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REPRODUCTIVE SUCCESS, FOOD SUPPLY, AND THE EVOLUTION OF CLUTCH-SIZE IN THE GLAUCOUS-WINGED GULL

by

JOHN GORDON WARD

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ABSTRACT

Lack (1947) proposed that, in nidicolous birds, clutch-size has evolved to correspond, on average, to the most productive brood size. The limit is normally set by the maximum number of young the adults can adequately feed to fledging. Recent studies using gulls to test Lack's hypothesis have shown that the most common and most productive clutch-size do not coincide. Recent increases in human refuse may have been a factor in these results. In this study, the Glaucous-winged Gull *Larus glaucescens* was used to test Lack's hypothesis. Experiments were designed to test the possible effects of refuse on the birds' capabilities of raising extra young. Both normal (1-3 chicks) and supernormal (4-6 chicks) broods were set up on both a colony (Mandarte Island) where refuse was used by the gulls and on colonies (Cleland Island and islands (QCI) in the Queen Charlotte Islands, B.C.) where refuse was not used. The results did not support Lack's hypothesis. Chicks grew better on Cleland and QCI, where only natural food was used, than on Mandarte where both refuse and natural food was used. On Cleland, chicks in all brood sizes reached an average weight of 1000 g (adult weight) before fledging. On Mandarte, the maximum weight was significantly below 1000 g for most brood sizes. Numbers of chicks fledged for each brood size increased with increasing brood size on all the colonies. Post-fledging survival rates indicated that on Cleland, chick survival was similar for normal and supernormal broods. On Mandarte, chick survival was better for the normal broods than for supernormal broods. The contribution to future breeding populations by individuals from different brood sizes was highest for a brood of six on Cleland, but was highest for a brood of three on Mandarte. The results are contrary to what Lack predicted both because a supernormal brood on Cleland was the most productive and because on Mandarte refuse did not give the birds an advantage over those colonies where refuse was not available. On Cleland, Pacific Sandlance was the predominant food. On Mandarte Pacific Herring was the predominant food. On Mandarte in 1971, I found that refuse formed up to 25 percent of the chick diet even though significantly more time was required by the adults when foraging for refuse as opposed to natural foods. The duration of the average foraging trip increased with chick age but this was due to an increased use of refuse by the adults as the chicks got older. Reasons for the high success on Cleland and QCI are discussed including both the possiblility of a recent change in the abundance of sandlance and the possible influence of reproductive effort on adult mortality. A winter study was carried out in south-western British Columbia in order to assess the use made of refuse sites during the winter by the Glaucous-winged Gull. I found that up to 65,000 glaucous-winged gulls wintered in the lower mainland region of British Columbia and that between 70 and 90 percent of these birds were using refuse sites.

Relatively few birds were using the intertidal zone, possibly because it is not exposed to any extent during daylight hours. The numbers of gulls in this area are discussed in relation to known information on the total population along the west coast of North America.

TABLE OF CONTENTS

Chapter			Page
I			
	A	Introduction	1
	B	Study Area	8
	C	Chick Addition Experiment - Rationale	11
II	Chick Growth And Survival		
	A	Introduction	14
	B	Growth Rates and Asymptotic Weights	14
	C	Chick Mortality and Fledging Success	33
	D	Post-fledging Success	41
	E	Summary	49
III	Food Utilized By Breeding Gulls		
	A	Introduction	51
	B	Diet of Adult Gulls Prior To Chick Hatching	52
	C	Chick Regurgitations	54
	D	Feeding Observations on Mandarte in 1971	57
	E	Discussion: Evolution of Clutch-Size	75
	F	Summary	83
IV	Use Of Refuse Dumps By The Glaucous-Winged Gull		
	A	Introduction	85
	B	Daily Activity During the Winter	86
	C	Numbers of Gulls and Their Use of Refuse Dumps	90
	D	Discussion	104
	E	Summary	108

Page

LITERATURE CITED 109

APPENDICES 115

LIST OF TABLES

Table		Page
1	Numbers of different brood sizes set up on the colonies in the different years.	15
2	Average age (days) (± SE) at which the asymptotic weight was attained by chicks in the different sized broods.	25
3	Average growth rates (g/day) (±SE) and sample size (n) for chicks ranked according to growth rates in the individual broods.	26
4	Average asymptotic weight (grams) (±SE) and sample size (n) for chicks ranked by growth rate as shown in Table 3.	28
5	Average growth rates (g/day) (±SE) for the different brood sizes with respect to the breeding season.	30
6	Nestling mortality rates for Mandarte in 1969 and Cleland in 1970. The number of chicks dying during each age interval is expressed as a percent of the total number of chicks at the beginning of the interval.	34
7	Percentage of deaths due to different factors on Mandarte in 1969 and Cleland in 1970.	36
8	Percentage survival rates of first year birds as related to brood size. These survival values are based on the number of live sightings of birds away from the colony.	42
9	Average asymptotic weight (grams) (±SE) of all individuals for different brood sizes compared with the average asymptotic weight of those individuals seen alive away from the colony for Mandarte in 1969 and 1971.	44
10	Theoretical contribution to future breeding populations for broods one to six on Mandarte in 1962, 1969, and 1971 and Cleland in 1970.	45

Table		Page
11	Pellets collected on Mandarte in 1969 and Cleland in 1970 classified as to whether garbage or non-garbage items. A more complete listing of species of natural food is found in appendix 4.	53
12	Average duration of foraging absences (±SE) for adults with both normal and supernormal broods.	60
13	Change in length of average foraging trips (minutes) (±SE) with chick age for both normal and supernormal broods on Mandarte in 1971.	62
14	Average number (±SE) of foraging trips made per day by adults with respect to the age of the chicks and the brood size.	65
15	Average duration (minutes) (±SE) of foraging trips for different food types with repect to brood size on Mandarte in 1971.	68
16	Roost counts for the winter seasons between 1969 and 1972 for the lower mainland area of B.C.	92
17	Numbers of gulls counted at or near refuse sites.	94
18	Comparison of roost and refuse site censuses. These figures do not include the numbers of gulls for the roosts and the refuse sites on Burrard Inlet.	97
19	Numbers of birds along the intertidal census areas (shown in fig. 14) and the age composition of those birds.	99
20	Percentage age composition of gulls at three different refuse sites.	102

LIST OF FIGURES

Figure | Page

1 Map of the west coast of British Columbia, Canada showing the location of the three different sites on which the experiments testing Lack's hypothesis were performed. 9

2 Map showing the location of the winter study area which included Vancouver, British Columbia and the surrounding municipalities. 12

3 Average growth curve for a brood of three chicks on Mandarte, Cleland, and QCI. The straightest portion of the curves was taken to be between 6 and 26 days. Some of the 5% confidence limits are put in to show the amount of variation associated with each curve. 17

4 Graph showing lines obtained when Ricklefs' conversion factors for a logistic and Gompertz curve are applied to the growth curve for a brood of three chicks from Cleland in 1970. The conversion line for the von Bertalanffy form is curved upwards even more than the Gompertz. 19

5 Average growth rates (between 6 and 26 days of age) for different sized broods on Mandarte, Cleland and QCI. The values for the average growth rate and their standard errors are in appendix 1. 21

6 Average asymptotic weights of the different brood sizes on Mandarte and Cleland. The values and standard errors are in appendix 2. 23

7 Percentage fledging success for the different brood sizes on Mandarte, Cleland, and QCI. 37

8 Absolute numbers of chicks fledged for the different brood sizes on Mandarte and Cleland. 40

Figure		Page
9	Percentage composition of food types found in chick regurgitations on Mandarte, Cleland, and QCI.	55
10	Change in average total time spent foraging each day by a pair with respect to the age of the chicks and the various brood sizes.	64
11	Change in frequency of food types in the diet of the chicks with respect to their age and brood size (Mandarte, 1971). 'n' is total on which percentages based. Percentage values in appendix 3.	67
12	Numbers of foraging trips for different food types classified according to the time of day the adults returned (Mandarte, 1971).	74
13	Change in chick survival to breeding (b) with respect to brood size. The curve for adult mortality (q) with respect to brood size is a hypothetical one which would be required in order for a brood of three chicks to be optimum. (from Charnov and Krebs, in prep)	80
14	Map of winter study area showing location of refuse dumps, roost sites, and flight lines between refuse sites and roosts. Refuse sites: 1 - West Vancouver (closed Oct. 31/69); 2 - North Vancouver; 3 - Barnet; 4 - Terra Nova; 5 - Leeder; 6 - Port Mann; 7 - Burnaby (closed Oct. 31/69); 8 - Richmond; 9 - Vancouver.	87
15	Rate of departure from roosts in morning and rate of arrival at roosts in evening for Dec 20/68.	89

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CHAPTER I

A Introduction

The study described in this thesis had two aims. The first, which was experimental in approach, involved the testing of Lack's (1947) hypothesis on the evolution of clutch-size in nidicolous birds. The second aim, which was of a more descriptive nature, dealt with the utilization of garbage by winter populations of the Glaucous-winged Gull *Larus glaucescens* in south-western British Columbia.

In recent years the study of factors involved in the determination of clutch-size in birds has received much attention, with the initial impetus coming from the early work of David Lack. Researchers have looked at both the proximate (immediate causal) and ultimate (evolutionary) factors determining clutch-size, especially in the nidicolous species. In this study I was concerned with the ultimate factors influencing the evolution of clutch-size in a nidicolous species. Lack (1947) postulated that in nidicolous birds, the most common clutch-size has evolved to correspond with that brood size from which, on average, the most surviving young are produced. The limit to the number of young produced is normally set by the amount of food the parents can bring to the nestlings. Thus Lack considered the ultimate factor determining clutch-size to be the ability of the adult birds to provide food for the young.

The most successful of the studies investigating Lack's hypothesis have been those which took an experimental approach in order to see if the most common clutch-size corresponded to the most productive one. In the experimental studies, broods, which were larger than the most common one and which as a rule rarely occurred naturally, were set up by adding extra nestlings to broods just after the eggs hatched. Success of these supernormal broods was measured by both how many individuals fledged from the supernormal broods and how many of these individuals survived to breeding as compared to normal broods. If more young fledge from supernormal broods than from normal broods, then it is necessary to obtain post-fledging mortality rates before an adequate decision can be made concerning Lack's hypothesis.

Studies on the following species have generally supported Lack's hypothesis: European Starling _Sturnus vulgaris_ (Lack, 1948), Great Tit _Parus major_ (Lack, Gibb, and Owen, 1957; Perrins, 1965), Swift _Apus apus_ (Lack and Lack, 1952; Lack and Owen, 1955; Perrins, 1964), Pied Flycatcher _Ficedula hypoleuca_ (Haartman, 1967; Klomp, 1970), Black-faced Dioch _Quelea quelea_ (Ward, 1965), Snow Bunting _Plectorophenax nivalis_ (Hussel, 1972), Laysan Albatross _Diomedea immutabilis_ (Rice and Kenyon, 1962), Manx Shearwater _Puffinus puffinus_ (Harris, 1966), Rhinocerus Auklet _Cerorhinca monocerata_ (Summers, 1970), Pigeon Guillemot _Cepphus columba_ (Koelink, 1972), Common Puffin *Fratercula arctica* (Nettleship, 1972), Brown Booby *Sula leucogaster* (Dorward, 1962), and the Red-footed Booby *Sula sula* (Nelson, 1966). In these species the most common clutch-size corresponded to the maximum number of young that the adults could adequately feed to fledging. In some of these studies (eg. albatross and shearwater studies) the broods did not have to be followed beyond fledging because the normal broods were obviously producing far more individuals, and in better weight condition, than were the supernormal broods. In others (eg. Great Tit) the survival of young had to be followed after fledging in order to establish that the normal clutch-sizes were in fact the most productive ones.

Other studies did not appear to support Lack's hypothesis in that the most productive clutch-size did not correspond to the most common one. Mountford (1968) explained these results on the basis that the size of clutch produced by a genotype is not accurately determined, but will vary amongst individuals of the same genotype. Thus the numbers of different clutch-sizes produced by a genotype will form some frequency distribution. The number of individuals produced from each clutch will vary depending on the size of the clutch. As a result, the number of offspring produced by a genotype in any year will then be a product of the numbers of different clutch-sizes laid by that genotype and the fledging success associated with each of the clutch-sizes. Mountford suggested that the most productive and most common clutch size may or may not correspond depending on the shape of these two distributions. However, at present there are no data supporting Mountford's modification of Lack's hypothesis. Studies on the Pied Flycatcher (Curio, 1958; Campbell in Lack, 1966), the Collared Flycatcher Ficedula albicollis (Lohrl, 1957) and the Heron Ardea cinerea (Owen, 1960) present circumstantial evidence which may support Mountford's idea. In the flycatcher studies the most productive clutch-size was larger than the most common clutch-size. In the heron study the most productive clutch-size was smaller than the most common. In all these studies the results included data on the post-fledging survival of the young.

The results of several other studies do not appear to support Lack's hypothesis even with the inclusion of Mountford's idea. In these studies the most productive clutch-size was larger than any normally found. Nelson (1964) found that the North Atlantic Gannet Sula bassana, which normally lays only one egg, could both incubate two eggs and fledge two young. In addition, more young were produced by the experimental broods of two young than by normal broods of one. The difference in fledging weight between the two brood sizes was small enough to preclude any differences in post-fledging mortality. Robertson (1971) found that the Double-crested Cormorant Phalacrocorax auritus could successfully raise up to six young. Normally they only raise a maximum of four young. In addition, the post-fledging survival was as high for chicks from supernormal broods as for those from normal broods. Both the Gannet (Nelson, 1966) and the Double-crested Cormorant are at present increasing in numbers. In the case of the Gannet, the species is presently recovering from earlier depredations by man. Lack (1966) argued that, because the Gannet is not presently in balance with its food supply, they are easily able to find enough food for more than one young. This argument could also apply for the Double-crested Cormorant.

The results of several studies on gulls also do not appear to support Lack's hypothesis. Coulson and White (1958) showed that the Kittiwake *Rissa tridactyla* could raise three young as well as two, but that over 74 percent of the pairs laid two egg clutches. They did not, however, have any data on post-fledging mortality. Harris and Plumb (1965) showed that the Lesser Black-backed Gull *Larus fuscus* could raise more chicks than normal. Again there were no post-fledging survival data. Vermeer (1963) found that the Glaucous-winged Gull could raise up to twice the normal number of chicks with equal success. In addition the post-fledging survival was higher for the supernormal broods than for the normal broods. Lack (1966) argued that these results did not contradict his hypothesis. In recent years there has been a large increase in the gull's food supply, mainly in the form of human refuse. This added food supply has enabled the birds to feed more young than normal. In the studies of gulls discussed above, no data were given indicating whether or not garbage was an important food source. In support of Lack's criticism, Spaans (1971) found that chicks fed garbage in addition to natural food grew better than chicks fed only natural food. Fordham (1970) and Hunt (1972) found that breeding success was better on those islands close to refuse sources. As can be seen from these studies more information is needed, both on the utilization of garbage by gulls used to test Lack's hypothesis, and on the post-fledging mortality of chicks from different sized broods.

In the first part of this investigation, the aim was to test Lack's hypothesis in a gull species in order to rule out the affect of garbage in the success of parents raising additional chicks. My study enlarged on Vermeer's work in order to determine, (1) how important garbage is as a food source in feeding the chicks, (2) whether the gulls could raise extra chicks where only natural food was available and/or used, (3) whether the Glaucous-winged Gull could raise extra chicks in more than one year and place, (4) how well the chicks grew prior to fledging, and how well they survived after fledging.

Recent increases in the amount of garbage discarded by man, besides influencing the success of brood manipulation experiments, may also be an important factor in the recent increases of gull populations (Brown, 1967; Harris, 1972). The provision of copious quantities of refuse by man may have permitted more birds to survive the winter than was possible in the past. In recent years, several people have studied the use made of human refuse by gulls during the winter months. The more extensive among these studies include the work on the Herring Gull *Larus argentatus* by Drury (1963) on the New England coast of the U.S.A. and Spaans (1971) in the Netherlands, and the work on the Dominican Gull *Larus dominicus* by Fordham (1968 and 1970) in New Zealand. Spaans showed that depending on the foraging conditions on the Wadden Sea, between 32 and 77 percent of the herring gulls in that region fed on the refuse sites during the winter. On the east coast of the U.S.A. up to 70 percent of the herring gull population used the refuse sites. In New Zealand, up to 50 percent of the gulls were at or near refuse sites and meatworks during the winter. In all of the above studies the gulls did use natural food sources, however, Spaans and Drury found that winter storms caused gulls which normally fed on the intertidal to switch to refuse sites.

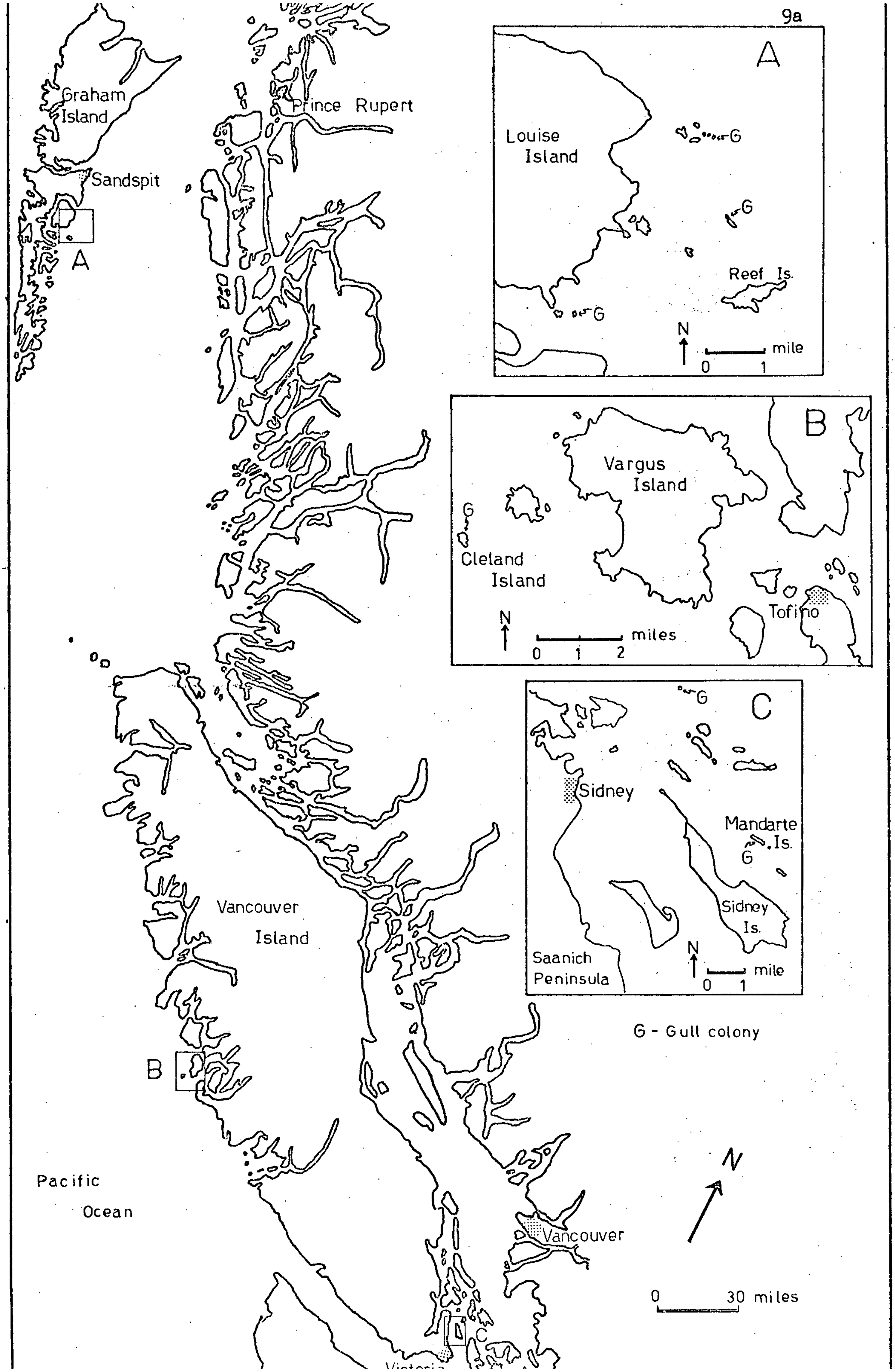
Along the west coast of British Columbia and Alaska, gulls feeding on intertidal areas have the added disadvantage of the extreme low tides generally occurring at night. The advent of refuse sites has provided a very attractive feeding area for the Glaucous-winged Gull and perhaps has contributed to their recent increase in numbers. The aim of the second part of this study was to investigate this use of refuse dumps by the Glaucous-winged Gull along the west coast and specifically in the lower mainland region of British Columbia.

