BREEDING BIOLOGY AND BEHAVIOUR OF THE COMMON MURRE (URIA AALGE AALGE(PONT.)) ON GULL ISLAND, NEWFOUNDLAND

SHANE PATRICK MAHONEY

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Breeding Biology and Behaviour of the Common Murre
(*Uria aalge aalge* (Pont.))
on Gull Island, Newfoundland

A Thesis
Presented to
The Department of Biology
Memorial University of Newfoundland

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
© Shane Patrick Mahoney
May 1979

Frontispiece

One adult murre and three chicks. It is at approximately this stage of development that young birds leave the ledges for the first time. Usually the male accompanies the chick to sea and cares for it during a period of perhaps two months. The chick may not return to the land for two years or more.

Abstract

The breeding biology and behaviour of the Common Murre (*Uria aalge aalge* (Pont.)) was studied on Gull Island, Newfoundland, during May through July in 1977 and 1978.

The origin of the Gull Island population was discussed as were the ledge population changes recorded over the breeding season. Reasons for the different patterns of attendance were suggested.

Breeding phenology was studied in detail. Eggs were weighed and measured and a number of their attributes (shape, volume etc.) were determined. Eggs of known age were collected, their embryos removed and their developmental patterns determined. Numbers of eggs laid and the chronologies of laying for both seasons were compared. Weights of eggs from replacement clutches and the time required to replace a clutch were defined.

Chicks were measured to calculate growth curves for weight and a number of other body parameters. Numbers of chicks were compared for both seasons as were the growth curves of chicks from both years. Fledging of chicks was recorded and observations were made on adult and chick behaviour at fledging. Different fledging schedules for both years were noted and possible reasons for the differences were suggested.

Breeding success, expressed as the numbers of pairs successfully fledging a chick, was recorded. Causes of egg and chick loss were recorded and the influence of predation was discussed in detail.

Observations were made on behaviour with particular attention being paid to those displays which involved characters of aggression. These displays were noted and their postures illustrated. The effects of high density nesting on the evolution of behaviour was discussed.

Results indicated that murres on Gull Island attained breeding success rates comparable with other areas but lower than most. Birds breeding at higher densities and on longer-established or "safe" ledges were most successful. Murres in this colony demonstrate a wide range of conflict behaviours with numerous appeasement displays functioning to maintain low levels of high intensity aggression.

Acknowledgements

I wish to thank Dr. Threlfall for supervising this work. His encouragement and suggestions were invaluable and contributed much, not only to this thesis, but to my entire M.Sc. program.

For their help throughout both years of this study I offer my sincere gratitude to Jim Foley and Frank Lapointe. I thank Jim for the valuable data his observations provided and especially for his preserverance on those wet and miserable days when any other occupation would have been preferable. To Frank, as well, I offer my thanks for help in gathering data; I particularly thank him for the drawings contained in this thesis and for printing and mounting many of the photographs. All of these have, through their meticulous preparation, contributed greatly to this work. The drawings, in particular, have been invaluable in their precise illustration of Common Murre behaviour. I thank both Frank and Jim for their help in repairing and transporting the Toyo raft.

To the Melvin family at St. Michaels I express sincere appreciation for their wonderful hospitality and for the opportunity to experience their truly Newfoundland way of life. To Mrs. Melvin I say thank-you for the many "lunches", I thank Wynn-Anne for her nail polish, Michael for his chain saw and Peter for his prayers.

To Mr. Louis Melvin I extend a very special note of thanks. I thank him for showing me the skills of Newfoundlanders - skills of boats and twine and knowledge of the sea and wind - skills which have made us Newfoundlanders the independent men we are. Finally I thank him for his warnings, for caution offered to a novice and delivered with

his usual keen perception of the "balance of things"; that he did not mind a few "whale backs" in his twine was also appreciated.

I express my gratitude to Dr. Gordon Bennett and Mr. David Jennings who proof read parts of this thesis. I thank Mr. Roy Ficken for photographing the behaviour illustrations and the embryos.

