9 A died in hatching B chick C shows bill	2	1
221	June 7	June 10	3	July 9 3 chicks	3	3
210	June 5	June 9	3	July 4 A and B show bill C pipped	3	2
224	June 6	June 10	3	July 9 3 chicks	3	3
154	June 4	June 9	3	July 4 A chick B shows bill	3	2
166	June 8	June 12	3	July 10 3 chicks	3	3
188	June 6	June 11	3	July 4 A and B pipped	3	2
171	June 5	June 10	3	July 9 A addled 2 chicks	2	1
	TOTAL		30		27	19
	HATCHING RATE				90%	
	FLEDGING RATE					1.9 per pair

When lifting the screened frames after four nocturnal 8-hour coverings off the nests, more than half of the frames were found partly covered by grass and straw. This indicates that nest building can be active during the night during the incubation period.

Summary of the Egg Stage

1. The bulk of egg-laying in 1961 and 1962 occurred in the last week of May and first two weeks of June. Marked females laid at about the same date each year.
2. No support was found for the Fraser Darling Effect that there is a greater synchronisation of breeding at greater densities.
3. Egg-laying is uniform throughout a 24 hour period. The mean egg-laying interval is 54.86 ± .63 hours.
4. For three members of the Laridae, egg-laying and incubation take longer in larger birds with larger eggs.
5. The mean clutch size for 479 initial clutches in 1962 was 2.82 ± .02. The difference between the means of the clutch size in the first and second half of the laying season was statistically insignificant. More clutches with two eggs were started in the second than in the first half of the laying season. No effect of density on egg production was observed.
6. Repeat laying occurs 11 to 12 days after the initial clutch has been destroyed.
7. The share of the sexes in incubation varies from one

pair to another, but the overall effect is a rather equal share.

8. The strength of the brooding urge depends on the length of the incubation shift, how far the bird is advanced in the incubation period and varies in the individual birds. Variations in nest relief are related to the degree of brooding intensity.
9. In close neighbouring pairs, the degree of aggressiveness of the individuals and the distance between their nests are factors which determine if coexisting incubation can be successful.
10. The incubation period is 26.9 ± .077 days.
11. The discrepancy between the percentage attentiveness during diurnal incubation (92% after the b- egg had been laid) and the percentage of incubation effectiveness is large in the egg laying period. Thirty-one and 53 percent of the full effectiveness of incubation are obtained after, respectively, the a- and b- egg are laid, which results in synchronous hatching.
12. No adverse effect on hatching and fledging rate could be observed in an experiment which prevented gulls from incubating during the night.

III - CHICK STAGE

A. Egg and Chick Mortality

The meadows were checked in 1961 and 1962 carefully and slowly so as not to disturb the breeding birds. In 1961, measurements on growth were taken on meadow D_3, which probably increased the mortality to a slight extent although extreme care was exercised (chicks were weighed in a bag and, after weighing, if they showed a tendency to run their heads were covered with grass).

Tables XV, XVI and XVII show respectively the breakdown for egg loss, chick mortality and fledging rates of 97 pairs which produced 266 eggs in 1961 and 479 pairs which produced 1386 eggs in 1962.

TABLE XV

EGG LOSS IN 1961 AND 1962

	1961	1962
Addled	48 eggs (18%)	140 eggs (10%)
Disappeared or eaten	24 eggs (9%)	59 eggs (4%)
Died during hatching	6 eggs (2%)	21 eggs (2%)
Pressed in air chamber, died in hatching		3 eggs
Egg moved down slope		3 eggs (1%)
Stepped on		3 eggs
Small yolkless egg		1 egg
Total unsuccessful	78 eggs (29%)	230 eggs (17%)
Eggs hatched	188 eggs (71%)	1156 eggs (83%)

TABLE XVI

CHICK MORTALITY IN 1961 AND 1962

Week of Life	Missing or Presumed Dead		Found Dead		Total Number of Deaths	
	1961	1962	1961	1962	1961	1962
1	26	144	27	50	53 (28%)	194 (17%)
2	3	20	14	45	17 (9%)	65 (6%)
3	2	10	7	28	9 (5%)	38 (3%)
4	2	10	5	20	7 (4%)	30 (2%)
5	2	1	1	14	3	15
6	-	--	1	7	1	7
7	-	2	2	3	2 (4%)	5 (2%)
8, 9	-	--	-	-	-	--
10	-	--	1	-	1	--
Total Loss	35	187	58	167	93 (50%)	354 (30%)
Number Fledged					95 (50%)	802 (70%)

TABLE XVII

SUMMARY AND FLEDGING RATE

	1961	1962
Total egg loss	78 eggs (29%)	230 eggs (17%)
Total chick mortality	93 chicks (35%)	354 chicks (25%)
Total number fledged	95 chicks (36%)	802 chicks (58%)
Fledging rate per pair of gulls	1 fledgling per pair	1.7 fledgling per pair

In both years the greatest egg loss was of those which did not hatch (or were addled) and most of the chick mortality occurred during the first week of life. The differences in percentages of egg loss, chick mortality and fledging rate in 1961 and 1962 were significantly different (p is respectively <.001, <.01 and <.001). The causes of egg loss and the rate of the weekly chick mortality were similar within these two years as can be seen from Table XVIII.

TABLE XVIII

EGG LOSS AND CHICK MORTALITY IN 1961 AND 1962

Cause of Egg Loss	% Egg Loss 1961	% Egg Loss 1962	Week of Life	% Chick Mortality 1961	% Chick Mortality 1962
Addled	61.5	60.8	Week I	57	54.8
Disappeared or eaten	30.8	25.7	Week II	18.3	18.4
Died in hatching	7.7	9.1	Week III	9.7	10.7
Other causes	--	4.4	Week IV	7.5	8.4
			Week V - X	7.5	7.7
Total	100.0	100.0	Total	100.0	100.0

The summer of 1961 was hot and the nature of the rocky substratum of the island accentuated the heat intensity. Several records of maximum temperatures in June and July of 1961 were far above the highest temperatures recorded in June and July of 1962 (The highest maximum temperatures in June and July of 1961 were respectively 81°F and 91°F; these for June and July of 1962 were respectively 71°F and 75°F -- recorded by the Victoria City Weather Office, 23 km. N. of Mandarte).

How the heat affected the incubation behaviour of the birds in 1961 is not known. The checking of the meadows in these weather conditions may also have caused more egg loss than would have been the case in milder weather.

The majority of the chicks in both years hatched during the last week of June and the first two weeks of July. In this period the embryos and chicks are most vulnerable to extremes in weather. During the first three weeks of July in 1962, the sky was often overcast and the number of hours of bright sunshine (Victoria City Weather Office) was lower in this year (188.5 hours) than during the same period in 1961 (242.6 hours). In 1961, the vegetation was nearly completely seared dry, leaving less hiding places for the young as well as the older chicks on the open meadows; in July 1962 green grass could be observed to some extent and the shrubbery also showed much green colour (in 1961 even the latter was scorched).

From Table XVI, it can be seen that the number of chicks found missing was greatest during the first week of life; this is due to the fact that the carcasses are harder to find at that stage and probably also to predation by gulls and crows. Crows take chicks mainly in the first and second week of life; after that the average chick becomes too big for crow predation. The predation by crows is probably very small, unless there is human interference; after which crow predation increases.

From the dead chicks found, the death causes can be summarized as follows:

<u>1961</u>

42 carcasses found, death cause unknown
12 pecked to death, and eaten by gulls
1 crushed by observer
1 maimed (cause unknown)
1 dropped down cliff
1 maimed and dropped down cliff

1962

90 pecked to death, and eaten by gulls
62 carcasses found, death cause unknown
3 eaten by crows
3 died, while wandering far from territory
3 caught in vegetation by aluminum band
2 dropped down cliff
2 died, of which the symptom was a loss of equilibrium
1 caught in crevice
1 died as a result of dwarfism in the 7th week ($\frac{1}{4}$th of the size of the average chick of that age)

In 1961 a greater proportion of dead chicks were found than in 1962. This is probably due to the fact that the smaller 1961 area was visited more often during the first two weeks after hatching than the extensive 1962 area. Once the dead birds reach a certain size it is hard to miss them.

In 1961 the proportion of "unknowns" was much larger than that of 1962. From the 42 "unknowns" 33 were found in the first two weeks after hatching. The large majority of these "unknowns" are thought to be casualties of weather conditions in 1961, since no clear external peck marks could be detected, which were found on the majority of dead chicks in 1962. Also the 1962 weather conditions left much more vegetation on the open meadows for shade and hiding places. From inspection of the island beyond the meadows on the east side and from the presence of large flocks of fledglings on the water in 1962, I observed that they were much more numerous in 1962 than in 1961.

From the above it is concluded that one of the main factors affecting chick mortality and fledging rate in 1961 and 1962 was the habit of the adults to attack strange chicks while the other main factor is thought to be the weather. Paynter (1949) and

Paludan (1951) also ascribe most of the chick mortality in Herring Gulls to this aggressive behaviour of the adults.

In 1962 the chicks were considered fledged after they were seen at the age of four weeks and older (constant checks in 1961, up till August 30, revealed that only relatively few died after the fourth week). In 1962, the "North East" area (see Map I) was thoroughly surveyed till August 12 and after that period the meadows were only searched for birds which were not over 30 days of age and for dead chicks, which were relatively easily detected at this time. In some cases, chicks were seen only two or three times during the first four weeks of life and if they were missed during the fourth week, they were presumed to be dead, although some of them might still have been alive. Probably relatively few died after the fourth week which were not recovered. Therefore the very few which were counted dead, but may still have been alive, probably balance the few which were regarded as fledged, but died and were unrecovered after the fourth week.

Of 479 initial clutches on the "North East" meadows in 1962, 401 c/3 clutches (clutch size of three) produced 1.79 fledglings per clutch and 70 c/2 clutches (clutch size of two) produced .99 fledglings per clutch. The difference is significant ($p < .001$).

TABLE XIX

FLEDGING RATE RELATED TO CLUTCH SIZE AND TIME OF BREEDING

Initial Clutch Size	Number of Cases	Number of Fledglings	Fledging Rate Per Clutch
three	401	716	1.79
two	70	69	.99
one	8	2	.25
Total	479	787	1.64

Initial Clutch Size Before June 3	Number of Cases	Number of Fledglings	Fledging Rate Per Clutch
three	216	397	1.84
two	19	21	1.12
one	2	0	-
Total	237	418	1.76

Initial Clutch Size From June 3 on	Number of Cases	Number of Fledglings	Fledging Rate Per Clutch
three	184	319	1.73
two	51	48	.94
one	6	2	.33
Total	241	369	1.53

The 401 c/3 and 70 c/2 clutches produced respectively .6 and .5 fledglings per egg. The difference did not prove to be significant. ($.20 > p > .10$)

The c/2 birds did not prove to be less effective than the c/3 ones in raising fledglings. It is shown in Table XIX that 237 clutches started in the first half of the breeding season produced 1.76 fledglings per clutch, while 241 clutches initiated in the latter half produced 1.53 fledglings per clutch. The difference is significant ($p < .05$) and is probably mainly due to the larger number of c/2 and c/1 clutches from June 3 on. (The difference between the number of fledglings produced per egg in the first and the latter half of the season was not significant. $.30 > p > .20$)

It has been observed that the habit of adults attacking strange chicks was one of the main factors affecting chick mortality. Chicks from nests within the shrub periphery of the meadows might suffer less from this type of aggression and therefore the fledging rate for nests within one meter of and inside the shrubbery was calculated. The fledging rate for 121 pairs, which had nests within the shrubbery of the "North East" area in 1962 was 1.69 per pair, which is rather similar to the fledging rate of 1.67 per pair for the whole "North East" area. The proximity of the shrubbery was therefore not as advantageous as expected, although it may play an important role in a hot summer like 1961, when most of the meadows were seared dry. The 1961 material was too small to make a similar analysis.