B Study Area

A large part of the study on the clutch-size question in the Glaucous-winged Gull was carried out during the summer months (1969 - 1972) on their breeding grounds. In order to test Lack's hypothesis as rigorously as possible, the study was carried out on two different types of gull colonies for more than one year. The first type included those colonies relatively close to large garbage sources. Here it was expected that the gulls would use refuse to feed their young. The other type included those colonies as far removed as possible from refuse sources. In this case it was hoped that gulls would only feed natural foods to their young.

The colony on Mandarte Island (lat. 48° 38' N, long. 123° 17' W) (fig. 1) was selected to fulfil the requirements of the first type of colony for three reasons. (1) It is a large colony with over two thousand breeding pairs. Although the colony at present appears to be full, the reproductive rates do not differ from those occurring when the colony was expanding. (2) I could compare my data with that of Vermeer who used the same colony. (3) It was relatively close to sources of refuse. The island, fully described by Drent <u>et</u>

Figure 1: Map of the west coast of British Columbia, Canada showing the location of the three different sites on which the experiments testing Lack's hypothesis were performed.



G - Gull colony

al. (1964), is located 4 1/2 miles ESE of Sidney, British Columbia, and only 30 miles from the Vancouver garbage dump.

The colony on Cleland Island (lat. 49° 10' N, long. 126° 06' W) (fig. 1) was selected to fulfil the requirements of the second type of colony. The island, described by Campbell and Sterling (1967), is located eight miles WNW of Tofino on the west coast of Vancouver Island. Again this colony is large with more than 1500 breeding pairs of gulls. No information is available as to whether it is expanding. Although the colony is not entirely removed from potential garbage sources such as the salmon fishing industry, it is the best that can be obtained anywhere along the west coast and still be readily accessible. The nearby Tofino garbage dump is very small and seldom used by gulls during the summer (Campbell, personal communication).

In the summmer of 1972, the study was carried out on the northern part of the British Columbia coast. In this region the colonies are generally small (<100 breeding pairs) and if expanding appear to be doing so at a very slow rate. Three small colonies (lat. 52° 55' N, long 131° 34' W) (fig. 1) were selected in the Queen Charlotte Islands, British Columbia, and are located approximately 25 miles SSE of Sandspit. The colonies are located on three small rocky islets (collectively abbreviated to QCI in the text) and together contained a breeding population of only 135 pairs.

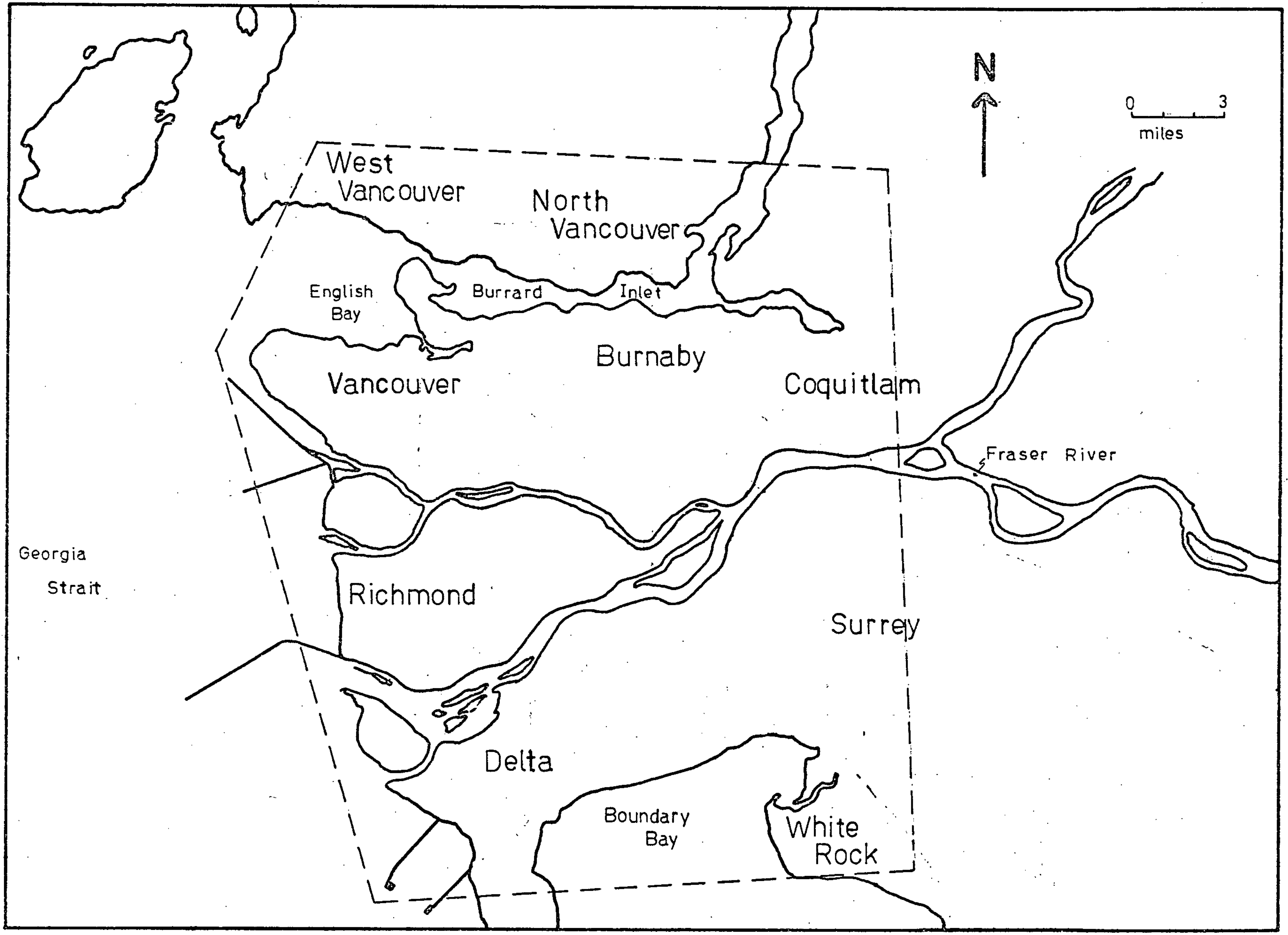
These colonies also fulfilled the requirements of being far removed from all garbage sources except the fishing industry.

The second part of the study, as mentioned in the introduction, was carried out during the winter months (1968 - 1972) in the lower mainland region of British Columbia. The boundaries of the study area, as shown in fig. 2, incorporated the city of Vancouver and a number of the surrounding municipalities. This study area only comprises a small part of the wintering range of the Glaucous-winged Gull. Some information is available from other studies done along the west coast of British Columbia and Alaska and will be incorporated in the discussion in chapter four.

C Chick Addition Experiments - Rationale

In many of the bird species used to test Lack's hypothesis, the broods have been formed by adding chicks at the time of hatching. This procedure has avoided problems involved in obtaining fertile eggs in similar stages of incubation. The chick additions have been done with the knowledge that the parent birds could have effectively incubated that many eggs. Various studies on passerines have confirmed that clutch-size was not determined by the number of eggs the bird could effectively incubate (studies listed in Klomp, 1970). The Gannet, unlike the passerine birds which have one large brood patch, uses its feet in order to incubate

Figure 2: Map showing the location of the winter study area which included Vancouver, British Columbia and the surrounding municipalities.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Vancouver
Burnaby
Coquitlam
Fraser River
Georgia Strait
Richmond
Surrey
Delta
Boundary Bay
White Rock

its single egg. Nelson (1964) showed that even with this method of incubation the bird could still effectively incubate two eggs.

The above type of assumption is not possible with the Glaucous-winged Gull or any of the other *Larus* gulls having a clutch of three eggs. These birds have three individual brood patches which permit effective incubation of only three eggs at any one time. The addition of extra eggs usually results in some or all of the eggs being unincubated for varying intervals of time. The final outcome is a greatly lowered hatching success for supernormal clutches relative to normal sized ones (Vermeer, 1963; Parsons, 1971). A somewhat different assumption then has to be made in the addition of extra chicks in these species. For the purposes of this study, it was assumed that the present brood patch arrangement is not in itself an ultimate factor determining clutch-size, but has evolved to correspond to the three egg clutch. If it were advantageous to have a larger clutch, a larger brood patch area could have evolved.

CHAPTER II

Chick Growth And Survival

A Introduction

The possibility exists that garbage has formed part of the chick diet for those studies testing Lack's hypothesis using gulls. This food source may have had a considerable influence on the success of these experiments. In this chapter, I describe the results of experiments designed to test the success of the Glaucous-winged Gull in raising normal and experimentally enlarged broods in two different types of situations. In one case only natural food was found in the chicks' diet. In the other, garbage made up an appreciable part of the diet. The criteria used to measure success included growth rates, maximum weight attained (referred to as asymptotic weight), mortality rates prior to fledging, fledging success, and post-fledging survival.

B Growth Rates and Asymptotic Weights

Methods: Large numbers of different brood sizes ranging from one to six chicks were set up during this study (Table 1). Vermeer's data (personal communication) from Mandarte Island showed that a large percentage of the larger broods lost at least one chick through mortality before the chicks fledged. As a result a large number of broods were required

Table 1

Numbers of Different Brood Sizes Set Up on The Colonies in the Different Years.

Location and Year		Brood Size 1	2	3	4	5	6
Mandarte	1969	63	56	48	50	36	53
Cleland	1969	12+	16+	18+	14+	17+	16+
Cleland	1970	152	94	101	52	37	40
Mandarte	1971	153	80	58	40	34	38
QCI	1972	31	18	30	5	14	

+ These values are the numbers of broods for which weights were available. The actual number set up was larger.

in order that I would be able to weigh complete broods in the older age classes. I defined a complete brood as one containing the same number of chicks as I had initially set it up with. In addition, the large sample for each brood size provided data for determining fledging success. Broods were formed either by removing or adding chicks three days or less old, or by leaving the broods as they hatched. Chicks were added to a nest within a day after the last egg in that particular nest had hatched. The adult birds did not appear to distinguish between their own and strange chicks. Also Tinbergen (1953) found that adult herring gulls did not differentiate between their own and strange chicks until their own chicks were over four or five days of age.

On Mandarte in 1969 and on Cleland in 1969 and 1970, chicks were weighed from hatching until fledging. On Mandarte in 1971, chicks were only weighed from 30 days of age to fledging. This provided asymptotic weights without the disturbance caused by handling young chicks in order to obtain growth rates. On QCI in 1972 only weights of chicks between hatching and 26 days of age were obtained. In all years chicks were weighed at two day intervals when possible.

The general shape of the growth curve obtained when weight was plotted against age is shown in fig. 3. Ricklefs (1967) presented a method for converting this sigmoid-shaped growth curve into a straight line. The slope of this line was

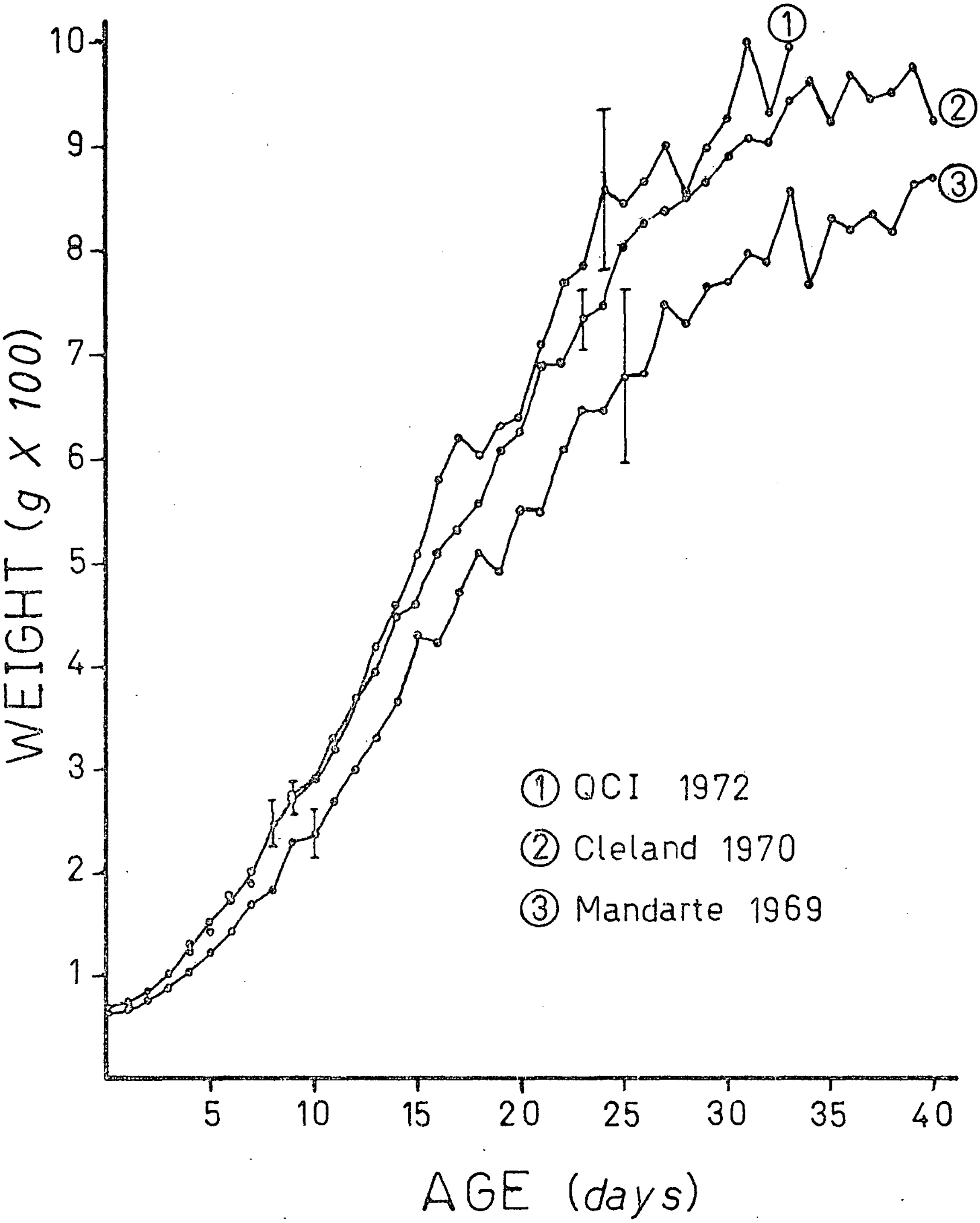


Fig. 3: Average growth curve for a brood of three chicks on Mandarte, Cleland, and QCI. The straightest portion of the curves was taken to be between 6 and 26 days. Some of the 5% confidence limits are put in to show the amount of variation associated with each curve.

a measure of the rate of growth at the inflection point of the growth curve. In his technique, Ricklefs assumed that the growth curve was approximated by one of three general curves: the logistic, Gompertz, or von Bertalanffy. As illustrated in fig. 4, none of Ricklefs's conversion tables for these forms were suitable for the growth curves in this study. Both the logistic and Gompertz conversion lines are curved through much of their length. This was Ricklefs criteria for rejecting any one of these forms as one approximating the shape of the growth curve in question. Because of the complex nature of Ricklefs method, and its poor fit, the method used by Spaans (1971) was used to calculate the growth rates in this study.

This method was found to be simple to use and still produced similar results. A linear regression of weight on age was calculated for each brood size using the weights of chicks between 6 and 26 days of age. It was during this age interval that the straightest portion of the growth curve occurred for all brood sizes. This method also approximates the growth rate at the inflection point and like Ricklefs' method permits a comparison of growth rates between brood sizes. This method has the added advantage of having the growth rates in the same units as the weights of the birds.

Different growth rates do not necessarily imply different asymptotic weights as will be shown in the results below. I determined the mean asymptotic weight for each brood size by

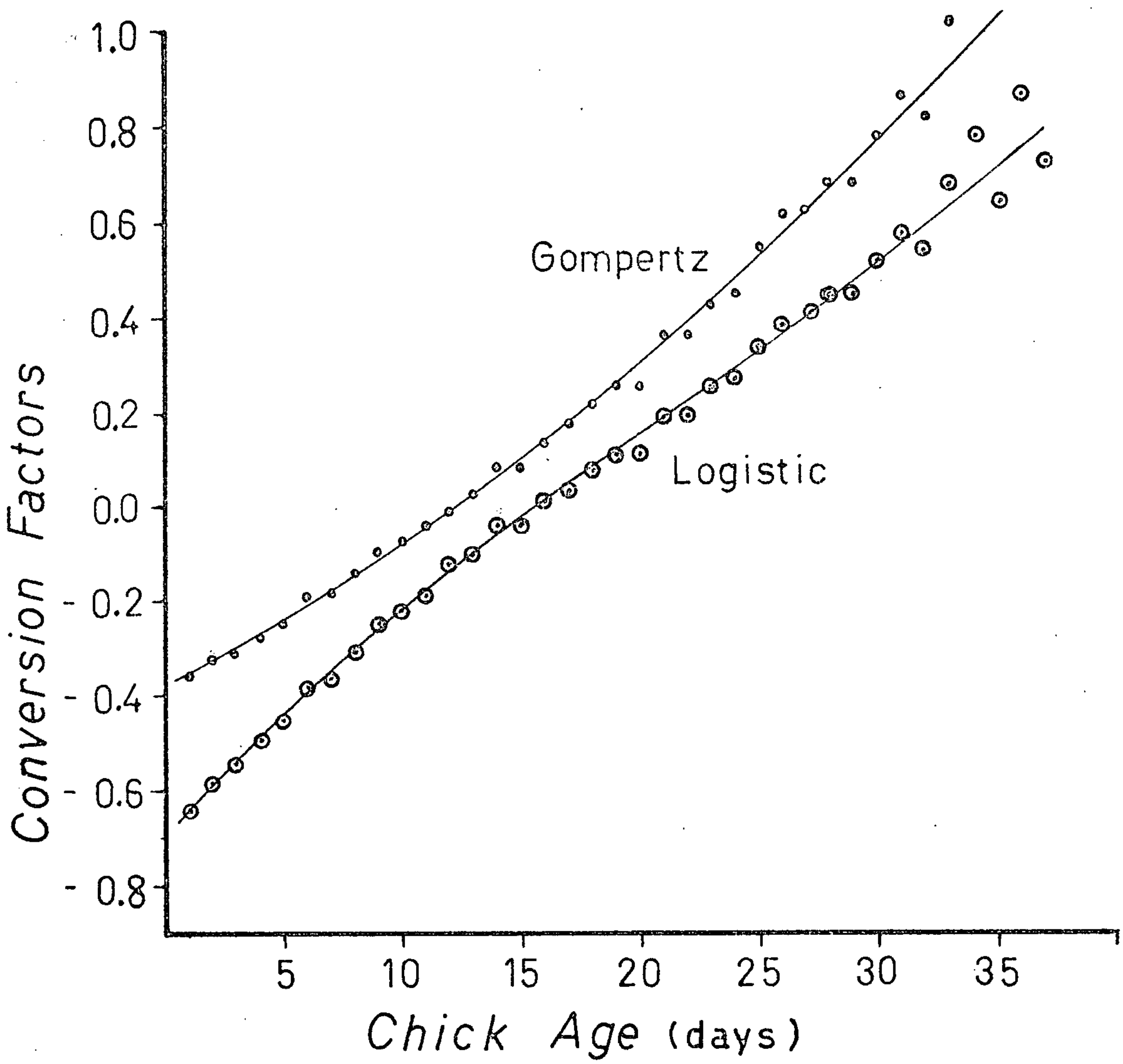


Fig. 4: Graph showing lines obtained when Ricklef's conversion factors for a logistic and Gompertz curve are applied to the growth curve for a brood of three chicks from Cleland in 1970. The conversion line for the von Bertalanffy form is curved upwards even more than the Gompertz.

averaging the maximum weights attained by individuals in that brood size. Chicks were not used if the last weight obtained for them was higher than all previous weights. Although the chick may have reached an asymptote, the possibility remained that the bird was still growing. Asymptotic weight was usually very similar to the fledging weight in this study and was used as a measure of chick condition at fledging. Together the above two measures served as good comparative indicators of how well the adults were able to feed chicks in different sized broods on the different islands.

Results: Growth rates varied depending on the colony, brood size, and year (fig. 5). The growth rates for Mandarte (1961) were calculated from data in Vermeer (1963). An analysis of covariance was done to test for differences in growth rates between brood sizes for each of the island-years (ie. Cleland in 1970, etc.). No significant differences were found. This was partly due to the large amount of variance associated with the growth rate for each brood size. On Mandarte in 1961 & 1969 and Cleland in 1970 there was a trend for growth rates to decrease with increasing brood size. In the case of Mandarte in 1969 this trend appeared to have some biological significance as indicated by the asymptotic weights presented below.