Particularly, I thank my wife Olivera, for typing this thesis and, most of all, for her consideration, patience and encouragement throughout the course of this work.

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Introduction

Many recent seabird investigations have developed as rigorous enquiries into the general principles of populations, adaption and evolutionary ecology (Ashmole, 1963; Birkhead, 1977; Cody, 1972). Such studies stand out in marked contrast to many of those conducted earlier which had as their focal points descriptions of natural history phenomena (Johnson, 1944). Such a transition has proceeded with (and grown out of) the concomitant emergence of the sociobiological theme which has attempted a definition of the "terms of reference" for inter-class comparisons (Wilson, 1975). This modern biological ambience has lent renewed importance to the study of social species.

The seabird family Alcidae, to which the Common Murre (*Uria aalge* Pont.) belongs, may have been evolved by the Cretaceous (Storer, 1952). The family is generally considered as belonging to the order Charadriformes, but considerable disagreement exists regarding its correct taxonomic position and its relevant subdivisions. Particularly, there is considerable evidence that strong relationships exist between the alcids and the Sphenisciformes (penguins) (Verheyen, 1958; Rabaey, 1963; Gysels and Rabaey, 1964). Further studies are clearly needed to decide the taxonomic position of the groups relative to each other.

The genus *Uria* is bispecific, with Common and Thick-billed (*Uria lomvia* L.) Murres being sympatric over parts of their ranges. Essentially the Thick-billed Murre is the more northerly species with various ecological and morphological adaptions which serve to reduce competition where both species overlap (Bedard, 1969; Spring, 1971).

The Common Murre breeds in colonies of up to a million individuals and is one of the most numerous seabirds in the northern Hemisphere (Tuck, 1960). Recent studies of this species have included an examination of its population characteristics (Leslie, 1966; Birkhead and Hudson, 1977), functional and morphological adaptations (Spring, 1971) and dispersal (Birkhead, 1974). Further investigations have examined the effects of various environmental contaminants on the species (Scott *et al.* 1975; Brown *et al.* 1973) and considerable attention has been paid to its breeding biology (Williams, 1974; Birkhead, 1977; Greenwood, 1964). Serious studies of the species' behavior have been much more infrequent with Birkhead's (1978) study representing an obvious exception.

Common Murres are distributed over the North Pacific and Atlantic Oceans and characteristically come to sea-cliff colonies in spring for breeding. In the Pacific they are found from California to Alaska, through islands in the Bering Sea and south to Hokkaido, Japan. In the eastern Atlantic their range extends northward to include Iceland, Bear Island, Novaya Zemlya and the Murmansk coast; southward they breed in the Baltic, the Faroes, Britain, Ireland and even in the Berlengas (Cramp *et al.* 1974). In the western North Atlantic they breed from Newfoundland (island) and the Gulf of St. Lawrence to about 56°N in Labrador, with a small colony in Greenland just south of the Arctic Circle (Tuck, 1960).

This species habitually nests in dense groups in close bodily contact and has been shown to share a number of common features with numerous other seabird groups (Lack, 1966). Such features include long expectation of life, deferred maturity and low reproductive output.

The objectives of the present study were (in general) two-fold.

Firstly, to examine the breeding biology of this species in what is a recent and small (about 600 breeding pairs) colony and secondly to examine the social behaviour of the species. For the latter endeavor emphasis was placed on those displays which showed characters of aggression.

Materials and Methods

The study was carried out on Gull Island, Witless Bay, Newfoundland ($47^{\circ}15'$N., $52^{\circ}46'$W.), during the summers of 1977 and 1978.

Gull Island, 27 km south of St. John's, Newfoundland, is the northernmost of 3 islands which comprise the Witless Bay Seabird Sanctuary, and is located 2.41 km from the nearest point of land. It is approximately 1.6 km long and .8 km wide with the long axis running in a true north-south line (Figure 1). The island attains a maximum elevation of 96 m (C.W.S. Map, 1969) and is heavily wooded except for a grassy perimeter ("Puffin slopes") and rock surfaces (Figure 2).