The fledging rates on the adjacent meadows D_3 and D_5 (with respectively 128 and 44 pairs of gulls) were respectively 1.84 and 1.77 per pair. The average territory size on meadow D_3 (19 m^2 per pair) was almost twice of that on meadow D_5 (10 m^2 per pair). The difference between the fledging rates at these densities did not prove to be significant ($.80 > p > .70$).

In 1961 the whole meadow D_3 was not checked as was the case in 1962, but comparing the 1961 and 1962 material for the similar area shows the differences in fledging rates even more than when comparing the 1961 fledging rate with that of the whole "North East" area in 1962. The fledging rates in 1961 and 1962 on meadow D_3 were respectively .98 and 1.84 per pair of gulls.

Approximately one chick per pair fledged from 10 nests on the higher part of the beach in 1962. The sample is small and the rings were not easily observed on these chicks, since their legs were often covered with water, and therefore they are not included in the calculated fledging rate.

The twelve replacement clutches in the "North East" area in 1962, produced from 31 eggs, 15 fledgings (fledging rate of 1.25 chicks per clutch). Two of these clutches started on June 30 (the last day of egg-laying in 1962) produced successfully one fledgling each.

Comparative figures from Paynter (1949), Paludan (1951) and Drost et al. (1961) on the fledging success of Larus argentatus are shown in Table XX.

TABLE XX

REPRODUCTIVE SUCCESS IN FOUR GULL STUDIES

Species	Colony and Study Period	Sample No. of Pairs	Average Fledging Rate Per Pair of Gulls	Authority
L. argentatus	Graesholm, 1944	87	.5	Paludan, 1951
"	Kent Island, 1949	100	.9	Paynter, 1949
"	Wilhelmshaven, 1956	107	.7	Drost et al. 1961
"	Wilhelmshaven, 1957	132	.4	" "
"	Wilhelmshaven, 1958	127	.7	" "
"	Wilhelmshaven, 1959	139	.9	" "
L. glaucescens	Mandarte Island, 1961	97	1.0	This Paper
"	Mandarte Island, 1962	479	1.7	" "

From Table XX, it can be observed that with respect to fledging, Larus glaucescens in 1962 was more successful than Larus argentatus in the studies undertaken at Graesholm, Kent Island and Wilhelmshaven.

B. Growth and Chick Addition Study

Growth -- The Glaucous-winged Gull is omnivorous in its feeding habits. A great variety of marine invertebrates, insects, fish, small mammals, discarded food and material from both garbage dumps and ships are devoured.

Table XXI and Figure III summarize weight records of 65 broods in 1961, up to 45 days of age (29 broods with one chick, 25 broods with two chicks and 11 broods with three chicks).

All chicks included in Table XXI and Figure III reached at least 30 days of age and were weighed periodically till at least this age. As can be seen from Figure III, most of the growth occurs during the first four weeks of life, after that the growth curve starts to level off.

The average weight at fledging for 55 birds in 1961 was 899 grams, with a range from 737 to 1403 grams (see Table XXVI).

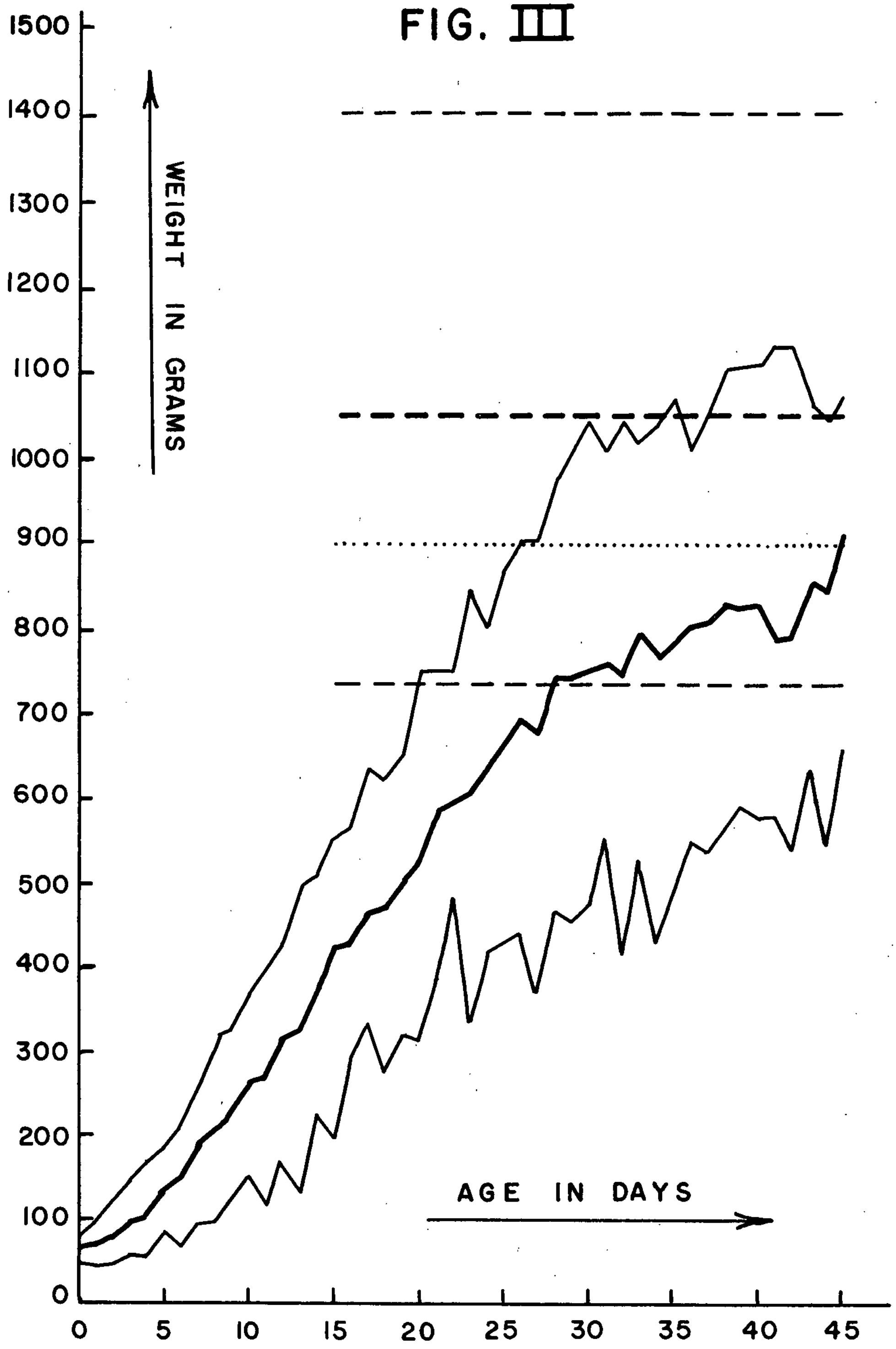
Thirty-one breeding adults in 1961 had a mean weight of 1051 gram with a range from 737 to 1403 gram.

These figures show that the average young gull at fledging reaches 86% of the weight of the average breeding adult.

Table XXII and Figure IV summarize separately the weight records of the 29 broods of one, 25 broods of two and 11 broods of three chicks, formerly included in Table XXI.

From Figure IV it seems that the growth of broods of one differs from broods of two and three. Older chicks were observed to compete actively for food while the single chick has no competitor. On the other hand, we know that the parents may adjust the frequency of feeding to the begging frequency of their young (von Haartman, 1953). In view of the above, and without showing the difference in growth statistically, no conclusion can be reached at this time.

FIG. III



ARITHMETIC GROWTH CURVES OF CHICKS COMPARED WITH AVERAGE WEIGHT AT FLEDGING AND AVERAGE WEIGHT OF BREEDING ADULTS IN 1961

━━━━━━ AVERAGE WEIGHT OF CHICKS
────── RANGE OF WEIGHT OF CHICKS
.... AVERAGE WEIGHT AT FLEDGING
━ ━ ━ ━ ━ AVERAGE WEIGHT OF BREEDING ADULTS
– – – – – – RANGE OF WEIGHT OF BREEDING ADULTS

TABLE XXI

GROWTH OF THE GLAUCOUS-WINGED GULL IN 1961 (AGE IN DAYS, WEIGHT IN GRAMS

Age	Sample	Mean	Range	Age	Sample	Mean	Range
0	67	65	46-77	23	53	610	334-849
1	54	70	44-93	24	34	634	416-801
2	59	79	47-119	25	52	667	430-863
3	38	97	58-147	26	31	697	441-906
4	51	104	54-167	27	41	681	379-906
5	38	137	85-184	28	40	745	467-976
6	33	150	76-212	29	33	746	453-1005
7	31	189	93-258	30	46	756	473-1047
8	25	206	95-317	31	31	771	557-1005
9	37	230	129-325	32	47	747	413-1047
10	32	265	153-368	33	35	798	529-1019
11	37	271	113-396	34	33	764	425-1039
12	25	314	175-430	35	32	784	481-1075
13	39	325	129-495	36	27	804	552-1010
14	35	369	229-509	37	39	811	538-1047
15	25	424	195-552	38	21	831	566-1104
16	43	431	289-566	39	28	828	594-1110
17	26	464	337-637	40	15	830	580-1110
18	47	469	272-623	41	17	789	580-1133
19	26	502	320-651	42	16	791	538-1133
20	39	527	311-750	43	15	857	637-1067
21	41	587	379-750	44	14	844	546-1047
22	27	599	481-750	45	9	913	665-1075