A one-way analysis of variance of the different growth rates with respect to the island-year showed significant

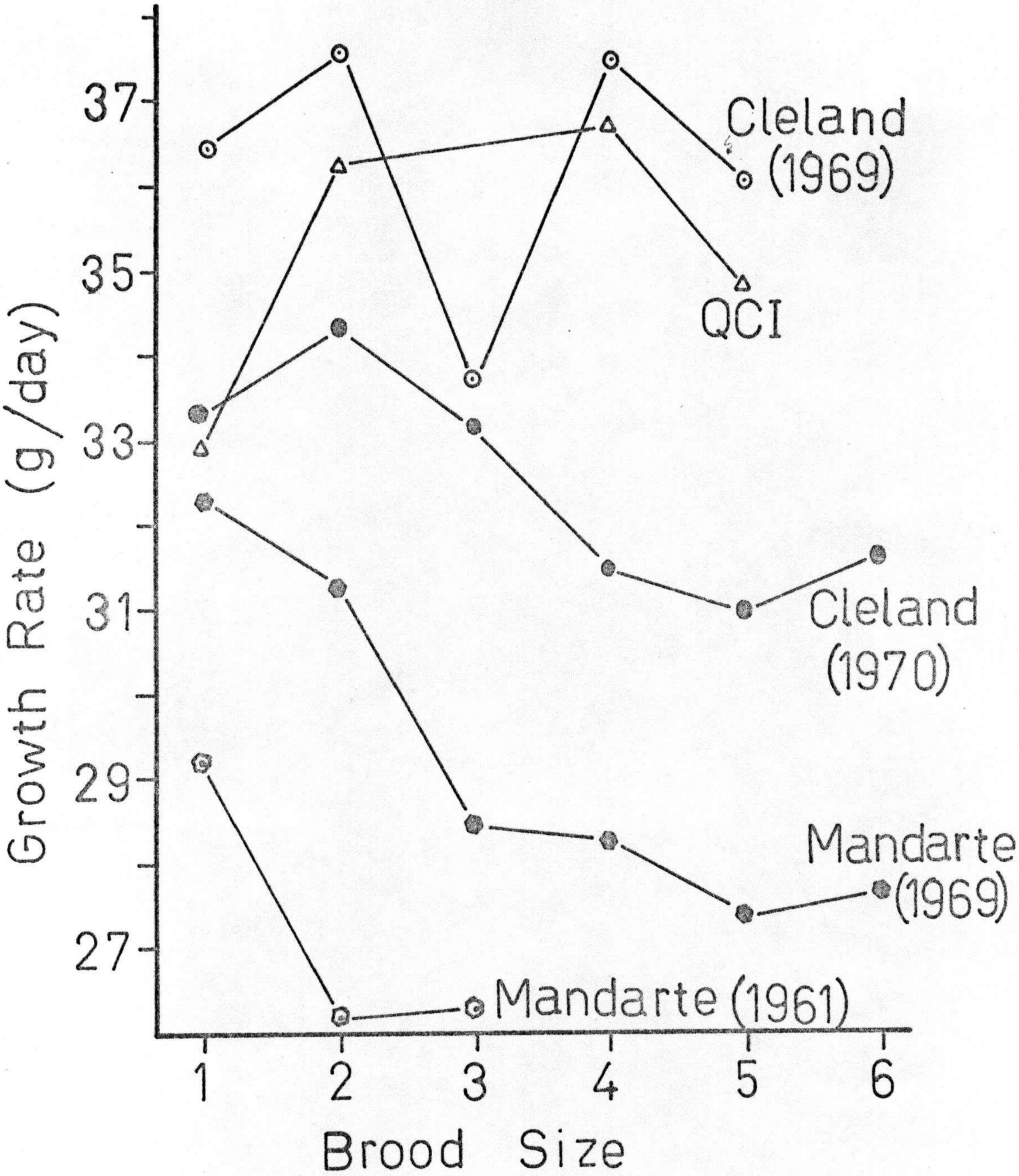


Fig. 5: Average growth rates (between 6 and 26 days of age) for different sized broods on Mandarte, Cleland, and QCI. The values for the average growth rate and their standard errors are in appendix 1.

differences ($P < 0.01$). As shown in fig. 5, Mandarte chicks always had the poorer growth rates.

For those island-years when growth was considered good (Cleland and QCI in all years), the two chick broods appeared to grow faster than the one chick broods. This difference, although it was not significant statistically, may have some biological meaning as discussed below.

The average asymptotic weights of chicks in the different brood sizes for the different island-years are shown in fig. 6. In both years on Cleland, chicks attained similar asymptotic weights for both normal and supernormal brood sizes. This weight was equal to the average adult weight of 1000 g obtained from a sample of 50 adult pairs weighed in 1969 on Mandarte. Thus in spite of the trend for a slightly slower growth rate in the larger broods on Cleland in 1970, a similar average asymptotic weight was attained in all the brood sizes. The few observations I had on the QCI chicks in 1972 indicated that the pattern of asymptotic weight with respect to brood size would be similar to that on Cleland.

A one-way analysis of variance of asymptotic weights of chicks for each of the different island-years showed significant differences ($P < 0.01$) between broods on Mandarte and on Cleland,. In contrast to Cleland the asymptotic weights of chicks on Mandarte appeared to decrease with increasing brood size in both years. These differences

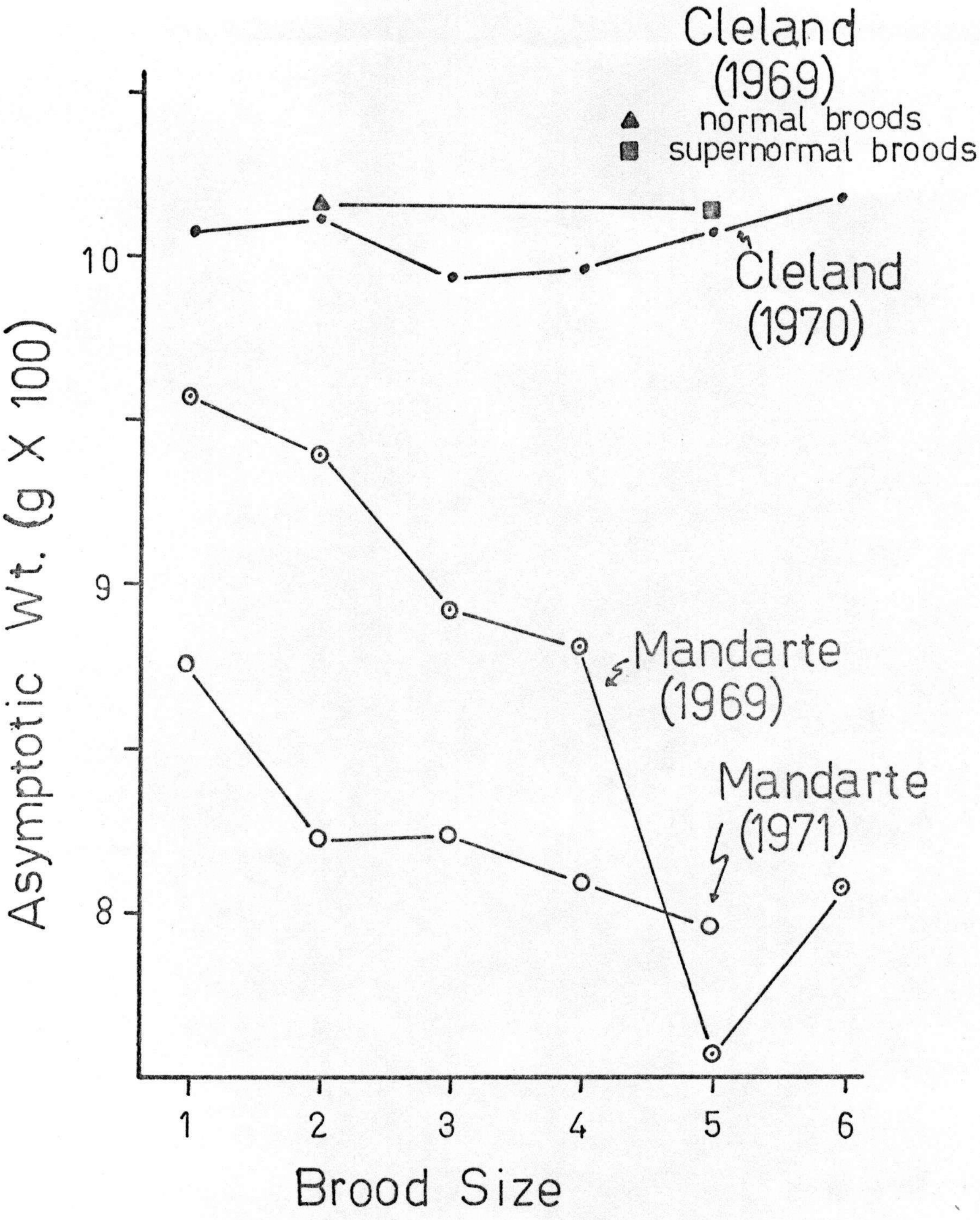


Fig. 6: Average asymptotic weights of the different brood sizes on Mandarte and Cleland. The values and standard errors are in appendix 2.

were significant (one-way analysis of variance; $P < 0.01$) in 1969 but not in 1971. On Mandarte in 1969 one and possibly two chick broods appeared to approach a maximum weight of 1000 g. This was not the case in 1971 when the average asymptotic weights of all brood sizes were well below the average adult weight.

Chicks appeared to reach an asymptotic weight (Table 2) at about 37 days of age. A one-way analysis of variance of these ages between island-years showed a significant difference ($P < 0.01$) between Mandarte in 1969 and the other two years. There were also some differences between brood sizes for each of the island-years. Generally the differences were no more than three or four days.

The growth rates given in fig. 5 do not show the pattern of growth rates for individuals in a brood. This pattern will give some indication of how a shortage of food during the chick stage will influence chick growth and most likely survival within a brood. The growth rates for individuals within a brood were ranked from fastest to slowest. The different ranks were then averaged for each brood size to obtain the data shown in Table 3. The data show that in the larger broods there was a considerable difference in growth rates between the chick ranked first and the one ranked last. On Cleland in 1970 the growth rate of the fastest growing chicks in brood sizes two to six appeared to be somewhat

Table 2

Average Age (days) (± SE) at Which the Asymptotic Weight Was Attained by Chicks in the Different Sized Broods.

Island & year	Brood Size 1	2	3	4	5	6	Average Age
Mandarte 1969	36.1 ±0.74 (19)	36.9 ±0.62 (29)	36.5 ±0.84 (26)	35.2 ±1.38 (14)	30.7 ±0.79 (24)	33.0 ±1.13 (8)	35.0 ±0.40 (120)
Mandarte 1971	38.5 ±0.72 (22)	36.4 ±0.71 (27)	36.5 ±0.52 (24)	38.2 ±1.23 (11)	40.7 ±1.39 (9)		37.6 ±0.37 (93)
Cleland 1970	36.7 ±0.38 (42)	35.8 ±0.36 (53)	36.5 ±0.39 (72)	37.7 ±0.43 (65)	37.5 ±0.55 (40)	37.6 ±0.52 (58)	36.8 ±0.24 (330)

(n) Number in bracket is sample size.

Table 3

Average Growth Rates (g/day) (±SE) and Sample Size (n) For Chicks Ranked According to Growth Rates in the Individual Broods.

Rank in brood	Brood Size 1	2	3	4	5	6
			Cleland 1970			
n =	(63)	(37)	(29)	(19)	(14)	(10)
1	33.4 ±0.64	36.5 ±0.70	36.9 ±0.59	35.6 ±0.82	34.9 ±1.38	35.2 ±2.24
2		31.9 ±0.66	33.7 ±0.70	31.7 ±1.00	32.4 ±1.42	32.2 ±1.83
3			29.5 ±0.90	29.0 ±0.90	31.0 ±1.30	29.1 ±1.85
4				24.9 ±1.33	27.7 ±1.01	26.8 ±2.87
5					25.7 ±1.01	25.3 ±1.72
6						22.5 ±1.98
			Mandarte 1969			
n =	(33)	(27)	(15)	(14)	(10)	(4)
1	32.2 ±0.99	33.6 ±0.77	33.5 ±2.65	32.3 ±0.99	30.5 ±1.96	32.1 ±2.13
2		28.2 ±0.84	27.3 ±1.49	28.9 ±0.82	27.5 ±1.94	29.3 ±1.31
3			24.0 ±1.47	26.4 ±0.92	25.1 ±1.64	27.2 ±0.91
4				23.4 ±1.04	23.3 ±1.80	25.7 ±1.27
5					20.1 ±2.07	21.0 ±2.11
6						17.5 ±1.47

faster than that for a single chick. Except for brood sizes two and three ($P < 0.01$), the differences were not significant statistically (t-Test). On Mandarte in 1969 this trend did not appear. On both Mandarte and Cleland those individuals ranked first for growth rate also had the highest average asymptotic weight (Table 4). This was similar for the other ranks in growth rates.

Some of the differences in individual growth rates within a brood will be due to competition for the available food. However, a part of this was most likely due to the differences in sex of individuals within a brood. In this species the males are heavier than the females and could be expected to have a faster growth rate. Snow (1960) showed this to be the case in the Shag *Phalacrocorax aristotelis* .

Sufficient data were also available for analyzing growth rates on Mandarte in 1969 and Cleland in 1970 according to whether broods were early or late. Broods were placed into one of the following three categories. The first, called early broods, included those broods with parents which were among the first ten percent of all pairs to lay eggs in the study area. The second, called mid-early broods, included those broods with parents among the first 10 to 50 percent. The third, called mid-late broods, had parents within the 50 to 90 percent range. No data were collected for broods with parents falling in the last 10 percent category.

Table 4

Average Asymptotic Weight (grams) (±SE) and Sample Size (n) for Chicks Ranked by Growth Rate As Shown in Table 3.

Rank in brood	Brood Size 1	2	3	4	5	6
			Cleland 1970			
n =	(34)	(19)	(23)	(15)	(5)	(4)
1	977 ±19.4	1037 ±24.0	1053 ±21.7	1092 ±29.6	1105 ±22.8	1149 ±37.6
2		969 ±25.7	989 ±21.1	1040 ±30.0	1033 ±55.3	1168 ±26.6
3			932 ±24.9	927 ±19.8	1019 ±22.2	1070 ±60.3
4				890 ±24.0	1020 ±35.6	990 ±49.7
5					899 ±15.7	945 ±37.8
6						895 ±40.7
			Mandarte 1969			
n =	(18)	(15)	(7)	*	(4)	*
1	958 ±34.2	988 ±26.1	936 ±27.3		837 ±71.5	
2		887 ±27.9	882 ±28.0		820 ±95.1	
3			865 ±38.8		749 ±63.9	
4					703 ±39.0	
5					668 ±67.8	

* Insufficient data were available for this brood size.

Growth rates for the different brood sizes with respect to the time of the breeding season are shown in Table 5 for Mandarte in 1969 and Cleland in 1970. An analysis of covariance, testing for differences in slopes with respect to time of season for each of the different brood sizes, showed no significant differences. On Mandarte in 1969 the trend was for growth rates to change as the season progressed, but the trend was not consistent for all brood sizes.

Discussion: Initially I had expected that the chicks on Mandarte would have faster growth rates than those on Cleland, since the colony was close to sources of refuse. The growth results in this study did not support this hypothesis. The growth rates and asymptotic weights on Mandarte were less than those found on Cleland in all years studied. Thus garbage, if used, did not appear to be a good food source for the Mandarte birds. This was contrary to what Spaans (1971) found for the herring gull in the Netherlands. Studies by Fordham (1964) in New Zealand and by Hunt (1972) on the east coast of the U.S.A. also indicated better breeding success on those colonies located closer to refuse dumps. The growth of chicks on Mandarte in 1962 (Vermeer's study) may have been more like that of chicks on Cleland and QCI as suggested by Vermeer's post-fledging data; however, no weight data were collected to bear this out. The decrease in asymptotic weight with increasing brood size on Mandarte suggests that these birds

Table 5

Average Growth Rates (g/day) (±SE) for The Different Brood Sizes with Respect To the Breeding Season. **

Brood Size	Early**	Mid-early**	Mid-late**
		Mandarte 1969	
1	29.6 ± 0.98	32.9 ± 1.13	33.1 ± 1.52
2	30.9 ± 0.84	32.5 ± 0.59	22.8 ± 2.64
3	30.1 ± 0.88	26.7 ± 0.94	24.9 ± 3.66
4	25.0 ± 1.45	29.4 ± 0.79	28.8 ± 0.98
5	29.4 ± 0.93	26.8 ± 0.74	26.6 ± 1.27
6	28.2 ± 3.32	27.3 ± 0.86	*
		Cleland 1970	
1	29.7 ± 1.91	33.3 ± 0.60	33.8 ± 0.86
2	34.9 ± 1.30	34.7 ± 0.53	33.9 ± 0.64
3	33.7 ± 1.10	33.3 ± 0.47	32.7 ± 0.89
4	32.5 ± 0.97	30.6 ± 0.74	32.6 ± 1.10
5	30.9 ± 1.18	30.3 ± 0.70	35.8 ± 1.47
6	32.4 ± 1.03	30.5 ± 0.68	34.8 ± 1.45

* No data available for this point.
** Explanation of early, mid-early, and mid-late on page 27.

even have trouble adequately feeding three chicks.

Harris (1964) obtained results for the herring gull similar to those on Mandarte. The herring gull chicks showed a decreasing asymptotic weight with increasing brood size for broods of one to three chicks. However, Harris concluded that food was not limiting for three reasons. (1) Single chicks should have grown faster than chicks in a brood of three if food was limiting. Harris did not think that this was occurring. (2) *Larus fuscus* (average adult weight 830 g) chicks being raised by *Larus marinus* adults (average weight 1800 g) should have received more food than normal and developed faster. This was not the case in Harris' study. (3) *Larus marinus* chicks, fostered by *L. Argentatus* and *L. Fuscus* parents, should not receive as much food as normal and grow slower. Harris' data indicated that they did not grow slower, supporting his argument. In this study I found that on Mandarte single chicks did grow faster than chicks in a brood of three although I could not show a statistical difference. In terms of Harris' first reason given above, food appeared to be limiting on Mandarte in 1969. This was most likely the case in 1971 as well.

On Cleland the data show that the adults are able to adequately feed broods up to double the normal size. All the brood sizes reached the same asymptotic weight at about the same age. In addition, the adults accomplished this result using only natural food (as is shown in the next chapter). The good conditions on Cleland applied for two successive years (1969 and 1970) in this study. Information for Cleland in 1971 (Henderson, personal communication) indicated that growth rates for a third successive year were also excellent. Thus within the limits of this study, it appears that on the average growth rates are very good on Cleland for both normal and supernormal broods. On Mandarte they are not even adequate for a brood of three. The growth results for QCI in 1972, some 300 miles north of Cleland Island, suggest that the conditions found on Cleland may be common along much of the outer coast of British Columbia.

In three different years (Cleland in 1969 and 1970, and QCI in 1972) two chick broods appeared to grow faster than one, although their asymptotic weights were not different. Harris (1964) obtained similar results for the Lesser Black-backed Gull as did Fordham (1964) for the Dominican Gull. Henderson (1972) showed that as brood size increased, the total effort required by chicks within a brood in order to elicit feeding by the parent remained the same. Thus as brood size increases, the effort required by any one chick in the brood in order to be fed decreases (assuming all chicks begging at the same time). Since the effort expended by an individual chick in order for it to be fed was dependent on its hunger level, then chicks in a brood of two would be fed at a lower hunger level than single chicks. Thus chicks in a two-brood can theoretically be fed more often. The net result of this would be a faster growth rate.

C Chick Mortality and Fledging Success

Methods: The rate of nestling mortality for different aged chicks in normal and supernormal broods was calculated using those broods for which complete data on the age of chick deaths were obtained. This excluded a number of broods for which only data on number of chicks fledging were available. Fledging success for the different brood sizes was calculated by expressing the total number fledging from each brood size as a percentage of the total number of chicks originally in that size. The log likelihood ratio test (G-test described by Sokal and Rohlf, 1969) was used to test for differences in the data for both prefledging mortality and fledging success.

Results: Detailed nestling mortality data were only available for Mandarte in 1969 and Cleland in 1970. Nestling mortality rates with respect to age and brood size are shown in table 6 for these two years. There were no differences statistically in the mortality rates between normal and supernormal broods. However, on both islands the mortality appeared to be higher in the supernormal than in the normal broods. This is reflected in the fledging success given below for all island-years. On both islands, the initially high rate of mortality in both normal and supernormal broods

Table 6

Nestling Mortality Rates for Mandarte in 1969 and Cleland in 1970. The Number of Chicks Dying during Each Age Interval is Expressed as a Percent of the Total Number of Chicks at the Beginning of the Interval.

	Mandarte 1969		Cleland 1970	
Chick Age (days)	Normal Broods	Supernormal Broods	Normal Broods	Supernormal Broods
n =	263	475	445	473
	%	%	%	%
0 - 5	6.5	8.0	5.2	4.0
6 -10	6.9	9.2	1.4	4.2
11-15	5.7	6.5	3.8	3.4
16-20	4.6	4.3	2.5	5.0
21-25	6.8	5.1	2.0	3.3
26-30	2.1	7.4	1.3	1.0
31-35	1.6	1.9	0.8	0.5
36-40	1.1	2.6	0.3	0.5
41+	2.2	5.0	0.3	0.0
Total loss	84	192	73	95
In Percent	31.9	40.4	16.4	20.1

n - Number of chicks at age 0.

appeared to continue longer in the supernormal broods. The mortality rates on both islands decreased significantly with increasing chick age (G-test; $P < 0.05$). Overall the mortality rates on Mandarte were significantly higher ($P < 0.01$) than those on Cleland.