A census of the murre breeding population on Gull Island was carried out in both 1977 and 1978. Counts were made from the island and by compassing the island in a fifteen foot inflatable Toyo raft outfitted with a 9.9 horsepower Johnson Outboard Motor. The murres were counted several times during the course of the breeding season and numbers of eggs and chicks were also employed as population indicators.

Egg-laying, incubation, and fate of eggs were investigated by making regular observations at a number of colonies with special attention being paid to numbers 2, 3, 4, 5, 7, and 9a (Figure 3). To facilitate identification squares of numbered masking tape and (or) nail polish were positioned on the eggs. These labels indicated the number of the egg and the date on which it was laid. Eggs registered in this manner were used to obtain information on incubation period, egg dimensions and on weight changes during incubation. Egg dimensions were recorded using dividers and a millimeter ruler.

Egg volumes were calculated employing a number of equations (outlined

Figure 1

Map of Newfoundland showing location of study area. Inset shows the area in detail.

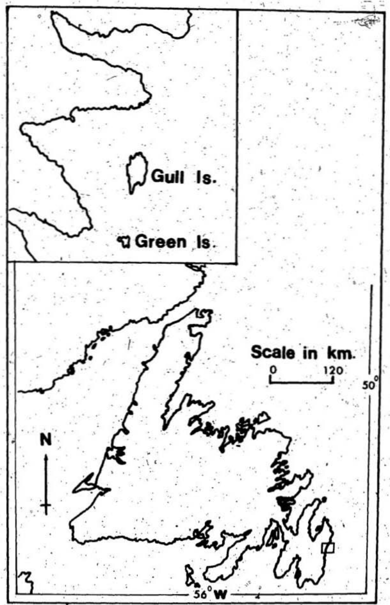

Gull Is.
Green Is.
Scale in km.
0
120
50°
N
56° W

Figure 2

Gull Island showing the vegetation zones.

1. exposed rock with lichens
2. grass and exposed peat
3. forest
4. open-water bogs

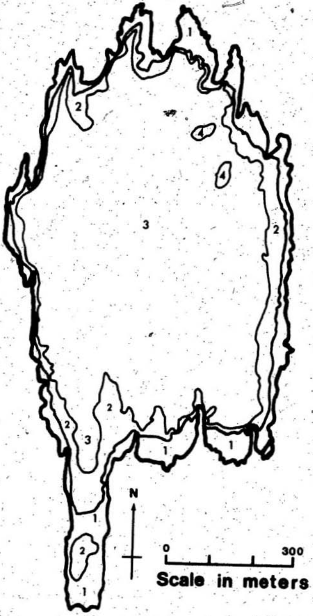
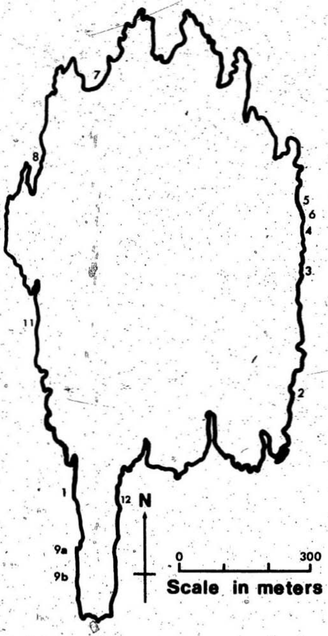

1
2
4
4
3
2
2
2
3
1
1
1
2
1
N
0
300
Scale in meters

Figure 3

Gull Island showing murre nesting sites.


7
8
5
6
4
3
11
2
1
12
N
9a
9b
0
300
Scale in meters

in table 6) and through water displacement experiments using 500 ml Pyrex beakers. Egg shapes were determined using the method outlined by Preston (1953), and by reference to Palmer (1962).

Fifty known-age eggs were collected in 1978 for a study of embryos. Eggs collected for this purpose were injected with 10 per cent formalin and returned to the laboratory. Here they were cracked and the shells and extraembryonic membranes dissected from the embryos which were dryed on a paper towel and weighed using an Ohaus 2610 g capacity triple beam balance sensitive to 0.1 g. Figure 4 shows the regions of the developing embryos that were measured.