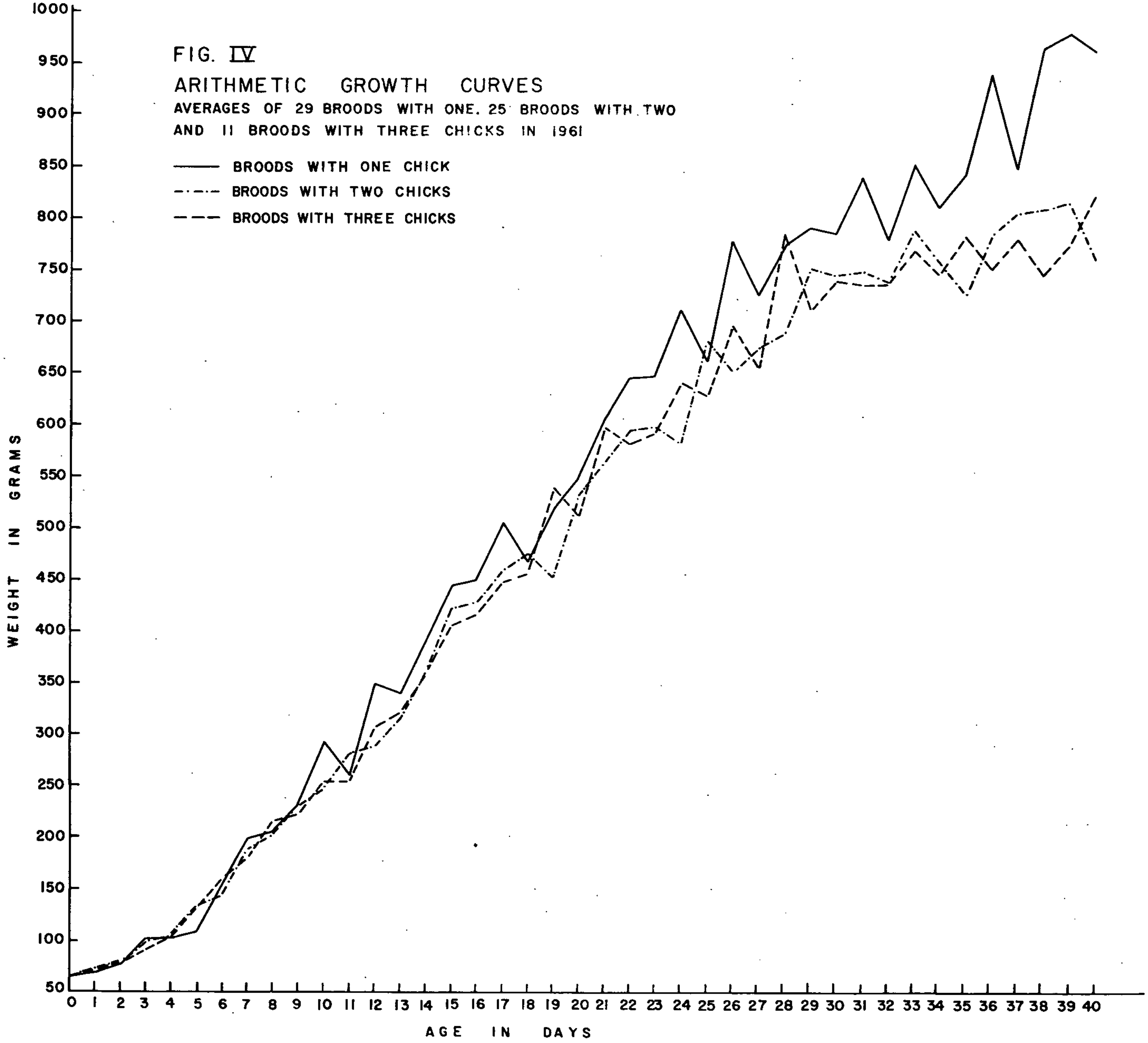


FIG. IV

ARITHMETIC GROWTH CURVES

AVERAGES OF 29 BROODS WITH ONE, 25 BROODS WITH TWO AND 11 BROODS WITH THREE CHICKS IN 1961

TABLE XXII

GROWTH OF 29 BROODS WITH ONE, 25 BROODS WITH TWO AND 11 BROODS WITH THREE GLAUCOUS-WINGED GULL CHICKS IN 1961 (AGE IN DAYS, WEIGHT IN GRAMS)

29 Broods with one Chick			25 Broods with two Chicks			11 Broods with three Chicks		
Age	Sample	Mean	Age	Sample	Mean	Age	Sample	Mean
0	19	65	0	27	65	0	21	65
1	15	69	1	18	72	1	21	70
2	16	76	2	27	80	2	16	79
3	12	101	3	12	99	3	14	91
4	12	102	4	26	102	4	13	110
5	10	108	5	11	135	5	17	133
6	9	152	6	16	144	6	8	159
7	9	199	7	13	187	7	9	181
8	9	205	8	10	203	8	6	215
9	11	231	9	18	232	9	8	223
10	10	293	10	8	247	10	14	255
11	14	259	11	19	283	11	4	254
12	9	349	12	12	289	12	4	308
13	11	341	13	16	317	13	12	322
14	11	393	14	14	357	14	10	360
15	8	444	15	9	423	15	8	406
16	13	449	16	19	427	16	11	416
17	5	506	17	11	459	17	10	448
18	14	467	18	23	476	18	10	456
19	8	519	19	9	452	19	9	541
20	8	548	20	17	531	20	14	511
21	14	604	21	15	563	21	12	597
22	5	646	22	11	595	22	11	582
23	15	647	23	26	598	23	12	592
24	8	713	24	14	582	24	12	641
25	11	661	25	28	681	25	13	628
26	7	780	26	13	652	26	11	698
27	9	731	27	20	675	27	12	654
28	13	774	28	15	687	28	12	786
29	8	792	29	13	751	29	12	711
30	13	786	30	19	746	30	14	740
31	9	842	31	13	748	31	9	735
32	11	778	32	23	738	32	13	736
33	8	854	33	14	791	33	13	770
34	6	811	34	17	759	34	10	745
35	12	844	35	12	725	35	8	784
36	5	940	36	14	785	36	8	751
37	10	848	37	19	806	37	10	782
38	5	965	38	11	808	38	5	746
39	4	979	39	17	815	39	7	775
40	4	962	40	7	758	40	4	824

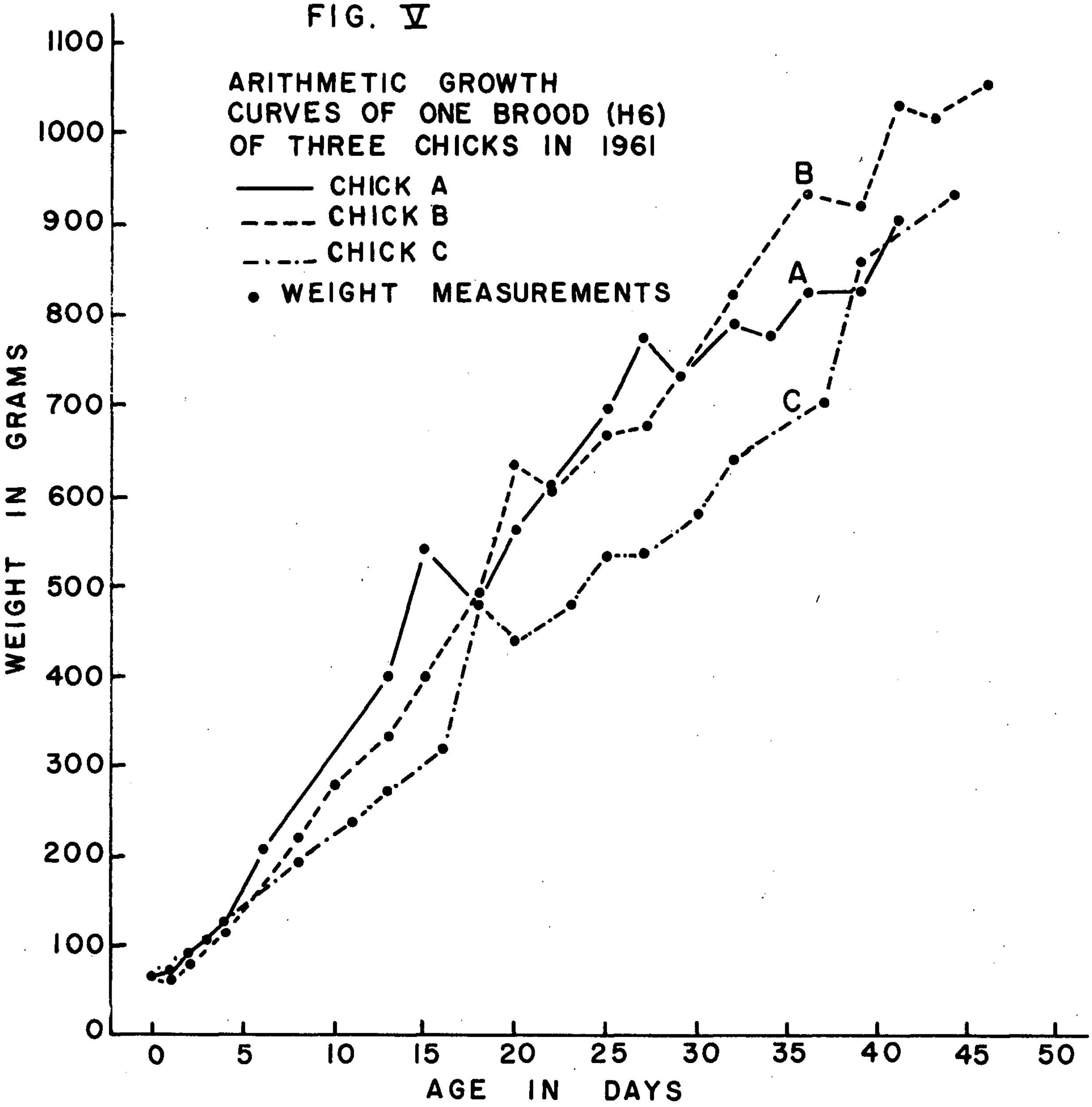
Generally the A and B chicks hatch before the C chick, but this does not mean that the first chicks sustain domiance in growth over those hatched last. From 11 broods of three chicks, in four cases the B chick, and in five cases the C chick, was heavier than its siblings at the end of the chick stage. The individuals of the other two broods of three showed about equal growth. From the 25 broods of two chicks, in ten cases the B chick gained more weight than the A chick, in seven cases the A chick gained more weight than the B one, in eight cases it was hard to decide which was heavier, or they gained weight at a similar rate. Figure V presents a typical example of the variation in growth of the individuals in one brood of three (brood no. H6: A and B chicks hatched two days before the C chick; the chicks were not always weighed on the same day, sometimes it took several days before a chick was caught again).

Chick Addition: Because of the growth curves in Figure IV showing no difference between growth in broods of two and three, a chick addition study was started in 1962 to test Lack's hypothesis (1954) "that the clutch-size of each species of bird has been adapted by natural selection to correspond with the largest number of young for which the parents can, on the average, provide enough food". The evolution of clutch and brood size is an important one, since it is closely related to the question of whether selection takes place on the individual level (Lack, 1947), or on the group level (von Haartman, 1955).

One- and two-day old chicks and pipped eggs were added to

FIG. V

ARITHMETIC GROWTH CURVES OF ONE BROOD (H6) OF THREE CHICKS IN 1961



97 nests on meadows D_5, D_{5A}, E, B, A and C. Nine supernormal broods of six, 65 supernormal broods of five and 23 supernormal broods of four were created in this manner. (of course the added eggs and chicks were not considered in the production figures of Tables XV, XVI and XVII). The addition was done when the original eggs in the nest were at the point of hatching or if the latter occurred, the chicks in the nest were one or two days of age. Table XXIII shows 50 from the 97 supernormal broods in which more than three chicks of each brood are considered to have fledged successfully. The first and second figure in column two indicate respectively the original and added number of chicks present in the nest right after hatching.