Table 7 shows that a large percentage of the chick deaths occurring on Mandarte and Cleland were due to pecking by other gulls. Rain appeared to cause relatively more deaths on Cleland than on Mandarte.

Fledging success, which is an indirect measure of nestling mortality, appeared to decline with increasing brood size in all years recorded (fig. 7) except 1962 (Vermeer's study). The differences in fledging success among the brood sizes for each island-year were significant (G-test) for Mandarte in 1969 and 1971 ($P<0.01$), and Cleland in 1970 ($P<0.025$). Broods on Cleland in 1970 and QCI in 1972 had a higher overall fledging success ($P < 0.01$) than did those on Mandarte in 1969, 1971, and 1962.

Discussion: In this study the pattern of mortality of chicks with respect to age does not differ greatly from that of other gull studies (Paynter, 1949; Paludan, 1951; Fordham, 1964; Vermeer, 1967; Parsons, 1971). These studies also showed that the highest mortality rates occurred in the chicks' first two weeks of life. Most likely the chicks' small size plays a large part in their vulnerability to both

Table 7

Percentage of Deaths Due to Different Factors on Mandarte in 1969 and Cleland in 1970.

Cause of Death	Mandarte 1969 Normal Broods	Mandarte 1969 Supernormal Broods	Cleland 1970 Normal Broods	Cleland 1970 Supernormal Broods
n =	84	192	73	95
	%	%	%	%
Killed by Gulls	59.5	66.7	42.5	40.0
Heavy Rain	1.2	3.0	20.5	25.3
Disappeared*	15.5	8.3	1.4	10.5
Unknown*	23.8	22.0	35.6	24.2

*disappeared: The chick disappeared and was assumed to be dead. No carcass was found.
*unknown: Carcass of dead chick found, but cause of death was not known.

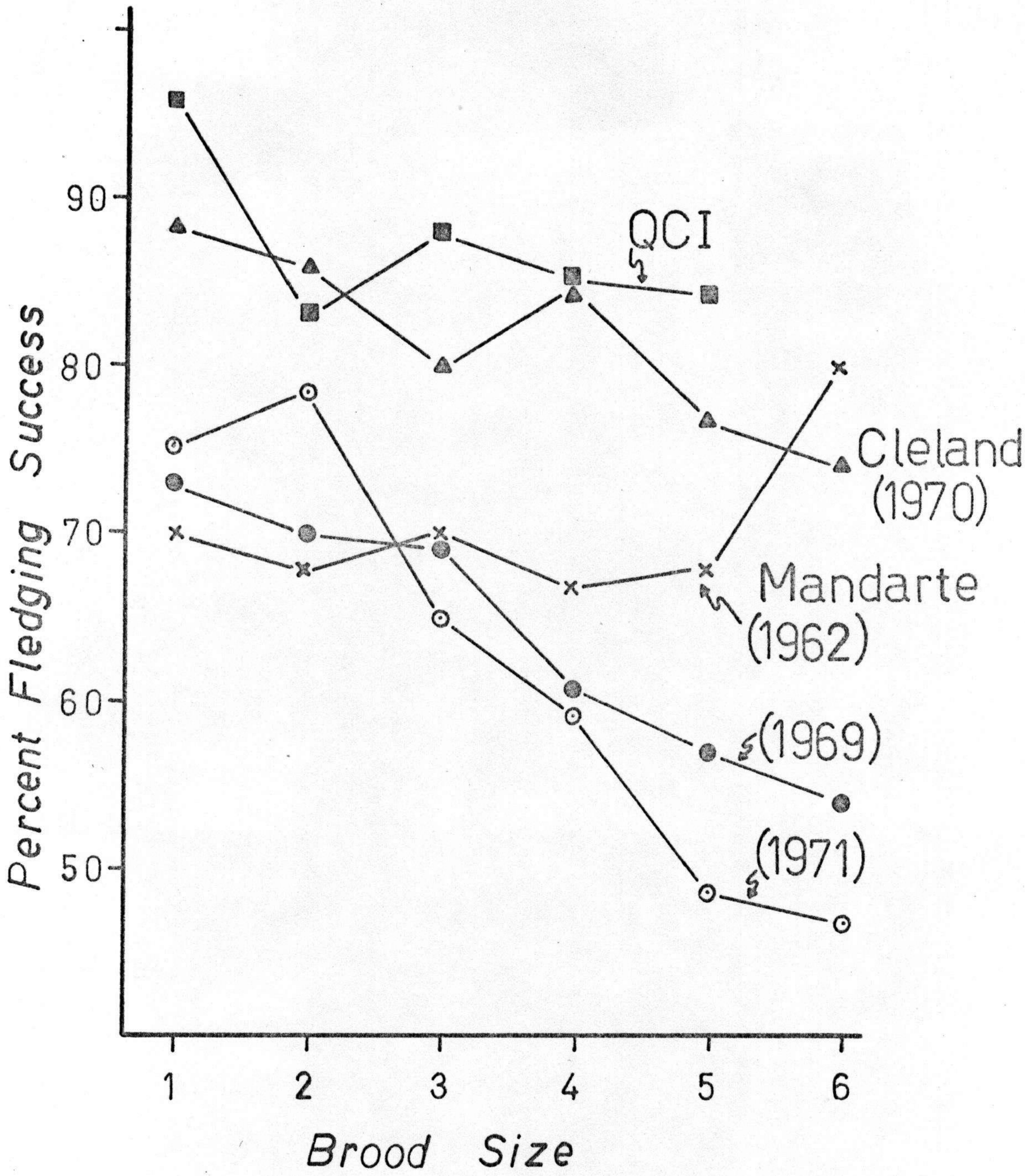


Fig. 7: Percentage fledging success for the different brood sizes on Mandarte, Cleland, and QCI.

attacks by other gulls and the weather. Harris and Plumb (1965) found that very young herring gull chicks in the supernormal broods suffered a high mortality relative to normal broods in a year of inclement weather. The adult birds were unable to adequately cover more than three chicks at one time because only one bird brooded the chicks at any one time. This study also showed that inclement weather can affect the mortality of young gulls. In this study the longer period of high mortality rates in supernormal broods could be a consequence of their slower growth. This would mean that the chicks are in a vulnerable size category for a longer period of time.

The reason for the lower mortality on Cleland and QCI than on Mandarte is not known, although it could be due to several factors. (1) The lower nest densities on Cleland and QCI may lower the number of adult-chick encounters. (2) Faster growth rates on these islands in general may result in healthier chicks better able to withstand inclement weather and/or attacks by other adults. (3) Perhaps there is better parental attendance on Cleland and QCI because food is more available and thus requires less time to obtain, as is shown in the next chapter. Fordham (1964) also noted that chick mortality due to attacks by adults increased when the food supply for a colony decreased.

The important consideration in this section is the fledging success and its relation to brood size. Contrary to Vermeer's findings, the percent fledging success decreased with increasing brood size on both Cleland and Mandarte. This type of trend is the one most commonly found in the literature. However, it should be kept in mind that although the percent fledging success decreased with increasing brood size, the absolute numbers of chicks fledged per brood size actually increased in all years (fig. 8).

Part of the decrease in fledging success with respect to brood size in this study may have been due to the disturbance during weighing. However, if this disturbance did have a deleterious affect, it operated only on the larger brcod sizes (4 to 6). There was no difference between this study and Vermeer's for normal sized broods on Mandarte. Even in 1971 on Mandarte when the chicks were not weighed until 30 days of age, the fledging success decreased with increasing brood size. In the larger broods the number of hiding spots within a territory may become critical resulting in chicks leaving the territory to hide when there is a disturbance. This in turn would increase their chances of being attacked by neighbouring gulls. Interestingly, the percent fledging success for a brood of six chicks on Cleland is still as high or higher than that reported in the literature for normal sized broods.

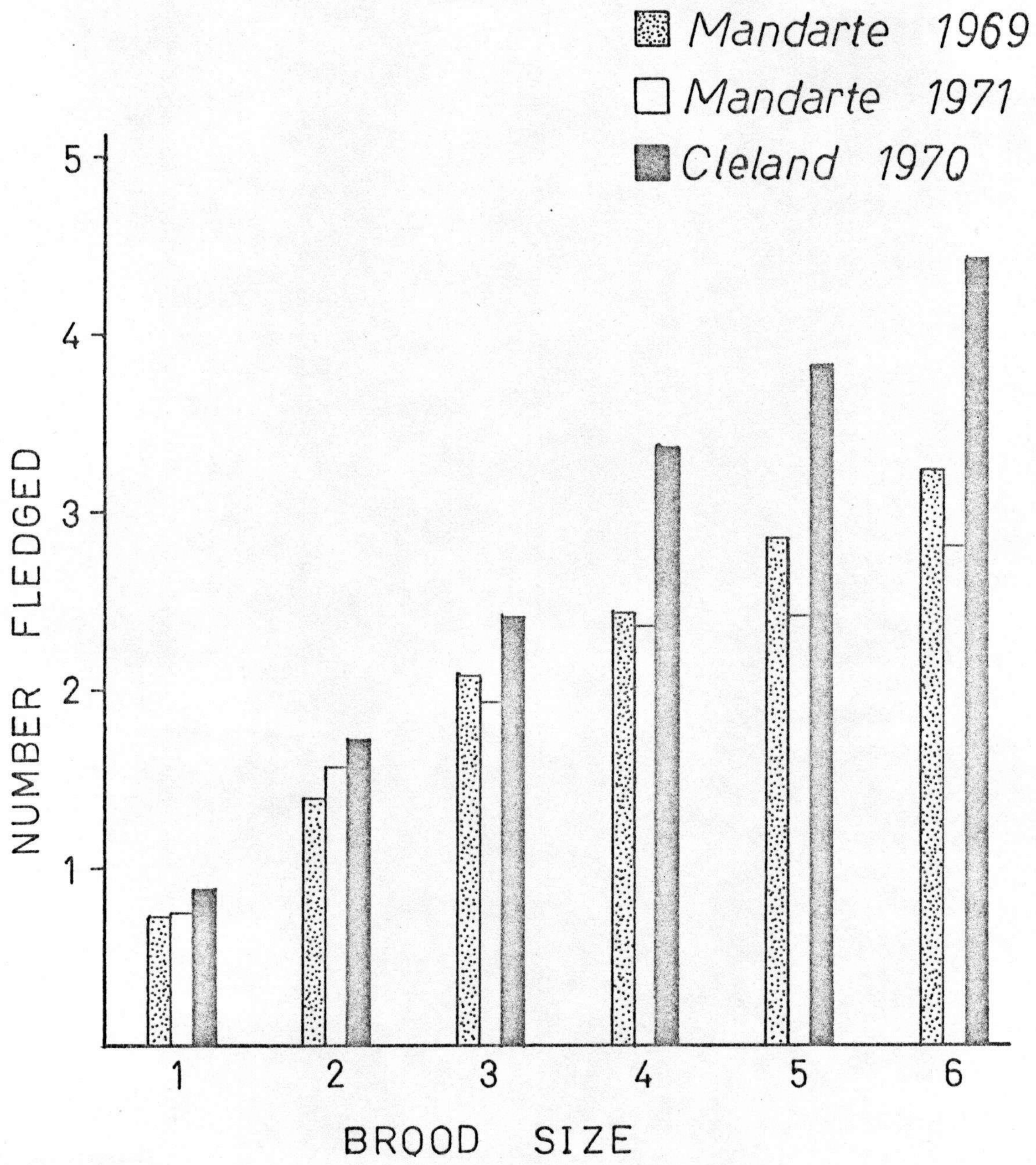


Fig. 8: Absolute numbers of chicks fledged for the different brood sizes on Mandarte and Cleland.

D Post-fledging Success

Methods: As many chicks as possible from different brood sizes were banded in 1969 and 1971 on Mandarte and in 1970 on Cleland. Estimates of post-fledging survival were derived from returns for these banded birds. I received some band returns for dead birds, but by far the most profitable returns were the live sightings (bands read with a telescope). The majority of these sightings were made by Ian MacGregor at refuse sites located between Vancouver and Seattle. Although the number of live returns for Mandarte was reasonably large (> 50 per cohort banded), the return for Cleland birds was small (16 out of 600 bands). Apparently the juveniles from Cleland Island do not come into the Puget Sound-Georgia Strait area in any number. Most of the 16 returns were obtained by MacGregor along the outer coast of the states of Washington and Oregon. The analysis of the sightings were done with respect to the brood size the chicks were in at the time the brood was initially set up. The first year survival rate is assumed to be proportional to the percentage of birds seen alive away from the breeding colony. In addition, Vermeer's data were reanalyzed incorporating the sightings of birds obtained in subsequent years.

Results: The results are shown in Table 8. On Mandarte in 1969 and 1971 the post-fledging survival for chicks in normal broods was higher than for those in supernormal broods.

Table 8

Percentage Survival Rates of First Year Birds as Related to Brood Size. These Survival Values Are Based on the Number of Live Sightings of Birds Away from the Colony.

Island & Year	Brood Size 1	2	3	4	5	6
Mandarte **	27.7	30.8	28.6	12.5	16.7	
1962	(47)	(146)	(171)	(120)	(90)	
Mandarte *	31.0	40.4	21.0	13.5	15.0	19.7
1969	(29)	(47)	(57)	(52)	(40)	(71)
Mandarte	20.0	21.0	20.0	13.0	8.0	10.0
1971	(100)	(109)	(93)	(82)	(72)	(81)
Cleland #		2.6			3.0	
1970		(267)			(300)	

* The differences in post-fledging survival rates between broods significant at $P < 0.025$ (G-test).

** The differences in post-fledging survival rates between broods significant at $P < 0.01$ (G-test).

(n) Number in bracket is the total number banded for that brood size.

\# Data combined for both normal and supernormal.

In 1969 the differences were significant (G-test; $P < 0.025$). There was no difference in post-fledging survival between normal and supernormal broods on Cleland in 1970. The analysis of returns for the chicks produced on Mandarte in 1962 showed that the survival for normal broods was significantly better ($P < 0.01$) than that for supernormal broods.

Table 9 shows a comparison of the average asymptotic weight (given in Appendix 2) for the different brood sizes on Mandarte (1969 and 1971) and the average weight of those birds seen alive away from the island. Although the sample size was small, the data suggest that the heavier birds had the best chance of surviving after fledging.

Table 10 shows the relative number of young per brood size that should survive to breeding. I have assumed that the recovery rates are proportional to the actual survival rates of the birds in their first year of life and that mortality in subsequent years is independent of brood size. In 1962 and 1971 on Mandarte, the broods of three chicks would contribute the greatest number of individuals to future breeding populations. In 1969 on Mandarte and 1970 on Cleland, a brood of six would contribute the most young.

<u>Discussion</u>: The data in this study suggest that the post-fledging survival of gull chicks was dependent on the asymptotic weight they attained prior to fledging. On Cleland

Table 9

Average Asymptotic Weight (grams) (±SE) of all Individuals for Different Brood Sizes Compared With the Averaged Asymptotic Weight of Those Individuals Seen Alive Away from the Colony For Mandarte in 1969 and 1971.

	Mandarte 1969		Mandarte 1971	
Brood Size	All Chicks	Fledged Chicks	All Chicks	Fledged Chicks
1	958 ± 32.9 (19)	988 ± 37.8 (7)	877 ± 28.3 (22)	957 ± 88.8 (5)
2	941 ± 21.5 (29)	943 ± 36.3 (14)	824 ± 30.5 (27)	867 ± 100.8 (4)
3	894 ± 16.3 (26)	944 ± 17.2 (8)	825 ± 31.8 (24)	965 ± 54.6 (3)
4	882 ± 38.5 (14)		810 ± 35.9 (11)	823 ± 65.2 * (4)
5	756 ± 27.3 (24)	894 ± 55.7 * (8)	797 ± 35.9 (9)	
6	809 ± 34.3 (8)			

* All supernormal chicks sighted were averaged to obtain this value.
(n) Number of individuals sighted for which asymptotic weights were available.

Table 10

Theoretical Contribution to Future Breeding Populations for Broods one to six on Mandarte in 1962, 1969, and 1971, And Cleland in 1970.

	Brood Size					
	1	2	3	4	5	6
			Mandarte 1962			
No. Of Chicks Fledged	0.73	1.40	2.10	2.70	3.40	4.80
Index of Chicks Surviving to Breeding *	0.19	0.43	<u>0.60</u>	0.34	0.57	-
			Mandarte 1969			
No. Of Chicks Fledged	0.70	1.40	2.07	2.44	2.85	3.24
Index of Chicks Surviving to Breeding *	0.22	0.57	0.44	0.33	0.43	<u>0.64</u>
			Mandarte 1971			
No. Of Chicks Fledged	0.75	1.56	1.95	2.36	2.43	2.81
Index of Chicks Surviving to Breeding *	0.15	0.33	<u>0.39</u>	0.31	0.29	0.28
			Cleland 1970			
No. Of Chicks Fledged	0.88	1.72	2.41	3.38	3.84	4.45
Index of Chicks Surviving to Breeding *	0.25	0.45	0.67	0.90	1.05	<u>1.26</u>

* Index is based on the number of sightings of birds away from the colony. It is assumed that there were no differences in the mortality after the first year.

where all brood sizes attained similar asymptotic weights, the post-fledging success did not differ between normal and supernormal broods. On Mandarte those broods with heavier asymptotic weights also had higher post-fledging survival rates associated with them. The detailed study on this aspect in the Great Tit by Perrins (1965) showed that post-fledging survival was influenced by the fledging weight. The heavier nestlings had the highest chances of survival in all years with the lighter individuals having a variable survival depending on the year.

In both 1969 and 1971 on Mandarte, single brooded chicks had the heaviest asymptotic weight suggesting that they should also have the highest post-fledging success. This was not the case for either year. Perhaps the chicks raised by themselves are at a disadvantage when competing for food after fledging, since they never had to compete with nest-mates as chicks.

The results Vermeer obtained in 1962 on post-fledging success (supernormal broods better than normal ones) were changed by later recoveries. However, I do not think the trends in post-fledging survival for Mandarte birds in this study will be changed by later returns. An explanation for Vermeer's results may lie in the nature of his sightings. He only had a small number of returns (<15% as opposed to up to 40% for this study) and all were from the Vancouver refuse dump or nearby parks in Vancouver. By chance there may have been more birds from supernormal broods than from normal ones at these sites. In this study, returns were obtained from many different places along the west coast. The later recoveries of Vermeer's birds included sightings at other places including sightings of these birds as adults on the colony. Vermeer had no weight data on his birds and this would indicate whether the result he got was logical. In this study the survival rates corresponded with the asymptotic weights. In addition, I reanalyzed my data omitting the returns during September and October, the months when the largest amount of first year mortality occurs (van Tets, 1968). The trends in the data were not changed by this procedure.

In actual fact then, Vermeer's experiment did support Lack's hypothesis, as did the data from Mandarte in 1971. In both these years a brood of three was the optimal size. In 1969 on Mandarte, a brood of six chicks would have contributed the largest number of progeny, although the broods of two were close behind. However, I think it is likely that adult gulls could not evolve a brood patch capable of successfully incubating six large eggs. If the gull evolved smaller eggs, in order to accommodate them all, the prefledging mortality could possibly increase as suggested in a study by Parsons (1971). He found that the survival of chicks from the 'C' egg which is the smallest egg was also the lowest. This would then remove the advantage gained by having a clutch of six eggs. If a clutch of six large eggs is dismissed as being impossible, then a two egg clutch was optimal on Mandarte in 1969. All the results from Mandarte, then, support Lack's hypothesis concerning the ability of parents to satisfactorily feed larger than normal numbers of offspring.

This was not the case for gulls on Cleland and perhaps for much of the west coast of British Columbia, if QCI can be considered typical of other colonies. In these places the contribution to future breeding populations by different brood sizes increased with each additional young added to the brood size. Although I discounted the possibility of a six brood on Mandarte and this would also apply for Cleland, it is quite conceivable for a gull to evolve brood patches capable of accommodating four eggs. This is perhaps demonstrated best by the shorebirds which have a brood patch arrangement such that they can incubate four large eggs (Lack, 1968). It would appear then that the results from Cleland do not support Lack's hypothesis. There are a number of reasons put forth in the literature which might account for this discrepancy. Because some of these involve the food supply, this part of the discussion will be dealt with at the end of the next chapter which describes the food situation on the different colonies.