Marked eggs were checked daily in 1977 and less often (usually every second day) in 1978 to determine hatching dates and pipping times. Once chicks appeared they were numbered by placing color bands and tape on the tarsi. Forty-seven chicks of known age were weighed and measured every second day in 1977 with twenty more chicks being subjected to similar analysis in 1978. In the latter season chicks were weighed less frequently in an effort to reduce chick loss due to human interference.

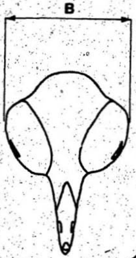
Chicks were weighed in a cloth bag suspended from a 300 g capacity Pesola Spring balance (sensitive to 1 g). Measurements taken with a millimeter ruler and dividers included culmen length and depth, tarsus, hand, forearm and middle toe. Wing chord measurements were taken along the outstreched contour of the wing, the tenth (outermost) primary was measured from the point the fleshy sheath emerged from the skin to the tip of the feather. A record of feather development from hatching to fledging was also kept.

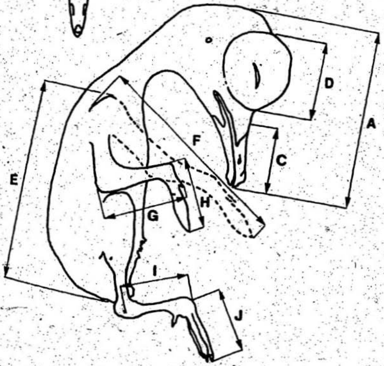
Rectal temperatures of chicks of known age were recorded using a YSI

Figure 4

Measurements taken on murre embryos

A. head length
B. head width
C. culmen
D. eye diameter
E. shoulder to tail length
F. arm length
G. forearm
H. hand
I. tarsus
J. middle toe


B


D
F
A
C
E
H
G
I
J

model telethermometer with #423 insert probe.

Identification of food items brought to chicks was made via direct observation of the prey in the adult murre's beak or by retrieving unconsumed specimens from the ledge surface.

Observations on behavior were conducted from vantage points at various distances from several ledges. Sites were chosen so as to minimize disturbance in the colonies. The oblique nature of the puffin slopes above the murre ledges and the presence of rock outcroppings allowed the observer to get, in some cases, within 10-15 m of the nesting murres without causing disruption of regular breeding activity. Observations were conducted using 7 x 35 Mayfair binoculars and/or a 15-60X Bausch and Lomb spotting scope, without the use of a blind. Most observations were conducted from distances greater than 50 m.

Results and Discussion

Part I: Breeding Biology

Population

The distribution and numbers of Common Murres in eastern North America are shown in figure 5. The species has generally increased in this region during the past forty years and Tuck (1960) associates this with a general warming trend in the marine environment (Hare, 1955).

The Common Murre population of Newfoundland is presently increasing, with an estimated 600,000 pairs nesting along the island and Labrador coastlines (Brown *et al.*, 1974). The species first colonized the Witless Bay Islands in about 1936 when small numbers were observed to breed on Green Island. By 1958 this population had reached approximately 50,000 pairs, a large, but not unsurpassed, increase; Tuck (1960) records an increase on Funk Island of more than 400,000 pairs for the same period.

The murre colony on Gull Island is a good deal more recent than that of Green and almost certainly represents an overflow from the latter population. Figure 6 demonstrates the increases that have occurred on both islands; several points are worthy of note.