TABLE XXIII

SURVIVAL OF 50 SUPERNORMAL BROODS IN 1962

Brood No.	Brood size after hatching	Number of chicks fledged	Age range (in days) of the young gulls in a brood, when last observed all together on the territory.
470	3 + 3	6	50 - 52
Reddie	3 + 3	6	46 - 47
Sorie	3 + 3	5	49 - 52
456	3 + 3	5	44 - 46
014	3 + 3	5	30 - 31
457	3 + 3	5	44 - 46
E	3 + 3	5	43 - 44
250	3 + 2	5	35 - 38
248	3 + 2	5	44
239	3 + 2	5	29 - 30 (4 of 5 chicks seen at 42 - 43)
463	3 + 2	5	43 - 45
Old 100	3 + 2	5	27 - 28
Old 85	3 + 2	5	42 - 44
218	3 + 2	5	29 - 30 (4 of 5 chicks seen at 33 - 34)
184	3 + 2	5	45 - 46
151	3 + 2	5	52 - 53
202	3 + 2	5	36 - 39
153	2 + 3	5	31 - 33
101	3 + 2	5	40 - 41
231	3 + 2	5	29 - 30 (4 of 5 chicks seen at 36-37)
274	3 + 2	4	39 - 41
L_1	3 + 1	4	52 - 53

TABLE XXIII Continued

M	3 + 2	4	46 - 47
Old 34	3 + 2	4	48 - 49
Old 11	3 + 2	4	52 - 53
A	3 + 2	4	45 - 46
226	2 + 3	4	54 - 55
267	3 + 2	4	37 - 40
179	3 + 2	4	48
460	3 + 1	4	37
464	3 + 2	4	41 - 44
41	3 + 2	4	28 - 30
52	2 + 3	4	32 - 33
37	3 + 2	4	38 - 39
48	3 + 2	4	29 - 31
Old 84	3 + 2	4	33 - 35
91	3 + 2	4	36 - 37
100	2 + 3	4	35 - 37
81	2 + 3	4	40 - 41
76	3 + 2	4	38 - 39
87	3 + 2	4	41 - 43
183	3 + 2	4	33 - 34
198	3 + 1	4	31 - 32
191	3 + 2	4	44 - 46
194	3 + 2	4	44 - 45
299	3 + 2	4	29
204	3 + 2	4	49 - 50
225	3 + 2	4	36 - 39
217	2 + 3	4	32 - 33
190	3 + 2	4	42 - 44

The adding of pipped eggs and chicks was done to nests in which laying had started before June 3.

That the chick mortality and survival of the supernormal broods is similar to that of normal broods is shown in Table XXIV, where the former are compared with normal broods (normal broods in which egg-laying had started before June 3) of one, two and three chicks.

TABLE XXIV

COMPARATIVE ANALYSIS OF MORTALITY AND FLEDGING RATES IN NORMAL AND SUPERNORMAL BROODS (B_1 TO B_6 INDICATE NUMBER OF CHICKS PRESENT IN A BROOD DIRECTLY AFTER HATCHING)

No. of Chicks Per Brood	B_1	B_2	B_3	B_4	B_5	B_6
No. of Nests	10	38	96	23	65	9
Mortality	3 (30%)	24 (32%)	87 (30%)	30 (33%)	104 (32%)	11 (20%)
No. of Fledglings	7 (70%)	52 (68%)	201 (70%)	62 (67%)	221 (68%)	43 (80%)
Fledging Rate per Brood	.7	1.4	2.1	2.9	3.4	4.8

Not enough broods of one and six are present to make a comparative analysis. But the adequate numbers of broods of two, three, four and of five show no statistically significant differences in mortality rates ($.99 > p > .98$).

Of the 145 unsuccessful chicks in the supernormal broods, 75 disappeared, while of the 70 dead chicks, the death causes can be summarized as follows:

35 pecked to death by gulls
25 carcasses found, death cause unknown
3 dropped down cliff
2 died of disease, of which the symptom was loss of equilibrium

2 were thin and probably starved?
1 eaten by gulls
1 caught in vegetation by aluminum band
1 diseased.

No chicks of the supernormal broods were weighed, to avoid disturbing them, but judging from the 1961 growth experience, they all seemed to be in healthy condition when last observed.

Only two meagre chicks in the 97 experimental broods were found dead later. This may have been due to starvation.

If there was a difference in weight between the fledglings of normal and supernormal broods, the chances of survival for the fledglings of the supernormal broods after they had left the island may have been less than these for normal broods. Lack (1948, 1954) tried to show that the survival rate in larger broods of Starlings was less after the birds had fledged, but the differences were not statistically significant. That in the Glaucous-winged Gull the survival for young gulls after departure from Mandarte Island in 1962, for supernormal broods was not less, but rather higher than in the normal broods is shown in Table XXV for 51 juveniles.

TABLE XXV

COMPARATIVE ANALYSIS OF THE SURVIVAL OF 51 YOUNG GULLS AFTER DEPARTURE FROM MANDARTE ISLAND IN 1962 (F_1 TO F_6 INDICATE THE NUMBER OF CHICKS CONSIDERED FLEDGED IN A BROOD BEFORE DEPARTURE FROM MANDARTE)

Number Fledged Per Brood	F_1	F_2	F_3	F_4	F_5	F_6
Total No. of Fledglings	47	146	171	120	90	12
No. Seen in Vancouver	2	7	13	14	13	2
% Seen per Young Fledged	.04	.05	.08	.12	.14	.17

The 51 juveniles (from nests in which laying started before June 3 in 1962) were seen in good health in the Vancouver area by R. F. Oldaker (reading of band numbers and colour combinations by telescope). The survival of the observed 20 juveniles resulting from normal broods, which fledged two and three chicks, is significantly different from that of the 27 juveniles of the supernormal broods, which fledged four and five chicks ($p < .05$). The number of juveniles observed in Vancouver is relatively small, but the survival rate of this small number is higher for the larger broods. It may be, that in the larger broods there has been a gradual and better adjustment for the acquisition of food in the chick stage due to competition of a larger number of siblings.

The results of this test do not seem to support Lack's (l.c.) hypothesis for this species. Lack (l.c.) argues that in the northern Larus, the upper limits of a clutch of three was originally set by the food requirements of the young, and the evolution of large eggs and three distinct brood-patches have merely provided a secondary reinforcement of this. The reason why the clutch is usually made up of three eggs is still unanswered, but it is probably not due to the evolution of large eggs, since in protracted laying a fourth egg can be produced within a similar interval as that between the laying of the a- and b-, and b- and c- eggs. It seems that the three brood-patches play a primary role for limiting the clutch size in the Glaucous-winged Gull as does the one brood-patch in the Laysan Albatross (Rice and Kenyon, 1962). In several cases

Rice and Kenyon added an extra egg to an albatross clutch, but in no case did two eggs hatch and they conclude that albatrosses are unable to incubate two eggs.

In a small scale experiment of addition before egg-laying, three eggs were placed into four empty Glaucous-winged Gull nests (in three nests a clutch of two, and in one nest a clutch of three was produced in addition to the eggs added) and three of these supernormal clutches were observed during hatching time. All eggs were addled. Rice and Kenyon's (l.c.) and this study (although the sample is small) seem to indicate that the brood-patches play a primary role in determining the clutch size of the Laysan Albatross and the Glaucous-winged Gull.

However, Rice and Kenyon's (l.c.) made a small scale chick addition experiment with the Laysan Albatross. In 18 additions of one chick, they found that in 15 cases both chicks died, at one nest a single chick died and in two nests both young survived, but one set was so emaciated that their survival to fledging was improbable.

The results of the chick addition experiments in the Laysan Albatross and the Glaucous-winged Gull are hardly comparable. Due to the limited feeding frequency in the albatrosses (Richdale, 1952; Rice and Kenyon, l.c.) it is not expected that more than one chick per brood could survive.

With respect to Glaucous-winged Gull chick production, 1962 was a favourable year seemingly due to the weather. Therefore more data are needed on gull chick addition, preferably in adverse weather conditions. Weather conditions may affect the feeding behaviour of the gulls. It is unlikely that food supply as such played a role in the greater chick mortality in 1961 than in 1962, since Glaucous-winged Gulls are omnivorous and have an extensive feeding range.

Two males and a female were observed on the Vancouver Garbage Dump, respectively on July 17, 1962, July 19, 1962 and July 30, 1962. On these dates they had broods respectively of 13, 39 and 31 days of age. Both before and after these dates, these adults were seen to attend chicks on Mandarte. This indicates that adults still go considerable distances (67 km.) while rearing flightless chicks.

To measure the frequency with which parent birds bring food to their young, a large series of observations is essential. No time in 1962 was available for a study comparing feeding frequencies between normal and supernormal broods.

C. Parent-chick and Chick Behaviour

Feeding -- After hatching, the frequency of mew and long calls increases when the chicks are stirring or moving around. There is much feeding and nest building activity and often chicks are presented nest material instead of food. Both male and female feed the chicks.

The feeding pattern may vary. A parent may go to the chicks, while giving the mew call (chicks can recognize their parent's mew call from all others over considerable distances); the chicks may peck at the bill, chest or even at the eye region; but will peck mostly at the bill tip of the parent which is nearest.(When the chicks grow bigger, they seem to peck most often at the whole bill, at the corners and inside of the bill). The parent regurgitates the food and may hold it in the bill or drop it on the ground. Pecking does not need to precede regurgitation. In some cases the parent may mew and regurgitate a fish and drop it and the less than a week-old chick will peck at it on the ground. Often a food item may be too large or too tough for the very young chicks to ingest and the parent takes off tiny bits and let the chicks take these from the bill tip. The male may still feed his mate at the early chick stage and when the male is feeding the chicks, his mate may sometimes come in from outside and take the food. In several instances, the female took a fish away which the male had just regurgitated in front of the chicks. The male would attack his own mate violently, while the latter would drop or walk away with the fish and swallow it at a certain distance from the nest. Those belonging to the same brood can all be fed at the same or at different times, often depending on how hungry and therefore how aggressive each individual is. It is not uncommon to see older chicks fight over a food item and pecks may be exchanged between siblings, but little harm seems to be done. The parents may swallow the regurgitated food again before the chick has had a chance to get it and they often try to avoid the food-begging young when these grow bigger. In some instances the consistent pecking of a chick seems to irritate the parent, which tries to avoid it and the chick may be pecked at.

<u>Flight</u> -- Chicks try out their wings and attempt to hop on the meadow at the end of the first week, this increases with age and when there is a breeze it becomes more frequent. In the last week before fledging the jumps become higher. Many of the fledged chicks land the first few times on the wrong territories within their meadow or on other meadows after they have been away, but most of them are able to return to their own territory. When a chick lands on a strange meadow, it is pushed and pecked from one territory to the next by both adults and chicks. The chick is moving like a pinball till it leaves the meadow ("Pinball action": ↗ • ↘ • ↗ — • is centre of a territory, → is chick's movement). If a chick lands on a different territory of the meadow where it was brought up, a short pinball movement occurs till it arrives on its own territory. The five to seven week old chicks will peck at and chase even adults other than their parents, when these come close or enter their territory. When flight is first attained and the gull chick lands on the water, the calling parent may accompany it. Many other gulls may join in the excitement and the parents attack any gull which is landing close or pecking the chick in the water. The parents may defend their chicks any place outside the breeding territory on the island. Chicks often leave the parental territory before they can fly and when disturbed swim away from the shore. A few will be swept away by swift tidal currents, but most of them make it back to the shoreline and on some occasions the parents will accompany them on their return journey.

Chicks hatching from nests on the higher part of the beach swim away from the shore when disturbed, even when they are in their second week. These come into contact with water several weeks before the chicks on the meadows and therefore the adaptation to the water for the former is a gradual one.