E Summary

Experiments using the Glaucous-winged Gull were carried out in order to test Lack's hypothesis on the evolution of clutch-size. Previous experiments had shown that this species could raise extra chicks but that the birds may have used refuse sites as a food source. In this study, experiments were carried out on both an island (Mandarte) where refuse is available to the birds and on islands (Cleland and QCI) where generally only natural food is available to the birds. Broods of one to six chicks were set up in the experiment in which growth rates, asymptotic weights, nestling mortality rates, fledging success, and post-fledging success were measured. Growth rates were best on Cleland and QCI in all years. Asymptotic weights of chicks in all brood sizes on Cleland and possibly QCI were equal to the average adult weight (1000 g). On Mandarte the chicks had significantly lighter asymptotic weights than those chicks on Cleland. Fledging success, which appeared to decrease with brood size, was significantly better on Cleland and QCI than on Mandarte. The absolute numbers of chicks fledged per brood size increased with brood size for all islands and years. Post-fledging survival was the same for normal and supernormal broods on Cleland. On Mandarte post-fledging survival was higher in normal broods than in supernormal broods. On Cleland the supernormal broods contributed the greatest number of individuals to future breeding populations. On Mandarte, normal broods contributed

the greatest number. Thus the results from Mandarte did support Lack's hypopothesis; but this was not the case for Cleland where the most productive brood size was larger than the most common.

CHAPTER III

Food Utilized By Breeding Gulls

A Introduction

The Glaucous-winged Gull, like the other gull species, is able to swallow food at the time of catching it and then regurgitate it for the young at the nest. Limited observation using scales placed in the territory of individual pairs showed that the birds could bring back a quantitiy of food weighing up to 20 percent of their own body weight. The number of such trips that the bird can make in a day will be determined by both the ease at which they can find the food and the distance the food is located from the colony.

Lack (1966) objected to Vermeer's chick addition experiment because it was conceivable that the adult gulls obtained large quantities of food at nearby refuse sources. As shown in the last chapter, on reanalysis, the results of Vermeer's experiment were not contrary to Lack's hypothesis on the evolution of clutch-size. As will be shown in this chapter, Lack's criticism concerning the use of refuse also turns out to be incorrect.

This chapter describes the food situation on the different islands studied, showing that the initial assumptions (see page 8) were correct concerning the type of food fed to the chicks on the different islands. Information is also presented on the relative availability of foods used on the different islands.

B Diet of Adult Gulls Prior to Chick Hatching

Methods: The fact that gulls regurgitate any undigested material in the form of a pellet lends itself as a means of testing, although not critically, for the presence or absence of garbage in their diet. An analysis of pellets collected on Mandarte in 1969 and Cleland in 1970 was carried out in order to determine the presence or absence of refuse in their diet. These pellets were collected on plots between May 11 and June 19 on Mandarte and between May 18 and June 22 on Cleland.

Results: Pellets of adult gulls on Mandarte in 1969 consisted of about 60 percent garbage (Table 11). The garbage found in the pellets included chicken, beef, and pork bones, paper, bottle caps, bits of glass, and string. On Cleland in 1970 there was less than one percent refuse in the pellets collected. Here the refuse was paper although the occasional beef or pork bone was seen outside the plots.

Discussion: This technique does not give absolute values for the use made of different food types. However the results did indicate that, prior to chick hatching, the gulls used far more refuse on Mandarte than they did on Cleland. Fish offal, if used by the Cleland birds, would not show up in the pellets and thus result in a bias towards natural foods.

Table 11

Pellets Collected on Mandarte in 1969 and Cleland in 1970 Classified as to Whether Garbage or Non-garbage Items. A More Complete Listing of Species of Natural Food Is Found in Appendix 4.

	Mandarte 1969				
Food Type	May 11-17	May 18-24	May 25-31	June 1-8	June 9-19
	%	%	%	%	%
Garbage	65.9	67.5	68.2	56.9	60.0
Natural	34.1	32.5	31.8	43.1	40.0
n =	473	1054	1110	1087	473

	Cleland 1970					
Food Type	May 18	May 24	May 31	June 8	June 15	June 22
	%	%	%	%	%	%
Garbage	0.7	0.5	0.0	0.0	0.0	0.0
Natural	99.3	99.5	100.0	100.0	100.0	100.0
n =	240	182	197	217	78	53

Observations by Henderson (1972) on the stomach contents of incubating gulls showed that the Cleland birds contained only Pacific Sandlance Ammodytes hexapterus whereas the Mandarte birds contained 29 percent garbage and the remainder natural food. This supports the basic conclusion drawn from the pellet counts that, prior to chick hatching, the birds on Mandarte use garbage in fairly substantial amounts whereas on Cleland they use very little.

C Chick Regurgitations

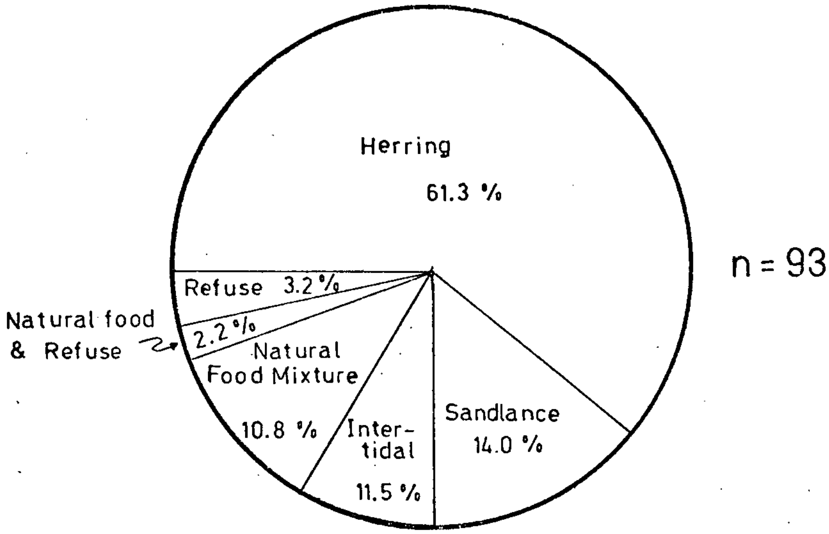
Methods: Gull chicks, when being handled, will occasionally regurgitate the food they have in their proventriculus. This provides an opportunity to determine the composition of food fed to the chicks by the adults. One objection to this method is the question of whether all food types are regurgitated by the chicks with equal ease. The work of Spaans (1971) indicated that they probably are.

During the regular weighing of chicks on Mandarte in 1969, Cleland in 1970, and QCI in 1972, all chick regurgitations were identified and recorded.

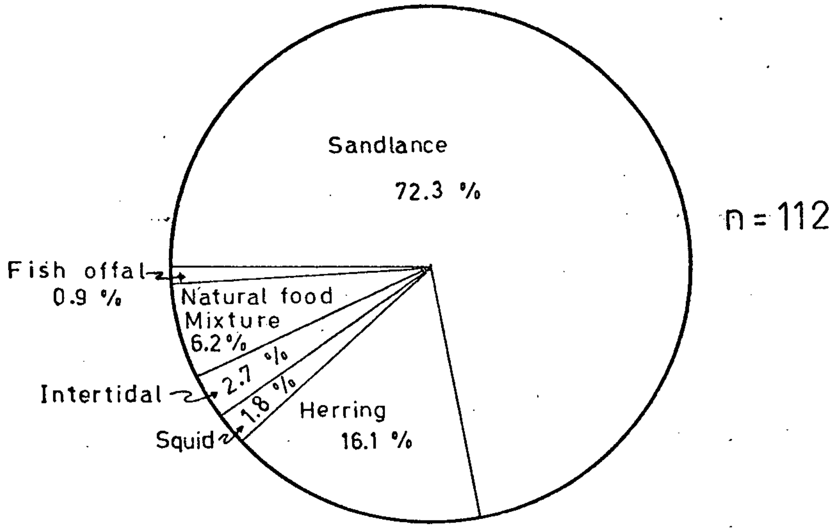
Results: On Mandarte in 1969 the majority of regurgitations were Pacific Herring Clupea pallasii (61.3 percent) (fig. 9). Refuse was only regurgitated 5.4 percent of the time. On Cleland in 1970 the majority of the regurgitations were Pacific Sandlance (72.3 percent). Fish

Figure 9: Percentage composition of food types found in chick regurgitations on Mandarte, Cleland, and QCI.

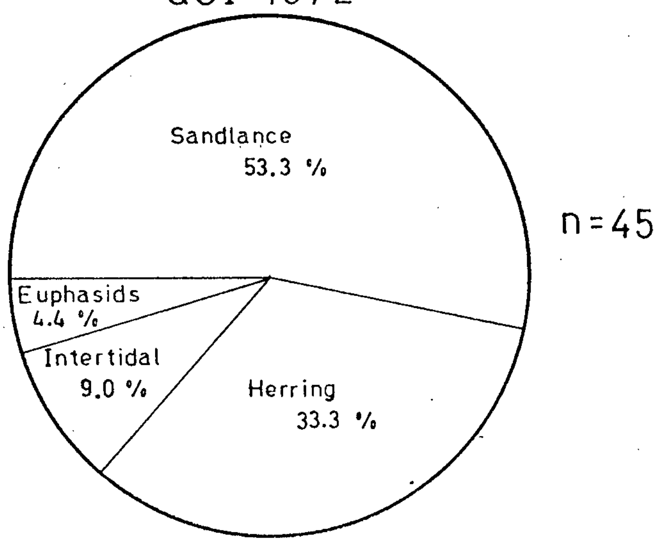
Mandarte 1969



Cleland 1970



QCI 1972



offal was found only once (0.9 percent). On QCI in 1972 sandlance and herring made up 86.6 percent of the regurgitations. The remainder were either intertidal organisms or small euphausids.

Discussion: These data also support the assumptions made at the start of the study concerning the usage of garbage on the different islands. Henderson (1972) systematically sampled chicks in 1970 on Mandarte Island, removing the food from their gullet. He obtained results similar to the chick regurgitations on Mandarte in 1969. These data also support the contention of Spaans that the use of chick regurgitations as a method of determining the diet of gull chicks does not differ greatly from the results obtained by directly sampling the gut contents of chicks.

On Cleland in 1970, fish offal was very rarely fed to the chicks. Observations by Henderson in 1971 on Cleland also supported this conclusion. During his observations, he saw no fish offal being fed (personal communication). Thus the birds on Cleland and QCI did not need mans' refuse in order to be able to adequately feed up to twice the normal number of chicks.

D Feeding Observations on Mandarte in 1971

<u>Introduction</u>: The growth results from Mandarte in 1969 indicated that the adults there were having difficulties feeding more than three chicks. According to Lack's criticism mentioned earlier, this should not have been the case. In 1971 on Mandarte a more detailed study was carried out on the food fed to the chicks in order to learn why. I wanted to know if garbage was fed more often to supernormal broods than to normal broods, and whether less time was required for the adults to obtain refuse than to obtain natural food. In addition, information was obtained both on the amount of time spent by adults in obtaining food for their chicks with respect to the brood size, and on the frequency of food types found in the chicks' diet.

<u>Methods</u>: Direct observations were made on pairs of gulls and their chicks in order to answer the above questions. There was a good opportunity to identify the food fed to the chicks by the adults because it was regurgitated before it had been digested to any extent. However, this method did have two disadvantages. First I could not see what was regurgitated in all the feedings because the view was partially obstructed either by grass or by the chicks themselves. In the analysis I assumed that the frequency of the unseen food types was similar to that seen by myself. Secondly, the proportion of food fed by frequency and by

weight may differ. I have a small amount of data suggesting that less garbage by weight than fish was brought back from a foraging trip. The weight of fish brought back from a foraging trip averaged 150 g (n = 10) whereas garbage averaged only 107 g (n = 7). A subjective impression of the weight of these two food types brought back per trip conformed with this as well. Thus the evidence suggests that perhaps garbage was overestimated by the frequency occurrence method and not underestimated.

Observations were made on 42 different pairs of gulls situated around three different blinds. ApppRoximately equal numbers of broods of one to six chicks were set up around each blind, although subsequent chick mortality changed these figures. Observation periods extended continuously from 0400 to 2200 hours and were made at each blind at six to eight day intervals. A total of 11 days of observation was obtained between June 23 and July 25. I recorded the arrivals and departures of the adult gulls being observed and the food they fed to their chicks.

Sixteen hours of similar observations (two eight hour periods) were carried out both on Mandarte in 1969 and on QCI in 1972. The absence of an adult was classified as a foraging absence only if the bird returned and fed the chicks with relatively undigested food.

Results:

(i) Foraging Absences: The average duration of a foraging absence or trip by adults with normal or supernormal broods on Mandarte, Cleland, and QCI are presented in table 12. I have included Henderson's (1972) data here for ease of comparison. Overall the Mandarte gulls spent more time on an individual foraging trip than did those on Cleland or QCI. The duration of a trip on Mandarte in 1971 was the longest (t-Test; $P < 0.01$) for all the years and places studied. The data also show a difference between parents of normal and supernormal broods, but it is not consistent from island to island and from year to year. With the exception of QCI none of the differences are significant statistically.

Discussion: Henderson (1972) suggested that adults with supernormal broods spend less time per foraging trip than do adults with normal sized broods. He theorized that the increased stimulation resulting from the extra chicks caused the adults to return sooner regardless of the amount of food they had obtained. The results of this study do not support his hypothesis. The data on foraging absences for Mandarte in 1971 showed no difference between parents with normal and supernormal broods. The data on QCI showed a significant difference between adults with normal and supernormal broods, but the adults with supernormal broods spent more time per foraging trip rather than less time as suggested by Henderson. The adults with supernormal broods on Mandarte in 1969 also

Table 12

Average Duration of Foraging Absences (±SE) for Adults with both Normal and Supernormal Broods.

Island & Year	Normal Broods (1 - 3) (minutes)		Supernormal Broods (4 - 6) (minutes)
Mandarte 1969	123 ± 8.0 (24)		140 ± 3.6 (13)
Mandarte 1970 #	156 ± 34.4 (22)		91 ± 5.1 (35)
Mandarte 1971 **	194 ± 6.6 (335)		194 ± 8.0 (275)
Cleland 1971 #	122 ± 13.2 (42)		93 ± 6.9 (86)
QCI 1972	69 ± 5.7 (20)	*	101 ± 12.6 (13)

Data from Henderson, 1972.
(n) Number in bracket is sample size.
* Difference between normal and supernormal broods significant (P<0.01) using t-Test.
** Mandarte 1971 significantly different from any of the other island-years (P<0.01) using t-Test.

appeared to be spending more time per trip than adults with normal broods. The situation does not appear to be a simple one and may be complicated by the availability of food. On Mandarte in 1971 the time spent on a foraging trip was relatively long. On QCI in 1972 it was relatively short. Henderson's conclusions were based on situations where the foraging time was intermediate between these two extremes.

The greater amount of time taken per foraging trip by adults on Mandarte suggest as do the growth data that food was harder to obtain there than it was on Cleland or QCI. More information on this aspect is given below.

(ii) Foraging Trips on Mandarte in 1971: In this particular year there were sufficient data for an analysis of the duration of the foraging trips with respect to the age of the chicks. Data in Table 13 show an increase in the average time taken with increasing chick age for both normal and supernormal broods. A linear regression of the duration of foraging trips on chick age showed a significant positive slope for both types of broods ($P < 0.01$). However, there were no differences in slopes between adults with normal broods and adults with supernormal broods.

The data collected in 1971 were also analyzed to see if the total amount of time spent foraging each day by adults changed as the brood size increased or as the chicks got older. Each pair of birds had a possible total of 36 hours

Table 13

Change in Length of Average Foraging Trips (minutes) (±SE) with Chick Age for Both Normal And Supernormal Broods On Mandarte in 1971.

	Chick Age (days)				
Brood Size	0-5	6-12	13-19	20-26	27+
Normal (1-3 chicks)	145 ±16.2 (32)	177 ±12.9 (61)	188 ±15.5 (50)	208 ±16.8 (58)	224 ±29.7 (20)
Supernormal (4-6 chicks)	158 ±27.3 (46)	195 ±15.7 (59)	208 ±30.1 (62)	221 ±74.3 (19)	217 ±47.2 (13)

(n) Number in bracket indicates the sample size.

Regression equations: normal - Y=142+3.4X
supernormal - Y=153+3.4X

each day in which to forage for food. A bird's foraging day was considered to extend from 0400 to 2200 hours (18 hours). If both members of a pair foraged continuously for the whole day, their total time spent foraging would be 36 hours. This never happened. Generally only one bird would forage at any particular time, although often in larger broods and the broods with older chicks, both members of a pair would be away foraging at the same time. The total amount of time spent foraging each day by a pair (fig. 10), on average, increased with increasing chick age and also with increasing brood size. A linear regression of these times on increasing chick age for each brood size (5 and 6 combined) was significant ($P < 0.01$) for broods four and five and just over the five percent level for broods of three ($P = 0.052$). There was not a significant slope for broods of one and two chicks. The slope of a regression of these times on brood size was also significant ($P < 0.01$).

The average number of foraging trips made daily by adults for the different brood sizes did not appear to change with chick age (Table 14). However, the number of trips made by adults did increase with increasing brood size. A two-way analysis of variance showed that there were no differences in the number of trips made daily with respect to the chick age but that there were differences associated with the brood size ($P < 0.01$).

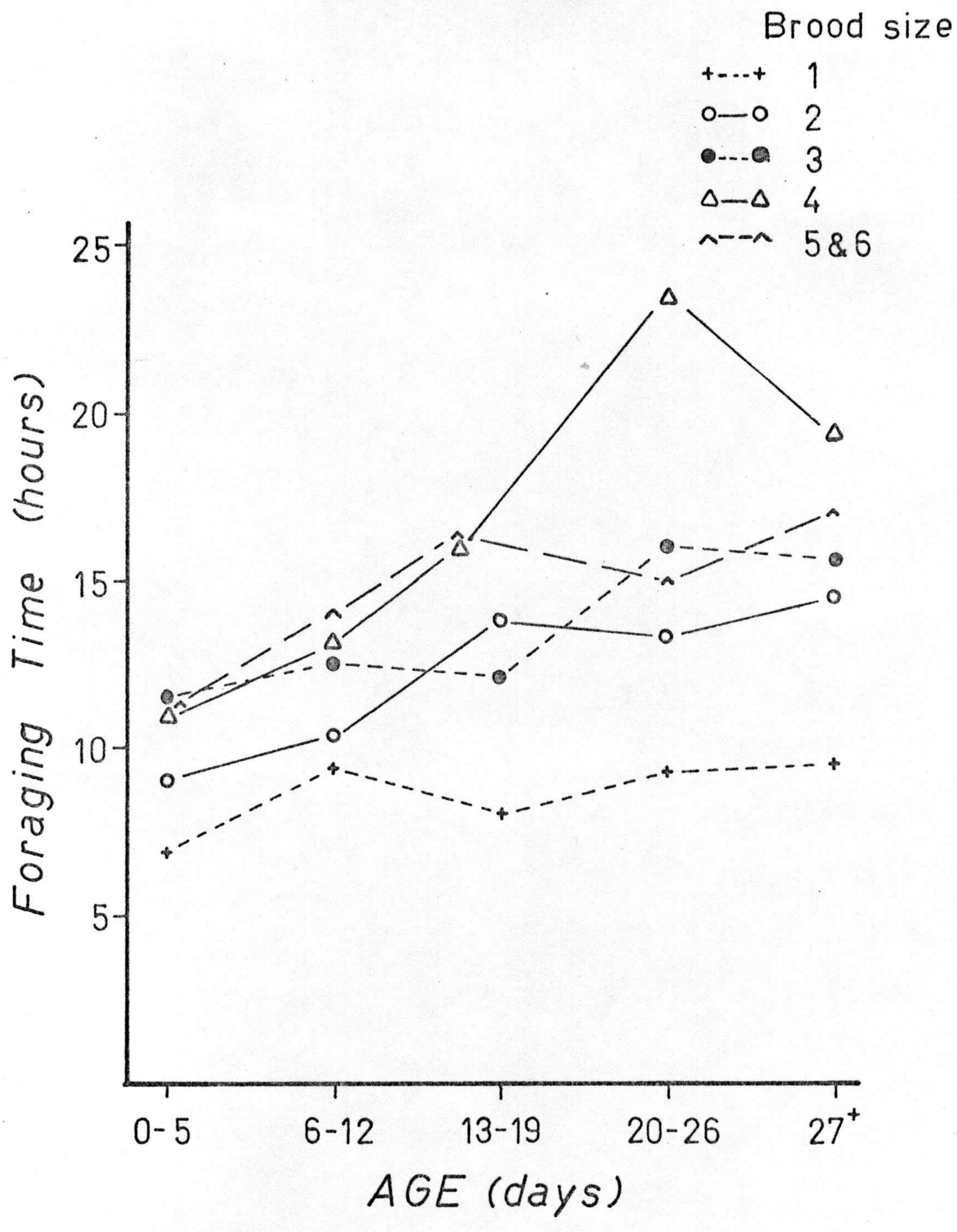


Fig. 10: Change in average total time spent foraging each day by a pair with respect to the age of the chicks and the various brood sizes.

Table 14

Average Number (±SE) of Foraging Trips Made per Day By Adults with Respect to the Age of the Chicks And the Brood Size.