From 1941, when Peters and Burleigh (1951) recorded 3000 breeding pairs, until 1958, the Green Island population increased to 50,000 pairs (Tuck, 1960). Between 1958 and 1974 the population further increased by approximately 24,000 pairs resulting in an estimated total population of 70,000 breeding pairs for the latter year (Brown *et al.*, 1974). The second period of increase (1958-1974), while of similar duration, was only one half the magnitude of the first (1941-1957). If these figures do adequately reflect the permutations in this population, then, certainly

Figure 5

Distribution and numbers of Common Murres in eastern North America (after Brown *et al.* 1975)

p= pairs
i= individuals
I= island

Colony # & Location	Size	Census year	Authority
1 Nunarsuk I.	150p.	1953	Tuck 1961
2 Quaker Hat.	30p.	1952	" "
3 Herring I.	475P.	1952	" "
4 Outer Gannet I.	17,700p.	1972	Nettleship & Lock
5 Gannet Clusters	17,500p.	1972	" "
6 Wester Bird I.	50p.	1953	Tuck 1961
7 Little Bird I.	725p.	1972	Nettleship & Lock
8 Bird I.	250p.	1972	" "
9 St. Mary's I.	4,120i	1972	Nettleship & Lock, 1973b
10 Wolf Bay	1,510i	1972	" "
11 Carrousel I.	4i	1972	" "
12 Gullcliff Bay, Anticosti I.	?i	1972	Nettleship
13 Heath Point, Anticosti I.	2i	1972	"
14 Shallop R., Anticosti I.	?2	1972	"
15 Bonaventure I.	17, 162p.	1974	Nettleship & Taylor
16 Bird Rocks, Magdalen I.	500-1000i	1973	Nettleship
17 Grand Colambier I, St. Pierre	40i	1964	Cameron 1967
18 Cape St. Mary's	2,500p.	1959	Tuck, 1961
19 Western Head, St. Mary's Bay	100i	1973	Nettleship
20 Great I, Witless Bay	2,800p.	1973	"
21 Green I., Witless Bay	74,000p.	1973	"
22 Gull I., Witless Bay	687 p.	1978	Mahoney
23 Baccalieu I.	2,500 p.	1959	Tuck 1961
24 South Cabot I.(= Little Cabot)	2,000p.	1973	Nettleship
25 Funk I.	500,000p.	1959	Tuck 1961
26 Guppy Islets	25i	1973	Nettleship

7

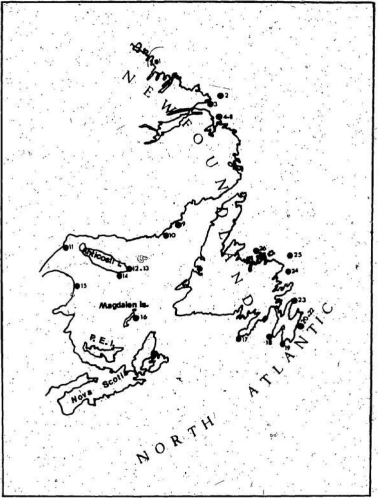
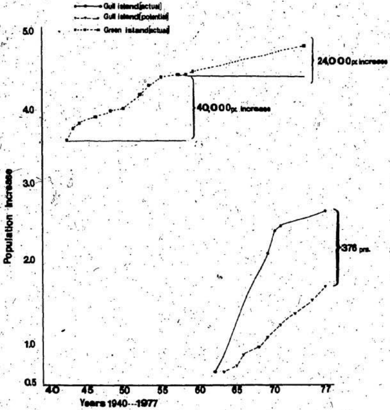

NEWFOUNDLAND
1
2
3
4-8
9
10
11
Anticosti I.
12-13
14
15
Magdalen Is.
16
P. E. I.
Nova Scotia
17
18
19
20-22
23
24
25
26
NORTH ATLANTIC

Figure 6

Changes in numbers of Common Murres breeding on Gull and Green Island (1940-1977).

Gull island[actual]
Gull island[potential]
Green island[actual]
5.0
4.0
3.0
2.0
1.0
0.5
Population increase
24,000px increase
40,000px increase
376 prs.
40
45
50
55
60
65
70
77
Years 1940---1977

since 1958, the rate of increase has experienced a marked reduction. It should be noted however, that accurate estimates of cliff-nesting populations are often difficult to obtain and the numbers they produce always involve some margin of error (Lloyd, 1968; Tuck, 1960). Nevertheless, the trends indicated certainly agreed with personal observations (Threlfall and Tuck pers. comm.).