Hiding -- Chicks on the meadows, at checking, usually hid during their first four weeks, many stopped doing so in their fifth, sixth or seventh week, while others still went into hiding right up to fledging or on rare occasions one or two days after fledging. Some chicks would hide very close to the nest, others would go long distances in the brush. Some chicks which were partially blind, fledged in an apparently healthy condition. The latter often came out of hiding at an early stage and were usually belligerent, probably due to the many attacks by adults.

Departure Before Fledging -- Some chicks wander far from their territory before fledging and probably most of them die, but some survive. One of three siblings on meadow A arrived one day on the camp beach, while the other two siblings still remained on the territory for another two weeks. This 47 day-old chick Y6, seemed to be emaciated when it arrived and was never fed by adult gulls as long as it stayed on the beach. Bread crumbs were occasionally thrown on the beach, and Y6, fledglings and adult would utilize them. How did it acquire its meals besides the occasional food remains which were distributed? This was made clear, when it was observed that when a gull fed its fledged young on the camp beach, Y6 would jump forward at the moment of regurgitation and dash off with a part of the food; chased by the adult. Not only Y6 would rush up to the food distrubution, other chicks on the camp beach did the same. They seemed to watch the food begging of the chicks and the oncoming swelling in the neck of the adult very closely, from a certain distance, and at the time of regurgitation, they would dash in. Y6 seemed to be very successful with this type of feeding at the times observed. After having spent about ten days on the beach, it seemed to be healthy.

Adoption -- The young gulls Y4 and Y5 were siblings on a territory at the shore edge of meadow D_3. Y4 fledged there, but Y5 disappeared at the age of 32 days and was later seen on the south club, where it was probably swept by a tidal current. It appeared to be emaciated and did much food-begging at the shore of South Rock (See Map I). Several observations later, Y5 still seemed very hungry and it often approached an adult on South Rock, which was on a territory and had an unbanded chick of its own. Although Y5 was very aggressive when there was a food distribution, it seemed to be avoided and only its own chick was fed by the adult. One day, both chicks approached the adult and started food-begging and Y5, being the more aggressive or hungry one, swallowed all. After Y5 had moved some distance, the other came closer and started food-begging, but being not as aggressive as Y5, it was not fed. On another day, both chicks were observed to share a fish regurgitated by the parent. In the first instances, Y5 probably jumped forward, in the manner of Y6 on the camp beach, when there happened to be a regurgitation for the other chick. Later on, the parent of this chick probably grew accustomed to Y5.

Y5 appeared healthy after some time and on September 12 it was observed in Vancouver.

Summary of the Chick Stage

1. There was a statiscally significant difference in the percentages of egg loss, chick mortality and fledging rate in 1961 and 1962, which was thought to be due to the weather. The other main chick mortality was due to the habit of adults attacking strange chicks. The causes of egg loss and the rate of the weekly chick mortality were similar within these two years.
2. The fledging rates in 1961 and 1962 were respectively 1. and 1.7 fledglings per pair of gulls.
3. The c/3 clutches produced significantly more fledglings than the c/2 clutches in 1962, which seems to be mainly due to less eggs in the latter and not to the c/2 parents' inability to raise less fledglings because the c/2 birds did not prove to be less effective than the c/3 ones in raising fledglings.
4. The difference between the number of fledglings produced from clutches started in the first and second half of the laying season was statistically significant. The difference probably is mainly due to the larger number of c/2 and c/1 clutches present in the second half.
5. Fledging rates of nests in two different habitats, the open meadow and shrubbery were similar. No statistic-

ally significant difference was found between fledging rates of nests at different densities.

6. From comparison of fledging rates in Larus argentatus and Larus glaucescens, the latter seems to be more successful.
7. Most of the growth in the Glaucous-winged Gull occurs during the first four weeks of life. The average young gull at fledging reached 86% of the weight of the average breeding adult in 1961.
8. Although in 1961, the growth rate of broods of one differed from the growth rates of broods of two and three chicks, no difference in growth seemed to occur between broods of two and three.
9. Fifty supernormal broods in 1962 produced more than three fledglings each. Causes of mortality in normal and supernormal broods were similar.
10. Mortality and fledging rates in normal and supernormal broods were similar. Survival of juveniles after departure from Mandarte was possibly higher from the supernormal than in the normal broods. The results of the chick addition experiment do not seem to support Lack's hypothesis that the clutch-size of each species of bird has been adapted by natural selection to correspond with the largest number of young for which the parents can, on the average, provide enough food.
11. The limited number of brood-patches seem to play a

primary role in limiting the clutch size of the Glaucous-winged Gull.

12. Parent-chick and chick behaviour have been discussed. Adoption of six week-old chicks occurs.

IV JUVENILE STAGE

A. Age at First Flight and Departure

Age at First Flight -- Table XXVI shows the age at first flight of chicks in 1961, which is based on observations of first trial flight, the time of first departure from the territory and weight measurements taken for the last time. The average age at first flight for 67 brids was 43.8 days, ranging from 37 to 53 days (the average weight at fledging for 55 birds was 899 grams which is 86% of the weight of the average breeding adult; see Chapter IIIB on growth).

TABLE XXVI

AGE AT FIRST FLIGHT RELATED TO WEIGHT IN THE GLAUCOUS-WINGED GULL IN 1961

Age at First Flight (In Days)		Average Weight at Fledging (In Grams)	
Age	No. of Young	No. of Young	Weight
35-39	3	36	906
40-44	43		
45-49	20	19	885
50-54	1		
Total	67	Total 55	
Mean Age	43.8 Days	Mean Weight	899
Range	37-53 Days	Range	566-1133

Thirty-six and 19 of 55 chicks fledged at 35-44 and 45-54 days respectively and reached a mean weight of 906 and 885 grams respectively. The 19 fledglings (45-54 days) had reached a mean weight of 833 grams when last weighed at 35-44 days, which differs significantly ($p < .001$) from the mean weight of 906 grams of the 36 birds (which fledged at 35-44 days). From this it appears that the age at fledging is influenced by the rate of growth of the chicks.

Age at Departure -- Indirect evidence on the age at colony departure is given by the age at which healthy young capable of flight were last seen on Mandarte. All fledglings were easily observed and all were presumed to leave the island. A biassing factor may be mortality instead of emigration causing the disappearance, but this is small because dead fledglings are not likely to go undetected due to their size.

Table XXVII shows 38 last sightings over the period 20-28 August, ranging from 48-65 days old, with a mean of 56, the age at presumed departure. Some individuals probably escaped notice on days after their "last sighting", and that this figure is somewhat too low is shown by the ages of 97 birds still present on the island the last two days of observation, 29 and 30 August. The ages here ranged from 46-67 days old, with a mean of 56, i.e. identical to the group presumed seen on their last day on the island.

TABLE XXVII

LAST SIGHTINGS OF GLAUCOUS-WINGED GULL YOUNG ON MANDARTE ISLAND IN 1961

Age (In Days)	20 - 28 August Group	29 - 30 August Group
45 - 49	3	9
50 - 54	13	32
55 - 59	16	37
60 - 64	5	15
65 - 69	1	4
Total	38	97
Mean Age	55.7 Days	55.5 Days
Range	48-65 Days	46-67 Days

Thirty-five young seen for the last time before August 30 (August 30 was the last field day spent on the island in 1961) remained on the island after first flight for an average of 14 days, ranging from 6 to 27 days. This makes the average bird 58 days old at presumed departure from the island. From the above and the results of Table XXVII, an estimate of an average age of 57 days at departure from the island seems reasonable. Herring Gull juveniles at typical colonies leave about the same age (Goethe, 1956) as contrasted to the much longer period at Wilhelmshaven colony studied by Drost (1951, 1952) where breeding and feeding grounds are adjacent.

During the two weeks after first flight, the fledglings wander over the island. Short trips occur first between the parent's territory and the shore. Later more wandering occurs along the beach. In the last few days some individuals were seen in the same day on the north and south end of the island.

Some visit neighbouring Halibut and Sidney Island which are respectively 1 and 2 km. from Mandarte, and may come back, but when once beyond these, they did not seem to return.

B. Dispersal and Family Ties

Dispersal -- One of the areas where sewage and garbage attract large numbers of gulls is Vancouver (67 km. to the north of Mandarte). The bulk of the banded juveniles after departure from the island in 1961 and 1962 were observed by Oldaker (telescope observations on band numbers) in Vancouver in the latter half of August and in the first half of September, from then on the observed numbers of banded Mandarte juveniles decline rapidly, presumably due to greater dispersal. The average age of 44 banded Mandarte juveniles for the first time observed in Vancouver from August 17 to September 6 in 1961 and 1962 after departure from the island was 63 days, ranging from 53 - 73 days old. The shortest time interval for a banded Mandarte juvenile between respectively last and first sighting on the island and in Vancouver was three days.

The farthest recovery of a dead juvenile of Mandarte was from San Francisco, California. This juvenile was killed by flying into an object in San Francisco on November 8, 1961 after it had been observed on Mandarte on August 30, 1961. Occasionally they stray far inland. A juvenile which was banded on July 19, 1959, on Christie Island (30 km. N.N.W. of Vancouver) was recovered wounded on June 2, 1960 at St. Paul, Alberta. Other juveniles (and later as adults) show philopatry to local feeding grounds; they have been observed in the same local areas for years in succession. Table XXVIII gives only a few of many examples.

TABLE XXVIII

SIGHT HISTORIES OF GLAUCOUS-WINGED GULLS FROM TELESCOPE OBSERVATIONS IN VANCOUVER, B.C.

Date	Location
No. 587-75264, banded as chick on June 30, 1957 on Mandarte Is.	
February 6, 1959	Victoria Square
December 9, 1959 to Feb. 15, 1960	" "
December 21, 1960 to Mar. 13, 1961	" "
May 24, 1961	City Dump (Marine Drive)
December 16, 1961 to Feb. 27, 1962	Victoria Square
November 22, 1962 to Jan. 4, 1963	" "
No. 597-09367, Banded as a chick on August 1, 1958 on Mandarte Is.	
January 30, 1959	Stanley Park
April 16, 1959	City Dump
May 11, 1959	Stanley Park
November 21, 1959 to Mar. 12, 1960	" "
February 2, 1961	" "
May 16, 1961	City Dump (Marine Drive)
December 3, 1961	Stanley Park
December 24, 1961	" "
No. 597-55646, banded as a chick on July 27, 1959 on Mandarte Is.	
March 30, 1960	Campbell Avenue Docks
November 22, 1961	" " "
January 25, 1962	" " "
February 5, 1962	" " "
No. 517-04226, banded as chick on July 15, 1956 on Mandarte Is.	
August 12, 1959	City Dump (Marine Drive)
November 4, 1959 to Dec. 8, 1959	" " " "
February 18, 1960	" " " "
June 17, 1960	" " " "
August 3, 1960	Mandarte Island
November 4, 1960	City Dump (Marine Drive)
April 4, 1961	" " " "
May 11, 1961	" " " "
August 25, 1961	" " " "
March 14, 1962	" " " "
August 1, 1962	" " " "
August 27, 1962	" " " "
October 29, 1962	" " " "

Few one-year-olds, but more two- and three-year-olds, which were banded on Mandarte as chicks were seen on the island during the breeding season in 1961 and 1962. Two- and three-year-olds on the meadows were sometimes observed carrying nest material. Few chicks banded on neighbouring islands bred as adults on Mandarte Island (three of 75 banded gulls observed in 1959 and 1960 on Mandarte by G. F. van Tets were from the neighbouring San Juan County).