Chick Age	Brood Size 1	2	3	4	5 & 6
(days)					
0-5	2.4 ±.50 (5)	4.5 ±.50 (2)	4.6 ±.64 (7)	4.0 ±.89 (5)	4.4 ±.85 (9)
6-12	3.2 ±.46 (10)	2.9 ±.34 (7)	5.0 ±.69 (7)	3.9 ±.34 (10)	4.8 ±.72 (9)
13-19	2.8 ±.31 (8)	4.0 ±.57 (6)	3.9 ±.40 (7)	4.4 ±.50 (9)	5.1 ±.58 (8)
20-26	2.8 ±.32 (10)	3.3 ±.42 (6)	4.8 ±.36 (8)	5.0 ±.00 (2)	4.3 ±.85 (4)
27+	1.8 ±.37 (5)	3.7 ±.88 (3)	3.6 ±.88 (3)	4.5 ±.50 (2)	4.5 ±1.50 (2)
Average no. of Trips/day Over Season	2.7 ±.18	3.5 ±.24	4.5 ±.25	4.2 ±.25	4.7 ±.35

(n) sample size

Henderson (1972) also found that the number of foraging trips increased with increasing brood size. However, the trend he found was much more marked than the one in this study. As is shown in the next section, the increases with chick age in the total amount of time spent foraging daily by adults is linked with the change in the diet since the number of trips made per day did not change.

(iii) <u>Food Utilization and Availability</u>: The frequency at which garbage was brought back to the chicks (fig. 11) increased with increasing chick age for both normal and supernormal broods. There were no differences (G-statistic, Sokal and Rohlf, 1969) between normal and supernormal broods regarding the frequency of trips in which garbage was brought back to the chicks. However, there was a trend for parents with supernormal broods to bring back more garbage at an earlier chick age than the adults with normal broods. The majority of the category "fish" was made up of Pacific Herring. A more detailed listing of the food fed the chicks is given in appendix 5.

In this study the amount of time taken to obtain a food type (foraging trip) was used as a measure of the availability of that food type. As shown in Table 15 the foraging absence was significantly longer (t-Test; $P < 0.01$) for garbage than for herring, sandlance, or intertidal organisms. There were no differences in the length of the foraging absence among the

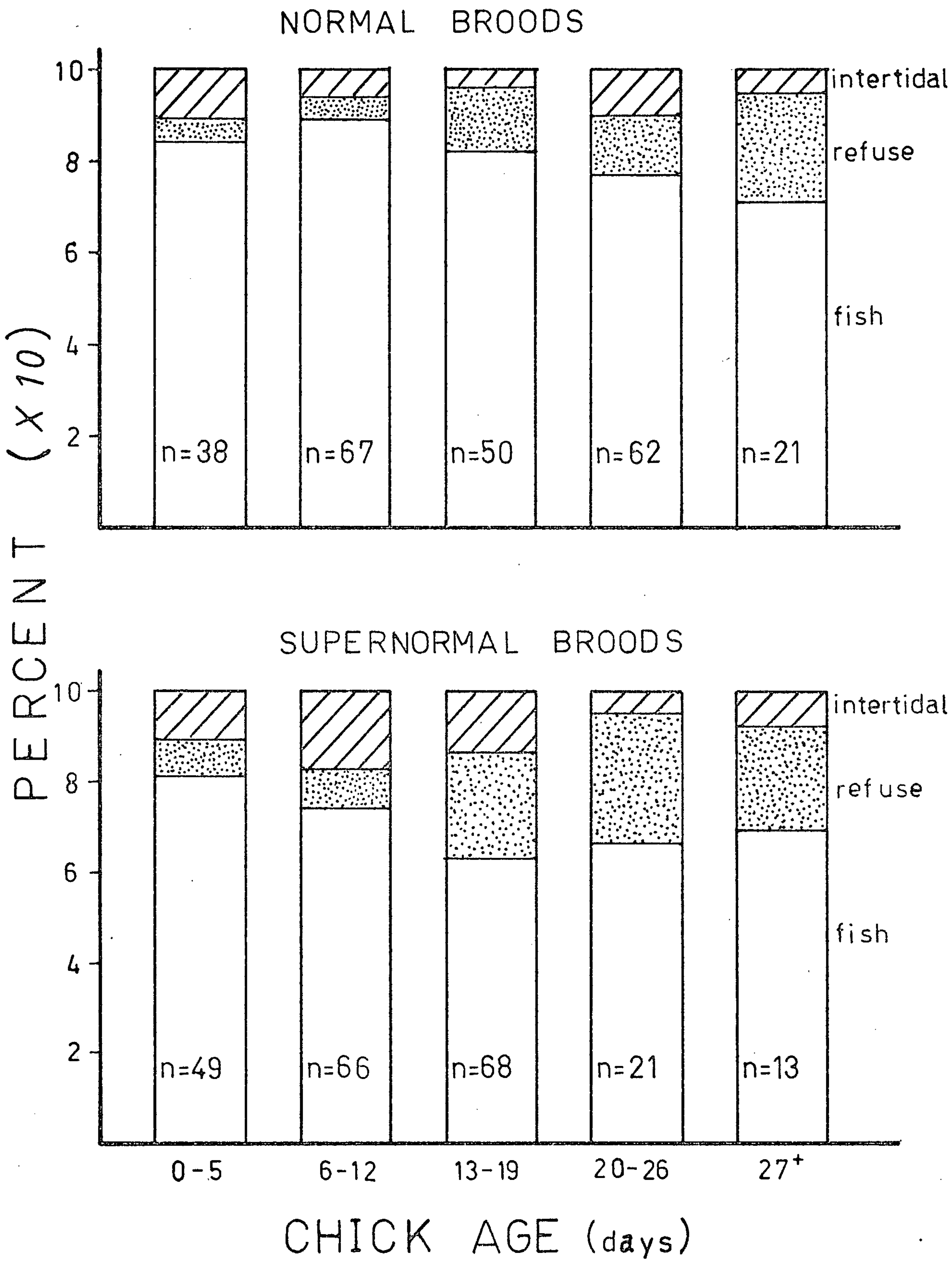


Fig. 11: Change in frequency of food types in the diet of the chicks with respect to their age and brood size (Mandarte, 1971). 'n' is total on which percentages based. Percentage values in appendix 3.

Table 15

Average Duration (minutes) (±SE) of Foraging Trips For Different Food Types with Respect To Brood Size on Mandarte in 1971.

Food Type	Normal Broods	Supernormal Broods
	(minutes)	(minutes)
Herring	172 ± 8.7 (144)	175 ± 11.5 (103)
Sandlance	199 ± 21.1 (38)	191 ± 23.4 (43)
Intertidal	163 ± 26.8 (14)	177 ± 35.1 (18)
Refuse *	271 ± 22.7 (25)	265 ± 24.9 (35)

* Using a t-Test, the difference between refuse and each of the other types was highly significant ($P < 0.01$).

natural food items. In addition, there were no differences between adults with normal and supernormal broods for the different food types.

As mentioned above, the average duration of a foraging trip for parents with either normal or supernormal broods increased with increasing chick age. A three-way analysis of variance of foraging absence with age, food type and brood size indicated that this increase was due to the change in the food type ($P < 0.01$) and not the chick age or brood size

The possibility of a change in the foraging absence with respect to date for each of the different food types was also checked. The linear regression of foraging absence on date resulted in a positive slope for both herring (0.7 min./day) and sandlance (0.9 min./day). The slope was not significant in either case but for herring it was just over the significance level ($P = 0.075$). There was no relationship for either garbage or intertidal foods.

<u>Discussion</u>: The food situation on Mandarte in 1971 was not quite what Lack (1966) suggested when he rejected Vermeer's experiments as not being a good test of his hypothesis. The birds did use garbage as he suggested but it probably formed less than 25 percent of the total diet. However, the fact remains that without garbage the birds may not have been able to raise as many young as they did. The most surprising result was the time required by the adults to

obtain garbage relative to the natural foods used. The reason why the birds used as much garbage as they did is unknown. The duration of the foraging trip for herring and sandlance did increase as the season progressed but the rate of increase was not sufficiently marked to make these two food types harder to obtain than garbage. It is possible that for some birds the difficulty in obtaining herring and sandlance increased to the point where garbage was a more "profitable" food type. The intertidal food was not a good alternative because its availability is limited to the single period of low tide each day.

There is another possible reason as to why the birds used more garbage later in the season. It was noted that when the adult birds regurgitated garbage, the chicks often would only peck at the food and turn away. If they did eat it, it was not with the same gusto with which they would eat natural food. Possibly as the chicks' food demands increased with age, the adults found it increasingly difficult to satisfy them with natural foods. When feeding the older chicks with refuse, the adults received signals from the chicks (e.g. not eating the food regurgitated) indicating that they were satiated. In actual fact the chicks would not be getting as much food as they needed.

Spaans (1971) found that chicks which were fed both natural food and garbage grew much better than those chicks fed only natural food. No data were available in this study in order to check this possibility. However, several reasons lead me to believe that chicks fed garbage in addition to natural food in this study would not grow better. (1) The very long time required to obtain garbage relative to natural foods should reduce the number of feeding trips which could be made by the adults per day. This would reduce the total amount of food that could be brought in any particular day. (2) The limited data (presented on page 58) also indicated that less refuse was brought back per foraging trip than herring. (3) Last, I do not think that the quality of the refuse was comparable to that of fish. However, I have no data on this aspect. In Spaans' study, part of the refuse fed the chicks was fish and fish offal discarded by the commercial fishing industry. If this is easily obtained, then it is not surprising that chicks fed this, along with other refuse and natural food, grew better than those fed natural food alone. In addition the refuse dumps were much closer to the breeding colony than was the case for this study. Some of the gulls in this study were probably foraging for refuse in Sidney (only five miles away). However this place could not provide food for very many gulls. Also some birds may forage in Victoria or Friday Harbour, both of which are about 15 miles distance from Mandarte. The nearest large source of available refuse is the Vancouver refuse dump some 30 miles away. The long foraging absences suggested that they were in fact using this source. Also, sightings have been made at this site of adults which had young on Mandarte.

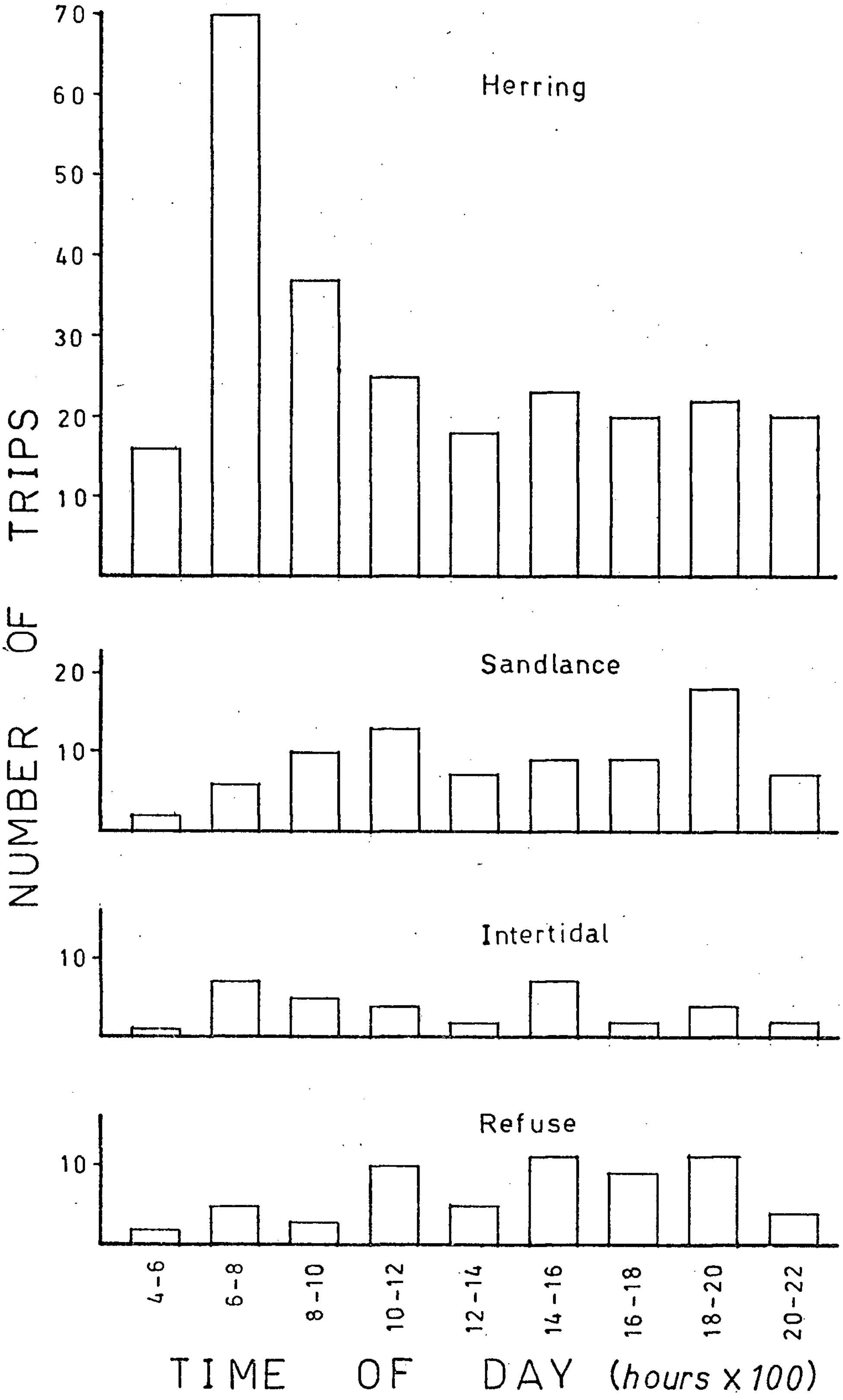
Spaans also found that the supernormal broods were fed more garbage than normal broods. This trend also occurred in this study but cannot be explained on the basis that it is a better food source.

On Cleland and QCI only natural foods were used. Thus the foraging times given in Table 12 for those islands were the times required by the adults to obtain natural food. A comparison of the foraging absences for natural foods between Cleland & QCI and Mandarte shows that on Mandarte the birds also took much longer to obtain natural food than did birds on Cleland or QCI. The difference may be due to a difference in the actual amount of food available and/or a difference in the numbers of gulls competing for the available food. For Mandarte, besides the 4000 gulls breeding there, there were an additional 3000 to 3500 gulls breeding on other islands in the general area (Drent, personal communication). This means that for Mandarte there were between seven and eight thousand gulls hunting for food within the same general area. On Cleland this number was probably less than four thousand.

(iv) <u>Diurnal Changes in Use of Food</u>: The foraging day (0400 to 2200 hours) was divided into nine two hour intervals. The time at which an adult returned with a particular food type during the day was assigned to one of the nine intervals on the basis of the food type. This was done for all trips involving herring, sandlance, refuse, and intertidal organisms. The number of returns per interval for the different food types is shown in fig. 12. More herring were brought back in the 0600 - 0800 interval than for subsequent periods during the day. The peak in returns for garbage did not start until the 1000 to 1200 hour interval. Sandlance and intertidal organisms were brought back in more or less equal quantities throughout the day.

<u>Discussion</u>: It would appear that there were differences in the frequency at which different foods (especially herring and refuse) were used throughout the day. The high frequency for herring in the early morning, relative to the rest of the day, may be related to its availability. Outram (1965) indicated that these fish, which feed on plankton, are still near the surface at daybreak but, like the plankton, move to deeper depths as the light intensity increases. This could in part explain why more herring are caught in the early morning. If herring availability decreases later in the day, then perhaps this explains why more of the subsequent foraging trips made by the gulls are to refuse sites. The intertidal results do not mean that intertidal food was available all day. This effect could be produced by the fact that the time of low tide advances each day, and over a period of several weeks, a low tide will have occurred at each of the intervals during one of the days.

Figure 12: Numbers of foraging trips for different food types classified according to the time of day the adults returned (Mandarte, 1971).



Herring
Sandlance
Intertidal
Refuse
NUMBER OF TRIPS
70
60
50
40
30
20
10
4-6
6-8
8-10
10-12
12-14
14-16
16-18
18-20
20-22
TIME OF DAY (hours x 100)

E Discussion: Evolution of Clutch-Size

The data presented in chapter two for Cleland and QCI did not support Lack's hypothesis. Lack predicted that adults should should not be able to adequately feed young in broods larger than normal. In this study, the adults were able to adequately feed both normal and supernormal broods using only natural food. In addition the limited number of sightings of juveniles from Cleland suggested that chicks from supernormal broods survived as well as those from normal broods.

A possible explanation for the above results concerns the nature of the food supply. The Pacific Sandlance was the major food fed to the chicks on Cleland. At present this species appears to be very abundant around both Cleland and QCI, as it was common to see gulls feeding on schools of these fish within a mile of the colony. Casual communication with fishermen suggest that this is the case along much of the British Columbia coast. However, to my knowledge no specific data are available on whether the sandlance has been as abundant in the past as it is today. Pritchard and Tester (1944) found that in the period 1939-41 the sandlance formed up to 40 percent of the summer diet of spring and cohoe salmon <u>Oncorhynchus</u> along the west coast of B.C.. Their study included both the west coast of Vancouver Island and the Queen Charlotte Islands. No data were collected by Pritchard and

Tester to indicate whether the sandlance was used by salmon in the winter as well. A paper by Macer (1966) on the sandlance in the North Sea indicated that these species may only be available in dense schools during the spawning season in the summer. If sandlance is only a seasonal food item for the salmon, then they might only be expected to use them if they were abundant.

A major decline in those salmon species preying on sandlance due to human fishing pressure could result in an increase in the numbers of sandlance. However, an examination of catch statistics for British Columbia did not indicate any major declines in the numbers of salmon caught since 1920. In addition, other species of fish are known to prey on sandlance, although their impact on the population is unknown. These predators include the Dogfish Shark Squalus suckleyi (Chatwin and Forester, 1953), and the Cod and Whiting (Gadidae) (Hart, 1949).

Pritchard and Tester also showed that the herring formed up to 50 percent of the diet of these salmon. In recent years the herring population on the west coast has declined (Taylor, 1964; Outram and Haegele, 1969). This could have two effects. First, this could result in present salmon stocks feeding even more heavily on sandlance. Second, the gulls which now rely heavily on sandlance on Cleland, may have used more herring in the past when this fish was more abundant. Interestingly, on

QCI herring formed a large part of the gulls diet and Taylor (1964) stated that herring populations in that area were one of the least exploited. A change in the availability of natural food and specifically the sandlance, cannot be discounted completely in explaining the results obtained for Cleland and QCI. However, circumstantial evidence suggests that an abundant food supply in the form of sandlance and/or herring has also been available to the gulls in the past.

Cody (1971) criticized the type of experiment performed in this study because the food supply was not measured. In this study only a small fraction of the total numbers of pairs on the colony were given extra chicks. It is possible that if all the pairs on the colony had four or more chicks, the adults would not be able to find sufficient food to raise the extra chicks as occurred on Mandarte. Considering the size of many of the colonies along the west coast (generally small), the distances separating them, and the ease at which adults obtained food on Cleland and QCI, I suspect that if every pair started out with a four egg clutch (assuming that they could incubate them) they would still be able to adequately feed the resulting chicks. However, no data are available to test this at the moment.

Wynne-Edwards (1962) and Skutch (1967) have argued that reproductive rates have evolved via group selection to correspond to the low mortality rates. This in turn has prevented the birds from overexploiting their food resources. However, I find it difficult to visualize how this type of selection could eliminate the individual producing a larger number of equally viable offspring.

Mountford's (1968) suggestion concerning the coincidence of the most productive and most common clutch-size does not apply in this study. When the frequency distribution of clutch-size is strongly skewed to the right as in the Glaucous-winged Gull (Drent *et al*., 1964), the most productive and most common clutch-size have to coincide. In this study the two did not coincide for Cleland where a six brood (never found naturally) was the most productive.

Another explanation of the results concerns the possible relationship between adult mortality and reproductive effort. Adult mortality, as suggested by Williams (1966) and Charnov and Krebs (in prep), could have a major affect on the total number of offspring produced by an individual during its lifespan. This would apply especially to long lived birds such as the Glaucous-winged Gull which has an annual mortality of 10 percent (Vermeer, 1963). If a larger brood has a higher adult mortality associated with it, then fig. 13 (after Charnov and Krebs) illustrates the relationship that would have to exist between brood size and adult mortality in order to account for an optimal brood size of three young on Cleland. The numbers of chicks surviving to breeding for the different brood sizes are plotted against brood size. This curve represents the relative contribution to future breeding populations by each brood size. The values are those given in chapter two. The other curve (labelled as q in fig. 13) is a hypothetical plot of adult mortality against brood size in order to produce the maximum fitness for a brood of three young. Here fitness is the difference between chick survival and adult mortality. In this case the rate of adult mortality has to increase with increasing brood size. The assumption is made that annual adult mortality does not change during the birds' life, but does change with brood size. Paludan (1951) and Ludwig (1967) have data which suggest that adult mortality does not change with age for adult gulls.