The colony on Gull Island began in the early 1960's. While Peters and Burleigh (1951) reported 50 pairs breeding on Gull Island in 1942, Tuck (pers. comm. to Haycock, 1973) observed loitering murres but no eggs or chicks from 1951 to 1961. In 1962 four or five pairs bred on the island and from that point onward the population has increased substantially. One hundred and thirty-six pairs were counted in 1969 (Haycock, 1973) and during the 1978 season a breeding population of 678 pairs was recorded. Table 1 records the population changes that have occurred at the various sites since 1971. Figure 7 shows how the murres have spread around the island during this same period.

The population increase recorded for Gull Island is beyond that possible for the original (1962) population. As figure 6 indicated there exists a difference of 356 pairs between the actual population recorded for 1977 and the predicted one based on a generous accumulate breeding success estimate of 60 per cent. Therefore, not only does the Gull Island population increase start very close to where the Green Island population's rate of increase begins to subside, but obviously recruitment from some external source must continually be involved to sustain the phenomenal rate of increase which continues to occur on Gull Island. While confirmation of this movement awaits banding studies, circumstantial evidence suggests

Table 1

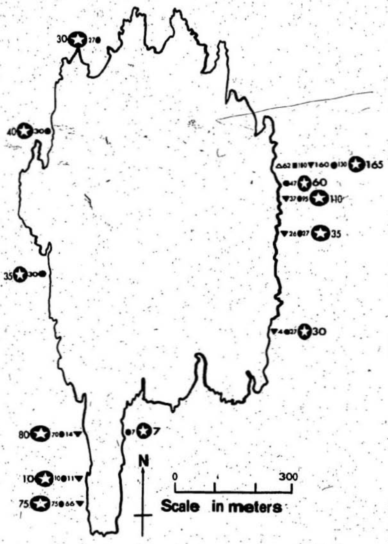
Population Changes For Gull Island (Nos. Prs.)

Year	Entire Is.	1	2	3	4	5	6	7	8	9a	9b	10	11	12	Source
1962	4-5	-	-	-	-	-	-	-	-	-	-	-	-	-	Tuck (pers. com.)
1969	136	-	-	-	-	62	-	-	-	-	-	-	-	-	Haycock (1973)
1970	260	-	-	-	-	180	-	-	-	-	-	-	-	-	Haycock (1973)
1971	316	14	4	26	37	160	-	-	-	11	66	-	-	-	Haycock (1973)
1977	589	70	27	27	95	130	47	27	30	10	75	10	30	7	This study
1978	687	80	30	35	110	165	60	30	40	10	75	10	35	7	This study

Figure 7

Changes in numbers of Common Murres breeding at individual sites on Gull Island (1969-1978). Observations discontinuous as indicated.

1969: Clear triangle
1970: Square
1971: Solid triangle
1977: Circle
1978: Star

30 ☆ 27 ●
40 ☆ 30 ●
△ 62 ■ 180 ▼ 160 ● 130 ☆ 165
● 47 ☆ 60
▼ 37 ● 95 ☆ 110
▼ 26 ● 27 ☆ 35
35 ☆ 30 ●
▼ 4 ● 27 ☆ 30
80 ☆ 70 ● 14 ▼
● 7 ☆ 7
10 ☆ 10 ● 11 ▼
75 ☆ 75 ● 66 ▼
N
0
300
Scale in meters

the Green Island population as the source of the murres breeding on Gull Island.

Murres, like many other seabirds (Nelson, 1966; Coulson and White, 1956), show a seasonal pattern of colony attendance. In overview this pattern sees a return to the colony after a period of absence, initially by experienced breeders and later by immature non-breeders. Once on the ledges, population changes occur as responses to a number of factors including egg-laying, incubation, chicks, feeding strategy and weather. The immature non-breeders leave the colony earlier in the season than breeding birds and are joined by some failed breeders. This exodus precedes the major departure which occurs at the time of fledging, and results in large segments of the population leaving within a relatively short period of time (figure 8).