Family Ties -- On September 5, 1961, two colour-banded siblings from Mandarte were observed being fed by an adult on the Vancouver City Dump. At the time of the observation they were respectively 57 and 58 days old and were last seen on Mandarte on August 30, 1961 at the ages of respectively 51 and 52 days old. The unbanded adult, probably their parent, which fed them on September 5, chased other juveniles which tried to get a share of the food. On September 16, 1961 another two siblings at the ages of 65 and 63 days old (last seen on Mandarte on August 30, 1961 at respectively the ages of 58 and 56 days old) were observed together on the Vancouver City Dump. This points to a strong bond in certain families as occurs from time to time in the Herring Gull (Drost 1951, 1955).

In certain cases feeding may go on for a long time after the juveniles have left the breeding colony. Oldaker observed how an unbanded juvenile was fed by an unbanded adult on January 12, February 6 and again on March 12, 1962 in Vancouver.

Summary of Juvenile Stage

1. The average age for the Glaucous-winged Gull at first flight ranged from 37 to 53 days, with a mean of 44 (43.8) days. The age of fledging is influenced by the growth rate of the chicks.
2. Young gulls start to leave the island at the age of 50 days, most are gone at the age of 60 days. On the average they leave the island at the age of 57 days.
3. After departure from Mandarte Island many young gulls arrive in Vancouver for the first time at the average age of 63 days.
4. There seems to be no general rule about the range of dispersal; some young gulls disperse far after first departure from the breeding ground, others show philopatry to local feeding grounds. A substantial number of two and three-year-olds (banded as chicks on Mandarte Island) visit Mandarte Island.
5. In certain Glaucous-winged Gulls a strong family bond occurs.

V POPULATION CONTROLS

Adult Mortality -- Fifty-nine of 68 colour-banded adults, trapped on their territories in 1961, were seen again in the summer of 1962. Since the island is densely populated and the gulls did not all come back to the same nest site, I may have missed a few. The majority of the observed banded adults on Mandarte were raised there, this being the largest known breeding colony of Glaucous-winged Gulls in British Columbia. A few bred on Mandarte, which were banded as juveniles on other islands (see chapter IVB). Once the gulls have bred in this relatively large colony, the probability that they will return to it later is high.

Tinbergen (1953) concludes that the Herring Gull in Holland usually returns to the same colony. Gross (1940) gives similar evidence for the Herring Gulls of the large Kent Island colony.

The adult survival for one year of the 1961 breeding birds was at least 86.8%. Drost et al. (1961), calculated the annual mortality for all banded adults, breeding and non-breeding Herring Gulls to be 10%. The average annual mortality of adult Kittiwakes, Rissa tridactyla, has been estimated 12% (Coulson and White, 1959), between 11 and 12% for the Arctic Skua, Stercorarius parasiticus (Williamson, 1959) and 13% for the Yellow-eyed Penguin, Megadyptes antipodes (Richdale, 1957). Thus the figures for five species of sea-birds are very close.

Twenty-four birds of the 68 colour-banded breeding adults in 1961 were seen in the Vancouver area in 1962 and 1963. None of the nine colour-banded adults, which were not observed on Mandarte in 1962, were among these 24 birds seen in the Vancouver area. This shows that the probability of a breeding bird appearing again on the island after a year's absence is rather small. Since the minimum annual adult survival in the Glaucous-winged Gull is 86.8%, and that one or two individuals may have been overlooked in the colony, or returned after a year's absence, (according Drost et al., 1961, this happened in the Wilhelmshaven colony) an estimate of a 10% annual mortality of adult Glaucous-winged Gulls seems reasonable.

Applying the formula $e = \frac{2-m}{2m}$ (where e = average expectation of further life and m = percentage annual mortality) used by Lack (1954) and knowing the mortality (m) to be .10, I find that the life expectancy (e) is 9.5 years for adults which start breeding for the first time.

From telescope observations on bands, I found several gulls breeding in their fourth year. In 1962, while observing incubation shifts on meadow C, I noticed four banded three year-olds, but none had a territory there and, from their behaviour and plumage, it seemed unlikely that they were breeding birds. Only once, in May 1962, was the copulation of a banded three-old female on a territory [illegible] seen. She may have bred that year. These observations indicate that three-year-old birds rarely breed.

From the above, I conclude that Glaucous-winged Gulls start to breed first in substantial numbers at the age of four. Drost et al., (1961), found that the Herring Gulls of Wilhelmshaven began breeding when they were from three to five years of age. Since the life expectancy for first-breeding adults has been calculated to be 9.5 years, the Glaucous-winged Gull which reaches maturity, should reach an age of 13.5 years, on the average, i.e., four years as immatures and 9.5 years when mature. These figures are identical to the ones obtained by Drost et al. (l.c.) on the Herring Gull, which are the most reliable for this species.

The oldest Glaucous-winged Gull recovered was 21 years (Canadian Wildlife Service Files). Drost and Schilling (1940) record six Herring Gulls which, in the wild, lived between 21 and 26 years. That the potential length of life in large gulls can be higher than the actual one has been shown by Steenstrup, 1847 (cited by Paludan, 1951), who mentions a Great Black-backed Gull, Larus marinus, on the Faroes, which lived 64 years and spent a life of partial liberty; it bred freely in the wild and in the fall it would return to the farm where it had been reared.

Population Controls -- Available counts of the Mandarte colony (main island alone) run as follows (compiled by Drent and Guiguet, 1961):

1915	450	pairs (incorrectly given as 225 in the above - pers. comm. R. Drent)
1921	350	pairs
1923	600	pairs
1927	(1000	pairs), a questionable estimate
1936	534	nests, a total count
1955	1500	pairs
1957-61	1800-2000	pairs
1962	2200	pairs

The estimate of 2200 nesting pairs in 1962 is based on the knowledge of the average territory size and the total number of breeding pairs in the "North East" area. In 1962 there were four times as many pairs as 26 years ago. This indicates an average yearly increase of 5.5% from 1936 to 1962. Knowing that the annual adult mortality for 1961-1962 was 10%, a theoretical 1000 adults at one year will result in 900 adults the year after. But if the present rate of increase continues 1000 mature birds at one year will result in 1055 birds the year after.

The fledging rate was 1.6 fledglings per pair for 1961 - 1962, this amounts to 800 fledglings per 1000 adults. Of 800 fledglings produced per 1000 adults, 1055-900 = 155 new adults must be recruited if the rate of increase is constant. This is a 80% mortality between fledging and maturation.

Maturation of the average Glaucous-winged Gull takes four years. It is assumed that the mortality in the second year approaches closely the annual adult mortality, which is known to occur in many birds (Lack, 1954). Therefore, around 70% of the total 80% mortality of the immatures should occur in the first year after fledging. The Herring Gull in Denmark, Fenno-Scandia and the U.S.A. have a mortality rate during the first year after fledging of respectively 62%, 57% and 60% (Paludan 1951, Hickey 1952, Olsson, 1958). After the first year mortality, these authors' figures disagree, especially in respect to adult mortality. The latter may be partly due to the fact that their data are based on the evaluation of the recoveries of dead birds, of which a large percentage was shot, or may possibly be due to the fact that the Danish gulls are sedentary, while the American and Fenno-Scandian gulls are migratory.

Capildeo and Haldane (1954) give the relation between fecundity (f), adult survival rate (s), and the age of breeding (a), when the population remains stable from year to year, in the following formula:

$$f = \frac{1 - s}{s^a}$$

If the adult survival and the age of breeding remains unaltered, the fecundity in a stable Glaucous-winged Gull population will be $\frac{.10}{.90^4} = .15$.

The fecundity (f) at the present rate of increase (using Capildeo and Haldane's (l.c.) formula as applied by Coulson and White, 1959, which interrelates fecundity, population change and average age at which a female starts to breed) is equal to:

$$\frac{\text{Number of young living one year produced by each female}}{2 \text{ X Annual adult survival}} =$$

$$\frac{1.6\ (1 - .7)}{2 \text{ X } (1 - .10)} = .27$$

where 1.6 is the number fledged per nest and .7 is the proportional mortality in the first year of life. Therefore the population will become stable if the present fecundity is reduced by approximately one half.

There seem to be two main factors concerned with the control of the Mandarte gull population, an annual fluctuation and the population increase over the years. One of the main factors playing a role in the annual fluctuation in the years 1961 and 1962 was the habit of the adults to attack strange chicks and the other main factor is thought to be the weather. The most attractive hypothesis for the gull increase over the years is that man is responsible through protection of the breeding gull colonies and through increase of the food supply during the winter. In the winter, the low tides fall mainly at night and adults and inexperienced young birds have little opportunity to utilize food from the intertidal zone. This has been offset by increasing numbers of garbage dumps, extension of harbours, and other human activities. Since gulls show a strong site tenacity, and tend to breed where they have been raised, it is fairly likely that the rise in the gull population in the Gulf of Georgia is not a result of immigration. Gulls are also known to have increased rapidly in Europe (Coulson and White 1959, Drost et al. 1961, Goethe 1956, Olsson 1958) and Eastern North America (Gross, 1955). From census data on breeding gulls in Finland they appear to have doubled their numbers in ten years and Grenquist (1961) ascribes the increase to the availability of fish scraps, garbage and sewage. More data, however, are needed from isolated gull colonies before the proposed hypothesis about causes of gull increase over the years can be firmly established.

GENERAL SUMMARY

Summaries will be found at the close of the first four chapters. The last chapter mainly is a summary in itself. It will suffice here to mention briefly the more important results.

1. The Glaucous-winged Gulls can maintain a strong pair-bond outside the breeding colony. Pair formation occurs on the territory. It was usual for pair-bonds to last for at least a year. Philopatry to the nest site was observed in the majority of cases.
2. No support was found for the Fraser Darling Effect that there is a greater synchronisation of breeding at greater densities. Egg-laying is uniform throughout a 24 hour period. The mean egg-laying interval is 54.86 ± .63 hours. For three members of the Laridae, egg-laying and incubation take longer in larger birds with larger eggs. The mean clutch size is 2.82 ± .02. The share of the sexes in incubation varies, but the overall effect is a rather equal share. The incubation period is 26.9 ± .077 days. The incubation attentiveness after the b- egg has been laid is 92 percent. Thirty-one and 53 percent of the full effectiveness of incubation are obtained after respectively the a- and b- egg are laid.
3. One of the chief causes of chick mortality was the habit of the adults to attack strange chicks and the other main mortality is thought to be due to the weather. Fledging rates in 1961 and 1962 were respectively 1. and

1.7 fledglings per pair of gulls. Fledging rates of nests in two different habitats and at different densities were found to be similar. Growth occurs mainly during the first four weeks of life. At fledging 86 percent of the weight of the average breeding gull is reached. The results of the chick addition experiment do not seem to support Lack's hypothesis that the clutch-size of each species of bird has been adapted by natural selection to correspond with the largest number of young for which the parents can, on the average, provide enough food.

4. The average age at first flight is 44 days, at island departure 57 days, at first arrival in Vancouver 63 days. The age at fledging is influenced by the rate of growth. There is no general rule about dispersal of the juveniles. A strong family bond can occur after island departure.
5. Annual adult mortality was 10%. Average longevity is 13.5 years. Mortality between fledging and maturation if the present rate of population increase is maintained is 80%. There seem to be two main factors concerned with the control of the Mandarte gull population, an annual fluctuation and the population increase over the years.