There is some reason to suspect that the adult mortality curve as related to brood size may take on some such form. Several people (Richhdale, 1947; Belopolskii, 1958; Fisher, 1967; Ingolfsson, 1967; Mercer, 1968; Hussel, 1972) have shown that adult weight does change during the breeding season. Hussel showed that in the Snow Bunting the weight loss for parents with supernormal broods was significantly larger than that for parents with normal broods. Both Belopolskii and Ingolfsson showed a weight loss in gulls during the breeding season. In the Glaucous-winged Gull the increased amount of energy expended by adults (reflected in increased time spent foraging) in raising extra chicks could take the form of a higher weight loss than normal during breeding. The major

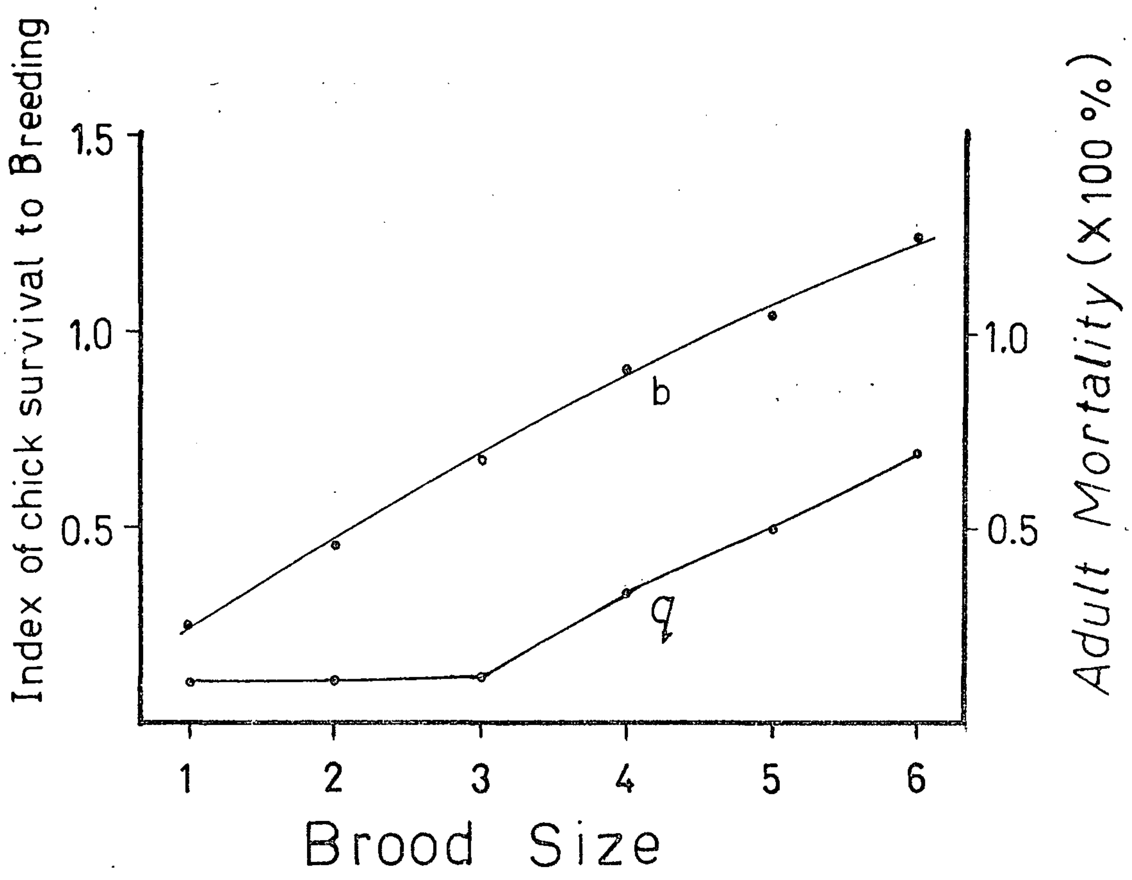


Fig. 13: Change in chick survival to breeding (b) with respect to brood size. The curve for adult mortality (q) with respect to brood size is a hypothetical one which would be required in order for a brood of three chicks to be optimum. (after Charnov and Krebs, in prep)

moult during and immediately after breeding could also accentuate this weight loss. Ward (1969) found that moult represents a major protein demand in birds. Drent (1967) calculated that the herring gull uses 20 to 33 percent of its daily net energy in incubating three eggs. The addition of a fourth large egg and the accompanying brood patch would increase the energy demand even more.

Differences in weight between adults could result in differences in mortality. Van Tets (1968) noted that the Glaucous-winged Gull had its highest mortality immediately after the breeding season which is the time when the birds should be at their lowest weight. Perrins (1965) showed that, at least in juvenile great tits, the weight of the birds had an influence on subsequent mortality rates. If adult weight losses associated with broods larger than three in the Glaucous-winged Gull were critical, then this could be reflected in a sharp rise in adult mortality. Higher mortality for adults with larger broods did not appear to occur during the breeding season. Only one instance of mortality was noted among 40 pair on Mandarte in 1971 and that concerned a bird with only one chick. Van Tets (1968) also noted that the Glaucous-winged Gull had a low summer mortality, whereas other species of gulls had a relatively higher one. Coulson (1960) noted that there was a mortality associated with breeding in the starling. Perrins (1965) found that parents raising supernormal broods had a higher mortality in one year but not in another.

This study is not the only one in which adult mortality could be operating as a factor in the evolution of clutch-size. Nelson (1964), who found that the Gannet could raise two chicks as well as they could raise one, also noted that the parents with supernormal broods were spending far more time foraging in the latter stages of raising their young than were parents with normal broods. In the Kittiwake (Coulson and White, 1958), only some of the older experienced birds raised the three-chick broods. Harris and Plumb (1965) and Pearson (1968) presented data which suggested that the Lesser Black-backed Gull could raise more than three young much like the Glaucous-winged Gull.

The possiblility also exists that adult mortality does not increase with increasing brood size. Kluyver (1970) found no relationship between adult mortality and brood size in the Great Tit although he did note a decrease in weight of adults during breeding (1952). Harris (1966) found that Sooty Shearwaters did not lose weight when trying to feed an extra young. This supports a suggestion by Hussel (1972) that adult feeding rates could have evolved along with the brood size. Possibly a feeding rate has evolved which prevents the adults from overworking themselves in trying to feed young, and thus lowering its chances of future survival. Bergman (1971) found that the Black Guillemot Cepphus grylle did not sacrifice itself for its young when the food supply failed. Hussel (1972) noted that Snow Buntings with supernormal broods (undernourished) still had a rest period even though there was a full 24 hours of daylight.

Too little is known about adult mortality and its relationship to reproductive effort in order to come to any conclusion concerning the Glaucous-winged Gull in this study. Presently the importance of adult mortality needs far more investigation. The results from Cleland and QCI do not support Lack's hypothesis as it presently stands. As discussed above, a recent change in the food supply does not appear to be the reason. The influence of reproductive effort on adult mortality may be an explanation of why this species has a brood of three and not four. Basically Lack's hypothesis is still correct but needs to be extended to include the possible influence of reproductive effort on adult mortality in long lived birds.

F Summary

This chapter described the food situation on the different islands, giving information on the foods used, its availability, and the time spent foraging for it by the adults. Prior to chick hatching, adults were found to be using refuse on Mandarte but not on Cleland. Chick regurgitations, collected while weighing chicks, showed that refuse was fed to chicks on Mandarte but only rarely on Cleland and QCI. Observations were also made on pairs of gulls in their territories on the colony. These indicated that gulls on Mandarte in 1971 had the longest foraging trip (in time) when compared to gulls for the other island-years. Gulls on QCI had the shortest foraging trips. In 1971 on Mandarte it was found that the time for a foraging trip increased with the age of chicks for both normal and supernormal broods. A three-way analysis of variance of foraging trip with chick age, food type, and brood size showed that the differences were related to changes in diet of the birds and not age of the chicks. It was found that more garbage was brought to the older chicks and that this food type took significantly longer to obtain than did natural foods. It was noted that the total amount of time spent foraging each day by pairs of birds increased with chick age and with brood size. The number of trips made each day did not change with chick age but did change with brood size. The results on Cleland and QCI did not support Lack's hypothesis. Possible reasons for this discrepancy are discussed in the last section of this chapter.

CHAPTER IV

Use Of Refuse Dumps By The Glaucous-Winged Gull

A Introduction

Many gull species congregate in areas of human habitation during the winter months. Several studies indicate that this is largely due to the presence of open-face garbage dumps. The attractive feature of these dumps is the tons of edible refuse (meat, bread, etc.) discarded daily by man and left lying exposed at these sites. The use of these food sources by the gulls is thought to be one of the major factors responsible for the recent increases in the gull populations. This large food supply has possibly allowed a larger number of birds to survive the winter than was possible before.

The Glaucous-winged Gull, which also utilizes refuse sites as a food source, winters along most of the west coast of North America with large concentrations occurring wherever large urban areas occur. One of the larger concentrations of this species occurs in the lower mainland area of British Columbia. Approximately one million people reside in this area. Perhaps the largest concentration of wintering gulls occurs in the San Francisco Bay area where gull numbers exceed 200 thousand; however, this number includes several species of gulls of which the Glaucous-winged Gull accounts for roughly 30 thousand of the total (Cogswell, personal communication).

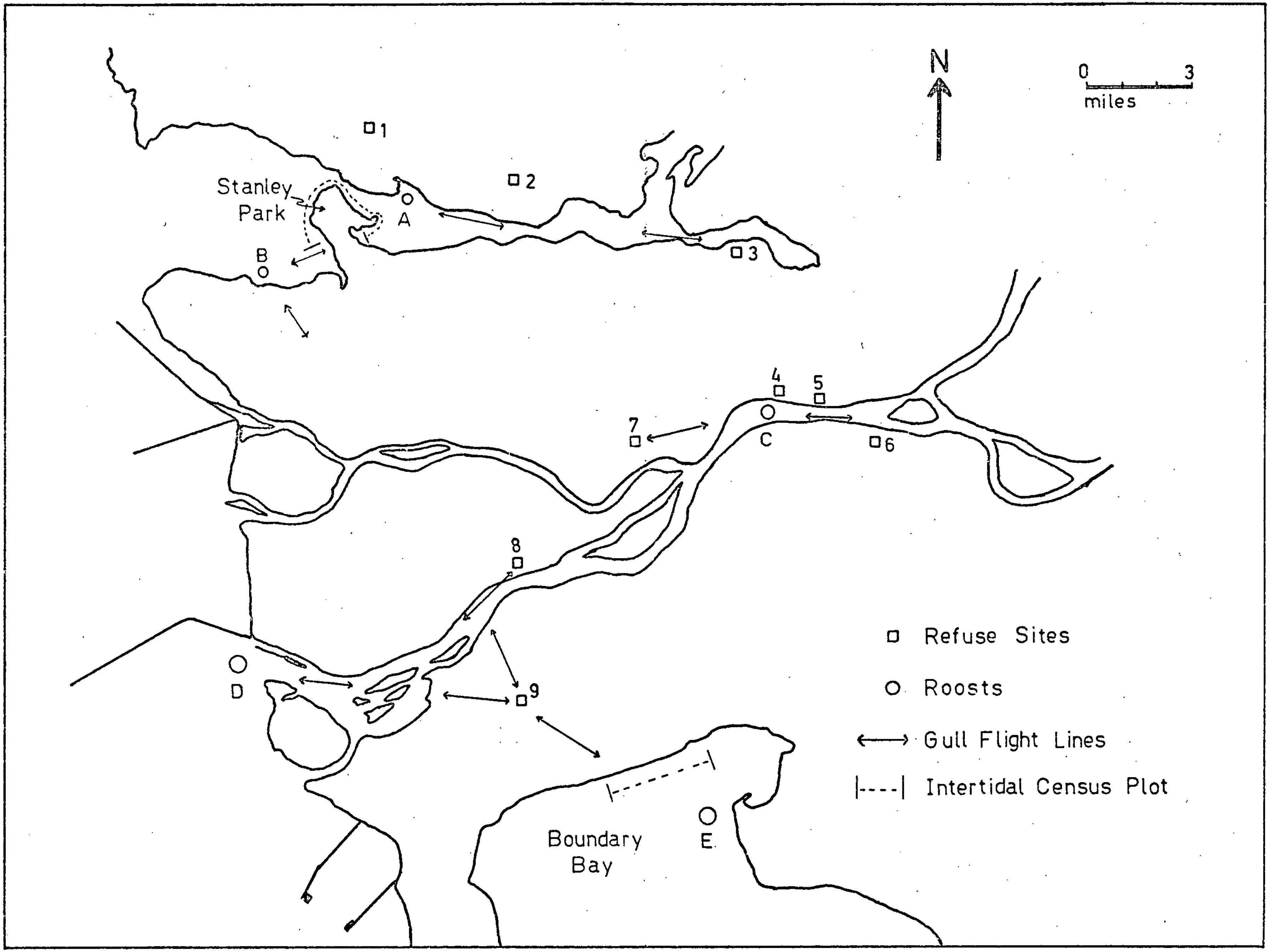
The lower mainland area (described in chapter one) was selected to serve as the study area because of the large numbers of glaucous-winged gulls wintering here and its easy accessability during the winter. The main purpose of this part of the study was to assess the use made of garbage dumps by these gulls in the study area during the winter, and to relate this to the total numbers of gulls in the area.

B Daily Activity During the Winter

The two major focal points for the gulls' activity in this area during the winter were the roosts and the refuse sites. The roosts were located at various points throughout the lower mainland (fig. 14) and were divided into two types. The first type consisted of log booms anchored in a body of water deep enough such that even at low tide it was still surrounded by water. Two of the roosts fall into this category and are labelled as A and C on figure 14. The other type of roost was located where extensive sand and mud flats form as the tide recedes. There were three roosts of this type and are labelled B, D, and E. Both types of roosts provide good protection from terrestrial predators. The second type of roost (mud flats) makes it possible for the gulls to stand on the shore without having to swim against an outgoing current and still be able to detect potential predators from afar.

The exodus of the gulls from these roosts started at

Figure 14: Map of winter study area showing location of refuse dumps, roost sites, and flight lines between refuse sites and roosts. Refuse sites: 1 - West Vancouver (closed Oct 31/69); 2 - North Vancouver; 3 - Barnet; 4 - Terra Nova; 5 - Leeder; 6 - Port Mann; 7 - Burnaby (closed Oct. 31/69); 8 - Richmond; 9 - Vancouver.


N
0
3
miles
1
2
3
Stanley
Park
A
B
4
5
7
C
6
8
D
9
Boundary
Bay
E
Refuse Sites
Roosts
Gull Flight Lines
Intertidal Census Plot

first light and continued for about a two hour period (fig. 15). The most rapid rate of roost departure occurred in the period of first light occurring prior to sunrise. From the roost the gulls proceeded to the various daytime sites which included refuse sites, log booms on nearby bodies of water, city parks, fields, fish docks, etc.. A small proportion of the birds as will be shown later, did remain on the intertidal areas to feed.

All the dumps are located either along the Fraser River or near Burrard Inlet (fig. 14). All are near some source of fresh water which is preferred by the gulls over salt water. Once the machines on the dumps started operating, the numbers of gulls feeding at the dump increased rapidly . During the day there was a constant turnover of gulls between the refuse sites and the nearby loafing sites which included logbooms or any large open area.

About two hours before dark, the gulls started to leave the refuse and loafing sites and move towards the roost sites. The flight lines of the gulls are shown in fig. 14. The peak movement of gulls unto the roost occurred between sunset and total darkness (fig. 15). Schreiber (1968) noted the same type of behaviour for the herring gull on the east coast of the U.S.A.. The roost counts which will be described in the next section were always made in the evening. It was found that in the morning the birds began leaving the roost before

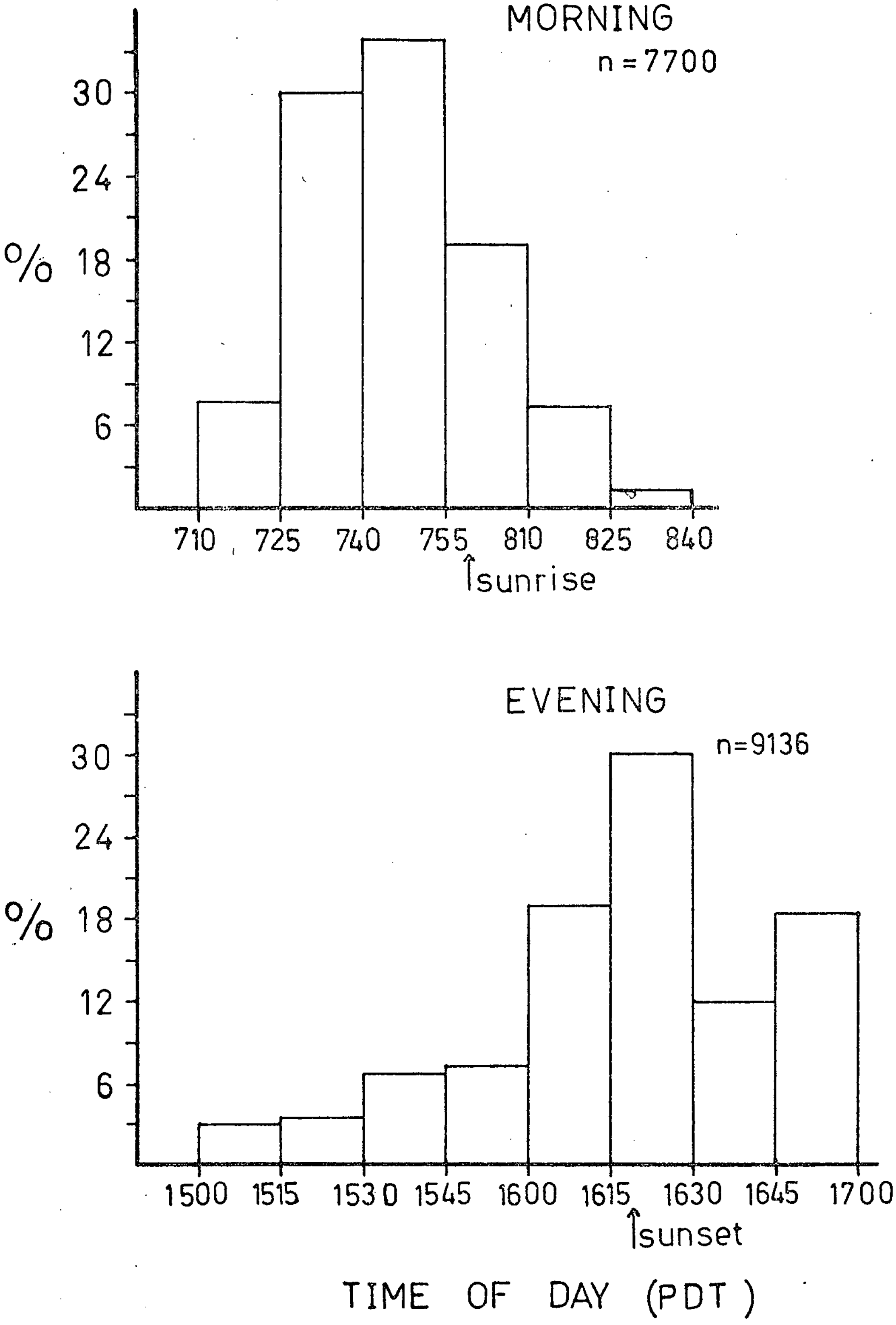


Fig. 15: Rate of departure from roosts in morning and rate of arrival at roosts in evening for Dec. 20/68.

it was light enough to accurately count them. In the evening all the birds coming to the roost could be counted before it was too dark.

C Numbers of Gulls and Their Use of Refuse Dumps

For this study, the numbers of gulls wintering in the study area were recorded for the months of October through to March over a period of four years (1968-72). The first year (1968-69) was spent learning the habits and movements of these birds. As a result only incomplete counts were obtained during that season.

Roost counts were carried out at all roosts in order to obtain estimates of the numbers of gulls in this area. In 1968-69 some roost counts were made in the morning but because some birds leaving the roost were missed, all subsequent counts were made in the evening. The counts at roosts C, D, and E were carried out at the same time because of possbile interchange between these roosts. This was especially evident for roosts D and E where gulls would switch from one roost to another depending on weather conditions. The numbers of gulls at roost C were more constant from count to count. The counts at roosts on English Bay and Burrard Inlet (roost A and B) were often not done or done on another day. It was not always possible to obtain sufficient observors to man all the roosts at one time. This deficiency was not particularily serious as there appeared to be little interchange between this area and the Fraser River delta.

The results of the counts are shown in Table 16. The majority of the gulls in the study area used roosts C, D, and E located on the Fraser River delta. Only about 12 percent of the birds were found to be using roosts A and B on Burrard Inlet and English Bay respectively. The winter population of gulls in the study area in 1969-70 numbered in the order of 45 to 50 thousand. In 1970-71 and 1971-72 the numbers were probably in the order of 55 to 60 thousand.