On Gull Island and in Newfoundland generally, murres usually return to land in March and take up residence in April or May. Even at these latter dates they may sometimes leave the island for periods of a couple of days or more. This situation is very much different from that which occurs in Britain where the birds return to the ledges in October or early November and essentially remain at sea only during the moulting period (Birkhead, 1976).

The seasonal pattern of attendance on Gull Island is represented in figure 9. Part a of this figure illustrates the population changes which occurred during the pre-laying period and shows that numbers alternated between high and total absence. No regular cycle of activity comparable to Birkhead's (1976) five to six day periodicity was observed for the Gull Island population. This greater irregularity may be due to the later return of the Newfoundland birds and their consequential lower level of

Figure 8

Composition profile of a "general" murre breeding population.

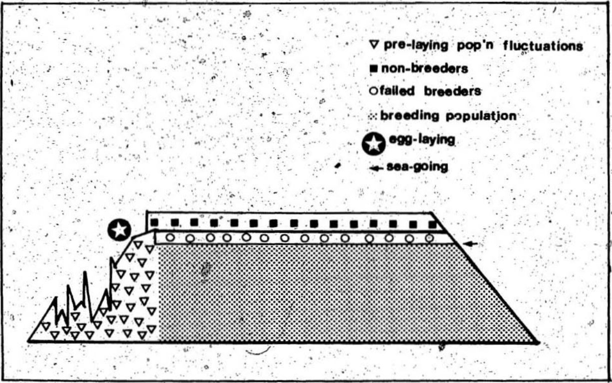
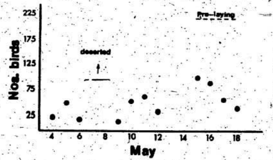
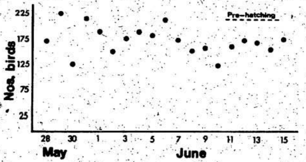
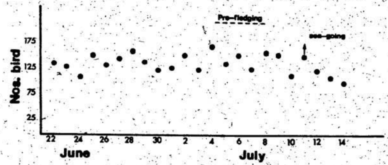

▽ pre-laying pop'n fluctuations
■ non-breeders
○ failed breeders
▨ breeding population
egg-laying
← sea-going

Figure 9

Seasonal attendance patterns of murres on Gull Island.


Nos. birds
225
175
125
75
25
deserted
Pre-laying
4
6
8
10
12
14
16
18
May


Nos. birds
225
175
125
75
25
Pre-hatching
28
30
1
3
5
7
9
11
13
15
May
June


Nos. bird
175
125
75
25
Pre-fledging
sea-going
22
24
26
28
30
2
4
6
8
10
12
14
June
July

acclimatization. At this stage weather exerts a strong influence on colony attendance (page 33), something Birkhead (1976) also noted for the Skomer population.

With the appearance of eggs and chicks the irregular patterns of attendance are lost. At these stages the murres are involved with the incubation of eggs and the brooding and feeding of chicks. Figures 9b and 9c show the more regular patterns of attendance during these prehatching and posthatching periods. As the first of these figures indicates attendance becomes more regular as the number of layings increase and more birds begin incubating.

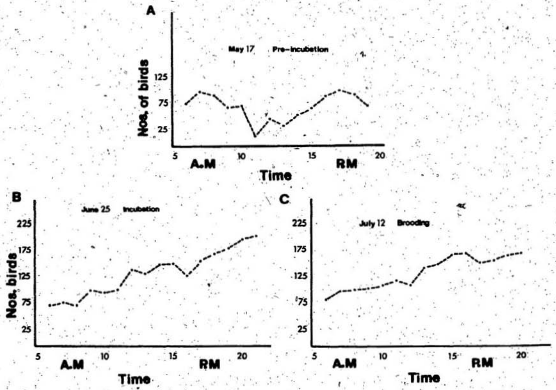
Attendance was also quite regular during the brooding period (figure 9c). Daily fluctuations did occur but they were of smaller amplitude than those observed for the pre-laying period especially, and for the early incubation period as well.