APPENDIX

BROODING TABLES

Nest No. Wide 1962

	Observations		Brooding Time in Minutes			No. of	
Date	Period	Mins.	Total	♂	♀	Shifts	Remarks
June 13	0655-0930	155	120	71	49	6	1 egg at 0930
" 14	0600-0800	120	59	59	--	1	
" 15	0740-0930	110	104	72	32	2	
" 16	0615-0930	195	191	191	--	1	2 eggs at 0930
" 18	0615-0930	195	195	195	--	1	
" 19	0545-0845	180	180	136	44	2	3 eggs at 0845
" 20	0610-0845	155	93	58	35	2	
" 21	0645-0830	105	105	--	105	1	
" 24	0540-0845	185	185	185	--	1	
" 25	0515-0830	195	195	195	--	1	
" 26	0630-0930	180	180	--	180	1	
Total		1775	1607	1162	445		

Nest No. 47 1962

	Observations		Brooding Time in Minutes			No. of	
Date	Period	Mins.	Total	♂	♀	Shifts	Remarks
May 25	0530-0830	180	109	--	109	1	2 eggs at 0830
" 26	0830-1035	125	113	65	48	2	2 eggs at 1035
" 27	0600-1100	300	286	181	105	5	3 eggs at 1100
" 28	0600-0800	120	118	89	29	2	
" 29	0615-1030	255	255	93	162	2	
" 30	0630-0930	180	180	130	50	2	
" 31	0630-0937	187	187	60	127	3	
June 1	0630-1030	240	239	214	25	2	
June 4	0600-0930	210	210	98	112	2	
" 6	0600-0900	180	179	152	27	2	
" 8	0550-0920	210	210	128	82	3	
" 10	0600-0900	180	180	145	35	2	
" 12	1510-1810	180	180	115	65	2	
" 13	0630-0930	180	179	118	61	2	
" 14	0530-0830	180	180	180	--	1	
" 15	0630-0930	180	180	58	122	2	
" 16	0615-0930	195	195	12	183	2	
" 17	0630-0930	180	180	129	51	2	
" 18	0615-0930	195	195	--	195	1	
" 19	0545-0845	180	180	112	68	2	
" 20	0545-0845	180	180	--	180	1	
" 21	0645-0845	105	105	89	16	2	A hatched
Total		4122	4020	2168	1852		

Nest No. 19, 1962

Date		Observations		Brooding Time In Minutes			No. of	
		Period	Mins.	Total	♂	♀	Shifts	Remarks
May	27	0600-1100	300	209	80	129	7	2 eggs at 1100 (1 egg at 1000 on May 26)
"	29	0615-1030	255	251	123	128	4	
"	30	0630-0930	180	179	39	140	3	3 eggs at 0930
"	31	0730-0937	127	127	63	64	3	
June	1	0630-1030	240	240	133	107	2	
"	2	0730-0945	135	135	135	--	1	
"	4	0600-0930	210	210	210	--	1	
"	6	0600-0900	180	180	116	64	2	
"	8	0550-0920	210	210	97	113	2	
"	10	0600-0900	180	180	50	130	2	
"	12	1510-1810	180	180	--	180	1	
"	13	0630-0930	180	180	150	30	2	
"	14	0530-0830	180	180	93	87	3	
"	15	0630-0930	180	180	--	180	1	
"	17	0630-0930	180	180	--	180	1	
"	18	0615-0930	195	195	61	134	2	
"	19	0545-0845	180	180	--	180	1	
"	20	0545-0845	180	180	52	128	2	
"	21	0645-0830	105	105	13	92	2	
"	24	0540-0845	185	185	32	153	3	A hatched
Total			3762	3666	1447	2219		

Nest No. Sorie, 1962

Date		Observations		Brooding Time in Minutes			No. of	
		Period	Mins.	Total	♂	♀	Shifts	Remarks
May	30	0735-0930	115	101	2	99	2	2 eggs at 0930 (1 egg at 0800 on May 28)
"	31	0645-0937	172	168	133	35	2	3 eggs at 0937
June	1	0652-1030	218	218	152	66	2	
"	4	0600-0930	210	210	210	--	1	
"	6	0610-0900	170	168	130	38	4	
"	8	0550-0920	210	209	62	147	3	
"	10	0600-0900	180	179	52	127	3	
"	12	1510-1810	180	180	8	172	3	
"	13	0630-0930	180	167	--	167	1	
"	14	0530-0830	180	179	90	89	2	
"	15	0630-0930	180	180	97	83	2	
"	16	0630-0930	180	180	19	161	2	
"	17	0630-0930	180	180	153	27	2	
"	18	0615-0930	195	195	--	195	1	
"	19	0545-0845	180	180	136	44	2	
"	20	0545-0845	180	180	--	180	1	
"	21	0645-0830	105	105	72	33	2	
"	24	0540-0845	185	185	108	77	2	
"	25	0515-0830	195	195	103	92	2	A and B hatched
"	26	0630-0930	180	168	73	95	2	
Total			3575	3527	1600	1927		

Nest No. 34, 1962

Date		Observations		Brooding Time in Minutes			No. of	
		Period	Mins.	Total	♂	♀	Shifts	Remarks
June	6	0600-0900	180	179	131	48	3	(Clutch started on May 27)
"	8	0550-0920	210	206	140	66	4	
"	10	0600-0900	180	178	41	137	3	
"	13	0630-0930	180	148	73	75	2	
"	14	0530-0830	180	180	68	112	2	
"	15	0630-0930	180	179	179	--	1	
"	16	0615-0930	195	194	63	131	2	
"	17	0630-0930	180	180	82	98	2	
Total			1485	1444	777	667		

Nest No. D, 1962

Date		Observations		Brooding Time in Minutes			No. of	
		Period	Mins.	Total	♂	♀	Shifts	Remarks
June	4	0610-0930	200	182	67	115	6	1 egg at 0930
"	6	0620-0900	160	144	121	23	6	2 eggs at 0900
"	8	0550-0920	210	210	99	111	5	3 eggs at 0920
"	10	0600-0900	180	180	--	180	1	
"	13	0630-0930	180	180	91	89	5	
"	14	0530-0812	162	160	107	53	5	
"	15	0630-0930	180	180	163	17	3	
"	16	0615-0930	195	195	41	154	2	
"	17	0630-0930	180	180	74	106	2	
Total			1647	1611	763	848		

Nest No. A, 1962

Date	Observations Period	Mins.	Brooding Time in Minutes Total	♂	♀	No. of Shifts	Remarks
May 31	0630-0937	187	144	--	144	1	1 egg at 0937
June 1	0630-1030	240	167	31	136	3	
" 2	0730-0945	135	116	14	102	3	2 eggs at 0945
" 4	0600-0930	210	210	--	210	1	3 eggs at 0930
" 6	0600-0900	180	180	15	165	3	
" 8	0550-0920	210	210	62	148	5	
" 10	0600-0900	180	180	128	52	2	
" 12	1510-1810	180	180	27	153	5	
" 13	0630-0930	180	180	71	109	2	
" 14	0530-0830	180	180	--	180	1	
" 15	0630-0930	180	180	--	180	1	
" 17	0630-0930	180	180	165	15	2	
" 18	0615-0930	195	195	--	195	1	
" 19	0545-0845	180	180	82	98	2	
" 20	0545-0845	180	180	20	160	2	
" 21	0645-0830	105	105	--	105	1	
" 24	0540-0845	185	185	74	111	2	
" 25	0515-0830	195	195	149	46	2	
" 26	0630-0930	180	180	--	180	1	(July 1: A and B hatched)
" 27	0630-0830	120	120	--	120	1	
Total		3582	3447	838	2609		

Nest No. Reddie, 1962

Date	Observations Period	Mins.	Brooding Time in Minutes Total	♂	♀	No. of Shifts	Remarks
June 1	0630-1030	240	84	84	--	1	1 egg at 1030
" 2	0730-0945	135	22	17	5	2	
" 4	0600-0930	210	208	93	115	4	2 eggs at 0930
" 6	0600-0900	180	177	167	10	3	3 eggs at 0900
" 8	0550-0920	210	210	210	--	1	
" 10	0600-0900	180	180	180	--	1	
" 12	1510-1810	177	177	33	144	3	
" 13	0630-0930	179	179	164	15	2	
" 14	0530-0830	179	179	179	--	1	
" 15	0630-0930	180	180	180	--	1	
" 16	0615-0930	195	195	195	--	1	
" 17	0630-0930	180	180	111	69	2	
" 18	0615-0930	195	195	141	54	3	
" 19	0545-0845	180	180	180	--	1	
" 20	0545-0845	180	180	180	--	1	
" 21	0645-0830	105	105	105	--	1	
" 24	0540-0845	185	185	116	69	2	
" 25	0515-0830	195	195	195	--	1	(June 30 A hatched)
Total		3290	3011	2530	481		

Nest No. M, 1962

Date	Observations		Brooding Time in Minutes			No. of	
	Period	Mins.	Total	♂	♀	Shifts	Remarks
June 4	0610-0930	200	190	134	56	4	1 egg at 0930
" 6	0600-0900	180	177	--	177	1	1 egg at 0900
" 8	0550-0920	210	206	97	109	2	2 eggs at 0920
" 10	0600-0900	180	179	127	52	4	3 eggs at 0900
" 12	1510-1810	180	178	148	30	5	
" 13	0630-0930	180	180	20	160	2	
" 14	0530-0830	180	178	93	85	2	
" 15	0630-0930	180	180	--	180	1	
" 16	0615-0930	195	195	66	129	2	
" 17	0630-0930	180	180	106	74	2	
" 18	0615-0930	195	--	--	195	1	
" 19	0545-0845	180	180	31	149	2	
" 20	0545-0845	180	180	140	40	2	
" 21	0645-0830	105	105	73	32	2	
" 24	0540-0845	185	185	46	139	2	(July 3 A and B hatched)
" 25	0515-0830	195	--	--	195	1	
Total		2905	2883	1081	1802		

Nest No. Bandie, 1962

Date	Observations		Brooding Time in Minutes			No. of	
	Period	Mins.	Total	♂	♀	Shifts	Remarks
June 13	0630-0930	180	171	58	113	4	1 egg at 0930
" 14	0530-0830	180	169	80	89	2	
" 15	0630-0930	180	178	78	100	3	
" 16	0615-0930	195	195	65	130	2	2 eggs at 0930
" 17	0630-0930	180	180	168	12	2	
" 18	0615-0930	195	195	195	--	1	
" 19	0545-0845	180	179	135	44	2	
" 20	0545-0845	180	180	50	130	2	
" 21	0645-0830	105	105	30	75	2	
" 24	0540-0845	185	185	47	138	2	
" 25	0515-0830	195	195	75	120	2	
Total		1955	1932	981	951		