During the same time period (1969-72), monthly censuses were made at all the known refuse sites in the study area. The size of the area made it impossible to cover all the sites in one day. As a result the area was divided into two parts and done on two consecutive days. Refuse sites around Burrard Inlet were done on one day and the remainder were done on the other. Again there appeared to be little interchange between these two areas.

The results are shown in Table 17. The numbers of gulls using the refuse sites in the study area increased rapidly in October and decreased rapidly in the first part of March. No counts were made of gull numbers in the study area during the summer months; however, their numbers were probably similar to those found in March and September. The majority of the birds were found in the general vicinity of the three largest roosts

Table 16

Roost Counts for the Winter Seasons between 1969 and 1972
For the Lower Mainland Area of B.C.

Roost Site	Year and Dates of Count					
	1969 - 1970					
	Nov. 7	Nov. 21	Dec. 5	Dec. 23	Jan. 9	Jan. 23
D	24,000	19,000	25,000	25,500	11,500	19,000
E	9,000	8,000	6,000	14,000	14,500	9,200
C	4,500	10,000	7,000	-	12,000	12,000
A & B	**	**	8,000	11,000	9,400	6,400
Total	37,500 (45,000)	37,000 (45,000)	46,000	50,500	47,400	46,600
	1970 - 1971					
	Oct. 30	Nov. 26		Dec. 31		Jan. 28
D	17,000	29,000		11,000		17,000
E	4,000*	11,700		26,000		13,700
C	11,700	17,000		15,700		15,000
A & B	8,500	7,400		6,500		4,200
Total	41,600	65,100		59,200		49,900

(cont'd)

Table 16 (cont'd)

1971 - 1972

	Nov. 9	Dec. 7	Jan. 18
D	30,500	16,320	11,790
E		19,456	11,339
C	16,400	17,000	12,840
A & B	**	3,500 ***	**
Total	46,900 (54,000)	56,300 (59,000)	36,000 (42,000)

Birds did not use the roost.
* Count low because of fog
** No count obtained for the roost
*** Count low.
(n) Estimate of numbers expected if all roosts counted.

Table 17

Numbers of Gulls Counted at or Near Refuse Sites.

Date	Refuse Sites * A	B	C	Total
1969 - 1970				
Oct. 6 - 7	6060	4730	3740	15530
Oct. 30 - 31	23100	5400	6610	35110
Dec. 1 - 2	17460	8130	7630	33220
Jan. 5 - 6	20470	4070	6280	30820
Feb. 5 - 6	26390	4680	4730	35800
Feb. 26 - 27	19670	7560	2500	29730
Mar. 19 - 20	8670	1095	925	10690
1970 - 1971				
Sept. 29 - 30	9700	1710	2850	14260
Oct. 29 - 30	26500	4780	6080	37360
Nov. 26 - 27	27380	8560	8030	44030
Dec. 30 - 31	28000	8450	5820	42170
Jan. 27 - 28	29840	5880	2695	38415
Feb. 25 - 26	19000	4620	2625	26245
Mar. 17	10020	4300	**	14320

(cont'd)

Table 17 (cont'd)

1971 - 1972				
Nov. 1 - 2	20500	7050	6860	34410
Nov. 30	23700	11880	**	35580 (42000)
Jan. 1 - 2	23500	5000	5510	33310
Jan. 27	23500	6390	**	29890 (33000)

* 'A' includes the Vancouver and Richmond refuse dumps: 'B' includes the Burnaby, Terra Nova, Port Mann, and Leeder refuse dumps; 'C' includes the West Vancouver, North Vancouver, and Barnet refuse dumps and the Campbell Ave. Fish docks.

** no count was made at this site.

(n) Number in brackets is estimated numbers at refuse sites.

as might be expected. The Vancouver and Richmond refuse dumps, which are located very close together, had the largest numbers of gulls (20 to 25 thousand) feeding there. Most of these birds were at the Vancouver refuse site which serves both Vancouver and the municipality of Delta. Approximately one million pounds of household garbage is dumped there daily during weekdays. Spaans (1971) showed a correlation between the number of gulls at a dump and the number of people using it. In addition the number of gulls will also be determined by how quickly the garbage is buried, the size of the area over which the garbage is spread, and whether the local authorities attempt to keep the birds away from the dumps.

Table 18 shows a comparison of the numbers of gulls counted at refuse sites and those counted at the roosts. The data for Burrard Inlet and English Bay were not included both because roost counts were incomplete and because the roost counts may not have represented the total numbers of gulls in the area. For this area it was noted that gulls would spend the night roosting on pilings, barges, etc. located throughout the inlet area. On the Fraser River delta, approximately 70 percent of the winter gull population were using refuse sites for feeding. A similar percentage was expected for birds on Burrard Inlet and English Bay.

As mentioned before, some gulls do use the intertidal area for feeding, although only a small portion of this area

Table 18

Comparison of Roost and Refuse Site Censuses. These Figures Do not Include the Numbers of Gulls for the Rcost and Refuse Sites on Burrard Inlet.

	Date		
1969 - 1970	Nov. 7	Dec. 5	Jan. 9
Dump census	28,900	25,600	24,500
Roost census	37,500	38,000	38,000
% gulls at refuse sites	76.0	67.4	64.5
	Average = 69.3 %		
1970 - 1971	Nov. 26	Dec. 31	Jan. 28
Dump census	35,940	36,450	35,700
Roost census	57,700	52,700	45,700
% gulls at refuse sites	62.3	69.2	78.0
	Average = 69.8 %		
1971 - 1972	Nov. 9	Dec. 7	Jan. 18
Dump census	27,550	35,580	29,890
Roost census	46,900	52,776	35,969
% gulls at refuse sites	58.7	67.4	83.1
	Average = 69.7 %		

is exposed during the daylight hours. In order to obtain an estimate of these numbers, counts on two sample areas (shown in fig. 14) were carried out in 1970-71. One sample site was a four mile length of shore on Boundary Bay. The other site was a six mile length of beach around Stanley Park in Vancouver. The latter area may not be entirely representative, but the biggest problem in selecting an area was to find one that was easily accessible for its whole length. The total length of shoreline was calculated for the area between White Rock and West Vancouver including Burrard Inlet and Indian Arm but excluding the waterfront area in Burrard Inlet. The numbers of gulls on the Boundary Bay sample area were used to compute the number of gulls feeding on the shoreline between White Rock and Point Grey. The Stanley Park sample area was used to determine the number of gulls for the remaining length of shoreline. The shoreline census accounted for only 3300 gulls or about five percent of the total numbers in the area (Table 19). This number could have been higher (but still less than 10 percent). The examination of pellets regurgitated by gulls at the refuse sites indicated that birds feeding along the intertidal zones were also visiting the refuse sites.

These birds also feed on the intertidal to a limited extent at night. Observation indicated that at any one time during low tides (occurring between 2200 and 0200 hours), up to 300 gulls were utilizing the mussel beds at the Second

Table 19

Numbers of Birds Along the Intertidal Census Areas (shown in fig. 14) And the Age Composition of Those Birds.

Date	Juvenile	Subadult	Adult	Total Numbers
	Age Class			
	%	%	%	
		Boundary Bay		
Nov. 10/70	6.3	9.5	84.2	158
Dec. 9/70	11.4	9.2	79.4	141
Feb. 16/71	18.1	8.7	73.2	127
		Stanley Park Seawall		
Nov. 17/70	20.5	18.0	61.5	122
Nov. 29/70	17.0	12.9	70.1	147
Dec. 8/71	13.5	12.9	73.6	163

Extrapolation of Sample Area to Whole of Study Area.

Average Number on Boundary Bay Site: 142
Average number on English Bay Site: 144

Shoreline Distances: White Rock to Point Grey 52.5 miles
Sample Area 4.0 miles

Number of Gulls 1860

Shoreline From Point Grey to West Vancouver 62.0 miles
Sample Area 6.0 miles

Number of Gulls 1483

Total Number of Gulls Caculated to be on the Intertidal Area

3340

Narrows in Burrard Inlet. Similar observations on Boundary Bay indicated that the birds might also be feeding on the mud flats at night. However, it was impossible to get close enough to the birds to check on their success rate. On Boundary Bay, the birds were generally very close together and not all actively hunting, suggesting that success may have been very low.

The numbers of gulls on refuse sites and on the intertidal area together still leave some 25 percent of the total number unaccounted for. Some of these birds will be utilizing refuse sources in places that were not counted, such as city parks, etc.. Others will be resting in areas missed during counting but still feeding on the dumps. Part of this difference will be accounted for by the difficulty involved in counting large flocks at a distance. Another source of error involved the C roost where up to 5000 gulls would come down the river to roost from outside the study area. Thus for this area at least 70 percent of the birds were using refuse sources. Considering the above sources of error, this figure will lie somewhere between 70 and 90 percent.

If the garbage dumps represent an easier source of food than the intertidal, then one might also expect to find a greater percentage of juveniles feeding on the dumps than on the intertidal area. Juveniles are considered to have more trouble obtaining food than adults. Counts were carried out in these two areas to verify this. The birds were classified as juveniles, subadults, and adults on the basis of their plumage characteristics. The results for the intertidal area, which included all birds seen on the census strip, are shown in Table 19. Only samples of birds were counted at the refuse sites (Table 20). The results indicated that there were no large differences in age compostion of the birds found on the intertidal and refuse sites. However, it is possible that the juveniles and subadults are underepresented in both areas. Kadlec and Drury (1968) found that, on the east coast of North America, the herring gull population with a 4.5 percent rate of increase consisted of 15 percent juveniles and 17 percent subadults. The Glaucous-winged Gull has also been shown to have a rate of increase of 5 percent (Drent et al., 1964). In this study, the values for the percentage of juveniles found were only similar to those of Kadlec and Drury for gulls at the North Vancouver refuse dump and at the other dumps when winter numbers were decreasing. Generally it would appear that the juveniles are under represented in the study area. The reason for this discrepancy may be due to a difference in the numbers of juveniles and adults which migrate. This differential type of migration does occur for the herring gull on the east coast of North America (Kadlec and Drury, 1968). It may also be that the Glaucous-winged Gull population is no longer increasing. However, new colonies are still being formed in the Puget Sound area (MacGregor, personal

Table 20

Percentage Age Composition of Gulls at Three Different Refuse Sites.

Date	Age aclass Juvenile	Subadult	Adult	Total Number in Sample
	%	%	%	
		Vancouver Refuse Site		
Oct./69	9.8	8.3	81.9	2813
Dec./69	7.1	8.9	84.0	2315
Jan./70	7.3	10.2	82.5	2190
Feb./70	13.1	14.1	72.8	2632
Mar./70	14.4	20.4	65.2	1330
Oct./70	4.7	4.9	90.4	887
Nov./70	5.4	8.9	85.7	3009
Dec./70	7.2	9.4	83.4	2316
Jan./71	6.3	9.2	84.5	2397
Feb./71	9.6	11.7	78.7	1403
		Terra Nova Refuse Site		
Oct./69	11.4	8.4	80.2	2573
Dec./69	12.4	12.0	75.6	1976
Jan./70	18.5	10.8	70.7	1715
Feb./70	20.0	14.9	65.1	999
Oct./70	11.2	8.3	80.5	881
Nov./70	6.1	9.1	84.8	1417
Dec./70	9.2	7.5	83.3	1180
Feb./71	15.8	12.5	71.7	1277

(continued)

Table 20 (cont'd)

	North Vancouver Refuse Site			
Jan./70	14.5	15.8	69.7	1318
Nov./70	14.2	9.4	76.4	1469
Dec./70	13.3	9.2	77.5	980
Jan./71	12.8	10.1	77.1	1162
Feb./71	20.2	13.1	66.7	1079

communication). As will be shown below the colonies in the Georgia Strait - Puget Sound area represent a small part of the total Glaucous-winged Gull population. Along the coast of Alaska it is not known whether the population is increasing, or how the migration of these birds affects the proportions of birds in different age classes found in this area.

D Discussion

As was shown in the last section, large numbers of gulls were using refuse sites in this area. However, Vancouver is not the only urban area with wintering populations of this species. San Francisco (30,000±), Tacoma (5000±), Portland (15-20,000), Victoria (6000±), and many other small urban areas together account for a large number of gulls presumably using refuse. The total number using refuse sources along the coast could be in excess of 150,000 individuals.

Some of these gulls using the refuse sites will be from colonies along the British Columbia coast. However, at least part and perhaps a large part of these birds have to be from colonies along the coast of Alaska. Present breeding populations for British Columbia and Puget Sound, Washington lie in the 50 thousand pair range. These numbers, plus the non-breeding birds associated with them, could only account for gulls using refuse sources but not those using natural food. MacGregor (personal communication) has made sightings on the Vancouver refuse dump of birds banded in the Kodiak area of Alaska. Isleib (personal communication) reported to me that there are large movements of glaucous-winged gulls through the Gulf of Alaska between the end of August and mid-November with the peak of movement in the latter part of September and in early October. This coincides with the large increases in gull numbers in the Vancouver area in October. Similarily the large exodus in this area during March matched the movement through the Gulf of Alaska in the spring.

Estimates of breeding populations for Alaska (Isleib, personal communication) are probably in excess of 150 thousand pairs. Willet (1915) reported three thousand pairs on Forrester Island, Alaska in 1914. This number is possibly higher now. A breeding colony south of Cordova, Alaska is estimated by Isleib at ten thousand pairs. These are but two of numerous other smaller colonies scattered along the Alaska coastline. Some of these birds winter in the Alaska region, utilizing both refuse and natural food. Sowl and Isleib (personal communication) estimated the winter population in Prince William Sound, Alaska at 40 thousand. Isleib further estimates winter numbers in excess of 100 thousand along the Gulf of Alaska coast. Many of the breeding birds leave the Alaska area during the winter and move south.

Some of these birds as discussed above do use refuse sites in major urban areas. However, the Glaucous-winged Gull also utilizes the natural food resources along the west coast of British Columbia in substantial numbers. Robertson (1973) reported numbers of glaucous-winged gulls of up to ten thousand in the Gulf Islands in British Columbia. These birds were using both human refuse and natural food. Robertson reported that numbers were greatest in this area during herring spawning in February and March. Observations by myself and R. Drent showed that up to 5000 birds were utilizing dead salmon on the Fraser and Harrison river in November and December. Robertson (study in progress) has noted large numbers of gulls (>30 thousand) along the west coast of Vancouver Island and the east coast of the Queen Charlotte Islands. No figures are available on the actual percentage of the glaucous-winged gull population using natural food during the winter; however, at present it appears to be as large as or larger than the number using refuse.

Recent increases in refuse sources may be linked to recent increases in glaucous-winged gull numbers. Large numbers of gulls appeared to have migrated from the Alaska area in the past as well when refuse sources were less abundant. Pearse (1923) reported large movements of gulls down the Strait of Georgia. Before the advent of the large garbage dumps and other refuse sources, mortality rates, especially those for juveniles, may have been much higher since natural food would be harder to obtain than refuse. The strategy of adults feeding juveniles away from the colony and letting them invade feeding territories as described for herring gulls by Drury and Smith (1968) would certainly have survival value under these conditions. The occurrence of winter storms would also heighten the effect of a hard to obtain food supply. Both Drury (1963) and Spaans (1971) found that winter storms caused birds which were using natural food sources to switch to refuse sites. In the past these would not be available. Perhaps with the increase in refuse dumps, less efficient feeders were able to obtain sufficient food to survive the winter.

There is little doubt that refuse sites along the coast attract large numbers of gulls, as is found in the Vancouver area. For example, when Seattle closed its refuse dump near Puget Sound and moved it inland away from the water, and thus away from the gulls, the numbers of gulls in the area decreased. Audubon bird counts indicated a drop in the local gull population from over 12 thousand gulls to around 2 or 3 thousand. However, it is not known whether populations of the Glaucous-winged Gull could maintain their present size without refuse sites. The large numbers using refuse sites suggest that this may be the case; but then it may also be that present natural food sources could support the population. Answers to the above questions may be forthcoming as methods of refuse disposal are changed.

E Summary

This part of the study was carried out in the general vicinity of Vancouver, British Columbia in order to assess the use made of refuse sites by the Glaucous-winged Gull. Counts of numbers of gulls in the study area were made at their roosts. Between 45 and 65 thousand gulls were counted in the various years of the study. Between 70 and 90 percent of these birds were feeding on refuse sites in the area. Some birds were feeding on the intertidal areas both during the day and at night. Counts of birds with respect to their age class (juvenile, subadult, adult) indicated that juveniles were under-represented in this area. Possible reasons for this occurrence are discussed. In the last section the data from this study are related to known information for the Glaucous-winged Gull population in North America.

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Appendix 1

Average Growth Rates (g/day) (±SE) for Brood Sizes One to Six Chicks on the Different Islands.

Island & Year	Brood Size 1	2	3	4	5	6
Mandarte 1961 *	29.2 ±2.54 (21)	26.2 ±2.09 (21)	26.3 ±2.01 (21)			
Mandarte 1969	32.3 ±0.70 (336)	31.3 ±0.50 (506)	28.5 ±0.63 (509)	28.3 ±0.58 (543)	27.4 ±0.62 (446)	27.7 ±0.70 (285)
Cleland 1969	36.5 ±1.62 (45)	37.6 1.06 (132)	33.8 ±0.59 (230)	37.5 ±0.77 (240)	36.1** ±0.94 (143)	
Cleland 1970	33.3 ±0.41 (491)	34.4 ±0.41 (584)	33.2 ±0.39 (667)	31.5 ±0.56 (590)	31.0 ±0.59 (486)	31.7 ±0.59 (577)
QCI 1972	32.9 ±1.27 (116)	36.3 ±1.14 (120)	36.5 ±0.69 (353)	36.8 ±1.63 (74)	34.9 ±0.81 (285)	

* Growth rates calculated using the average weights with age given in Vermeer, 1963.

** Data for five and six chick broods combined.

(n) Number of chick weights used in calculation of growth rates.

Appendix 2

Average Asymptotic Weight (grams) (±SE) for Brood Sizes One to Six Chicks on the Different Islands.

Island & Year	Brood Size 1	2	3	4	5	6
Mandarte 1969	959 ±32.4	941 ±21.5	894 ±16.5	882 ±38.5	756 ±27.3	809 ±34.3
	(19)	(29)	(26)	(14)	(24)	(8)
Mandarte 1971	877 ±28.3	824 ±30.5	825 ±31.8	810 ±35.9	797 ±35.9	
	(22)	(27)	(24)	(11)	(9)	
Cleland 1969		1015* ±8.1		1015* ±21.8		
		(253)		(29)		
Cleland 1970	1009 ±17.8	1013 ±14.8	994 ±13.8	997 ±15.8	1011 ±17.3	1020 ±17.3
	(42)	(53)	(72)	(65)	(40)	(58)

* Normal broods and supernormal broods combined.

(n) Number in brackets is the smaple size.

Appendix 3

Frequency Occurrence of Food Types (in percent) with Respect to Age and Brood Size for Mandarte in 1971.

	Food types fed to Chicks			
Chick Age	Fish*	Intertidal	Refuse	(n)
		Normal Broods (1-3)		
0-5	84.2	10.5	5.3	38
6-12	89.5	4.5	4.5#	67
13-19	82.0	4.0	14.0	50
20-26	77.0	6.5	12.9#	62
27+	71.4	4.8	23.8	21
		Supernormal Broods (4-6)		
0-5	81.6	8.2	8.2#	49
6-12	74.2	12.1	7.9#	66
13-19	63.2	11.8	23.5#	68
20-26	66.7	4.8	28.5	21
27+	69.2	7.7	23.1	13

* Fish includes both herring and sandlance.
# Remaining percentage (<6%) a mixture of refuse and natural food
(n) Number of foraging trips in which the food fed to the chicks was seen.

Appendix 4

Different Food Types Recognized in the Pellets Collected on Mandarte (1969) and Cleland (1970).

Food	Mandarte	Cleland
<u>Intertidal</u>		
Balanus sp.	*	*
Pollicipes polymerus		*
Mytilus sp.	*	*
Asteroidea (starfish)	*	*
Amphineura (chitons)	*	*
Clinocardium sp.	*	*
Polinices sp.	*	*
Strongylocentrotus drobachiensis	*	
Haliotus kamtschatkana	*	
Patellacea (limpets)	*	
Brachyura (crabs)	*	*
<u>Insecta</u>		
Hymenoptera (ants)	*	
<u>Refuse</u>	*	*
<u>Fish bones</u>	*	*

Appendix 5

Food Type Found in Chick Regurgitations and In Observed Feedings of Chicks by Adults.

Food	Mandarte	Cleland	QCI
<u>Pelagic</u>			
Clupea pallasii	*	*	*
Ammodytes hexapterus	*	*	*
Pholidae	*		
Cephalopoda (squid)		*	
<u>Intertidal</u>			
Clinocardium sp.	*	*	
Polychaeta	*		
Euphausiacea		*	*
Brachyura	*		
<u>Refuse</u>			
Bread & meat scraps	*		
Offal		*	