Nest No. F, 1962

Date	Observations		Brooding Time in Minutes			No. of Shifts	Remark
	Period	Mins.	Total	♂	♀		
June 12	1535-1810	155	135	66	69	5	1 egg at 1810
" 13	0630-0930	180	179	37	142	2	
" 14	0530-0830	180	147	45	102	3	
" 15	0630-0930	180	165	80	85	2	2 eggs at 0930
" 16	0615-0930	195	195	--	195	1	
" 17	0630-0930	180	166	82	84	2	3 eggs at 0930
" 18	0615-0930	195	177	177	--	1	
" 19	0545-0845	180	180	64	116	2	
" 20	0545-0845	180	180	--	180	1	
" 21	0645-0830	105	105	30	75	2	
" 24	0540-0845	185	149	46	103	2	
" 25	0515-0830	195	179	179	--	1	
" 26	0630-0930	180	180	180	--	1	
Total		2290	2137	986	1151		

Nest No. H, 1962

Date	Observations		Brooding Time in Minutes			Shift	Remark
	Period	Mins.	Total	♂	♀		
June 12	1655-1810	75	27	--	27	1	1 egg at 1810
" 13	0630-0930	180	30	7	23	2	
" 14	0530-0830	180	145	--	145	1	
" 15	0630-0930	180	169	45	124	3	2 eggs at 0930
" 16	0615-0930	195	185	103	82	2	
" 17	0630-0930	180	180	--	180	1	
" 18	0615-0930	195	178	37	141	5	
" 19	0545-0845	180	178	16	162	3	
" 20	0545-0845	180	180	43	137	2	
" 21	0645-0830	105	105	105	--	1	
" 24	0540-0845	185	185	5	180	3	
" 25	0515-0830	195	195	37	158	2	
Total		2030	1757	398	1359		

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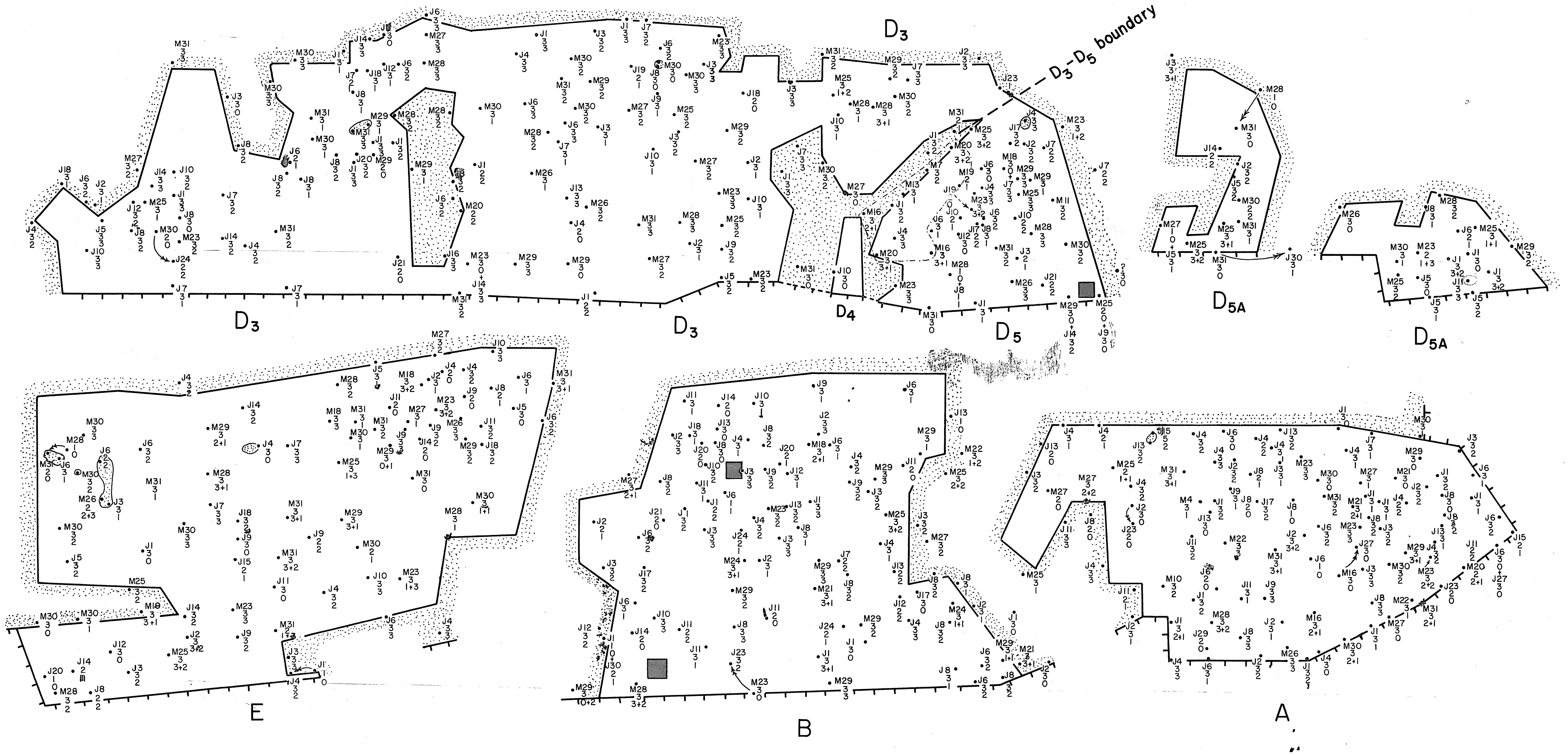


MAP III "NORTH-EAST" AREA (CHECKED IN 1962)

→ SECOND NESTING SITE BY A PAIR OF GULLS (PROTRACTED OR REPEAT LAYING)

0 6
METERS

M29 FIRST FIGURE INDICATES CLUTCH COMMENCEMENT (MAY 29)
3 SECOND " " CLUTCH SIZE (CLUTCH OF 3 EGGS)
2 THIRD " " FLEDGING RATE (2 FLEDGLINGS)

——— MEADOW BOUNDARY

M29
3
2+2 +2 INDICATES THAT 2 EXTRA CHICKS FLEDGED THIS NEST (CHICK ADDITION EXPERIMENT)

┴┴┴┴ CLIFF (FACING WATER) OR ENDING OF MEADOW AT SHORELINE

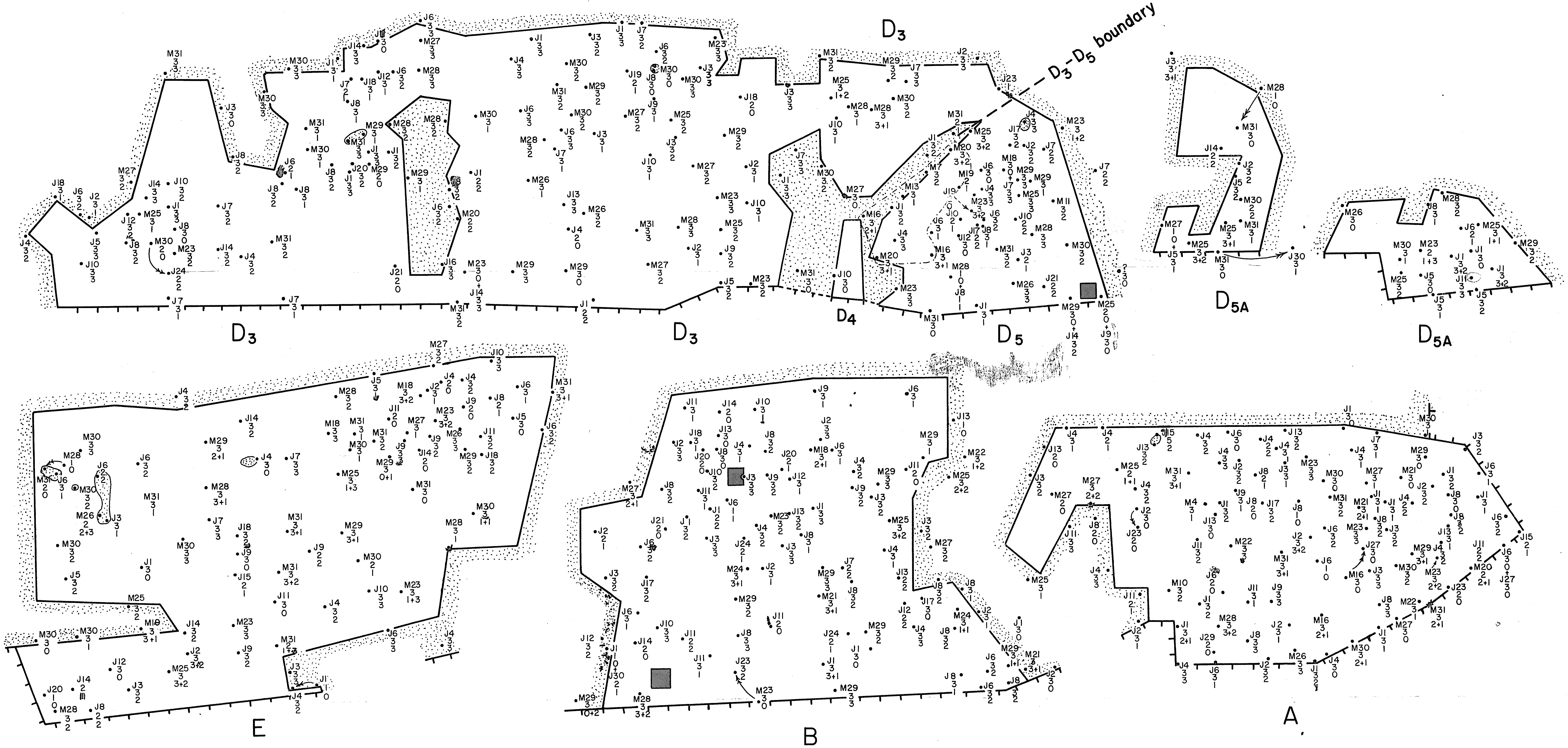
—·—·— NUCLEUS OF EARLY CLUTCH COMMENCEMENT

M29
3
0
+
J10
2
1 INDICATES PROTRACTED OR REPEAT-LAYING AT SAME NEST SITE

D3, D5, D5A
E, B, A MEADOWS

SMALL D 4 MEADOW NOT USED IN CALCULATION OF AVERAGE TERRITORY SIZE

■ BLIND ▨ BRUSH M = MAY J = JUNE



MAP III "NORTH-EAST" AREA (CHECKED IN 1962)

0 6
METERS

— MEADOW BOUNDARY

CLIFF (FACING WATER) OR ENDING OF MEADOW AT SHORELINE

-·-·- NUCLEUS OF EARLY CLUTCH COMMENCEMENT

■ BLIND

▨ BRUSH

M = MAY J = JUNE

→ SECOND NESTING SITE BY A PAIR OF GULLS (PROTRACTED OR REPEAT LAYING)

M29 FIRST FIGURE INDICATES CLUTCH COMMENCEMENT (MAY 29)
3 SECOND " " CLUTCH SIZE (CLUTCH OF 3 EGGS)
2 THIRD " " FLEDGING RATE (2 FLEDGLINGS)

M29
3
2+2 +2 INDICATES THAT 2 EXTRA CHICKS FLEDGED THIS NEST (CHICK ADDITION EXPERIMENT)

M29
3
0
+
J10
2
1 INDICATES PROTRACTED OR REPEAT-LAYING AT SAME NEST SITE

D3, D5, D5A
E, B, A MEADOWS

SMALL D4 MEADOW NOT USED IN CALCULATION OF AVERAGE TERRITORY SIZE