Birkhead (1976) noted a general increase in murre numbers on the ledges up until the time of fledging as a result of the piecemeal arrival of immature birds. This was not the case on Gull Island where these birds occurred almost exclusively in clubs, i.e. in loafing areas away from the breeding ledges.

Patterns of attendance over twelve to fourteen hour periods for an individual ledge were also recorded. In figure 10a the population changes for site number five during a continuous twelve hour period are recorded. Peak numbers are indicated for the early morning and late afternoon. While, the assumption is certainly interpretive, the pattern evidenced may indicate that at this time, many birds spend the hours of darkness at sea. If so, this would agree in part with Birkhead's observations which suggest that

Figure 10

Daylight patterns of attendance at site 5 during the pre-incubation, incubation and brooding periods.



A
May 17 Pre-incubation
Nos. of birds
125
75
25
5
10
15
20
A.M
P.M
Time
B
June 25 Incubation
Nos. birds
225
175
125
75
25
5
10
15
20
A.M
P.M
Time
C
July 12 Brooding
225
175
125
75
25
5
10
15
20
A.M
P.M
Time

in British populations non-incubating and non-brooding birds spend the night away from the ledges.

During the incubation and brooding periods (figures 10b, 10c) colony numbers gradually increased throughout the day reaching their maximum levels late in the evening. The lower levels recorded during early morning observations might mean that a number of birds had departed before the counts began. Certainly the steady increase in the late evening hours suggest that the greater percentage of the birds do remain on the ledges overnight.

The seasonal aspect to these daily fluctuations may be explained in terms of the gradual development of an increasingly affective tie to the land. As the breeding cycle progresses the appearance of eggs and chicks holds more birds on the ledges at all times of the day.

The most striking difference in colony attendance between the British and Newfoundland populations is seen in their respective arrival dates at the breeding site. The British populations return to the ledges after only a brief period of absence (approximately three months), while the Newfoundland birds remain away from the land for seven months or more. Birkhead (1976) views the early return of British populations as being closely associated with competition for nest sites, and cites the works of Dennis (1967) on Faire Isle (Scotland) murres and Nelson (1964) on Bass Rock (Scotland) Gannets (*Morus bassanus* L.) in support of his thesis. In both these instances population increases have coincided with earlier returns to the breeding ledges. In these situations the birds return to the colony soon after completion of the moult to ensure maintenance of their nest-site for the oncoming breeding season.

Certainly in situations of intense competition early establishment of nest-site ownership would be advantageous. Why then don't the Newfoundland populations, which breed at densities comparable to, and even greater than, the British populations, return earlier to their breeding ledges?

The mean annual air temperature for the month of January in the Skomer region is about 6^{0}C (Cramp *et al.*, 1974) which is higher than that for the month of May in the Witless Bay area. Furthermore, ledges in Newfoundland colonies are covered with ice and snow for extended periods of time and thus offer a sharp contrast to the situation in Britain. Weather then, might certainly be a factor in keeping Newfoundland murres at sea for longer periods of time. It should be noted here that *U.a. hyperborea* frequently lays its eggs on ice and snow (Belopolskii, 1957) but murres here may simply not have evolved this capacity. Possibly, if populations continue to expand, selective pressure may favor earlier return to the colonies, but in the present situation new colonies are being established and populations of longer residence continue to expand. These facts indicate that while certain colonies show very dense populations room for expansion does exist.

The varying schedules of colony attendence shown by different populations are undoubtedly responses to a multiplicity of factors. At present our knowledge of seasonal variations in diet of seabirds and the distrubution of their prey is meagre. In fact, even the distribution of seabirds themselves in the non-breeding season is only generally known and banding recovery data consistently present a biased view. Consequently, interpretation of the varying patterns of colony attendance remains sketchy. Much work is needed to elucidate the "why" of seabird movements and to round out our knowledge of their general biology.

Subspecies

Of the seven recognized subspecies of Common Murres (Salomonsen, 1944), those breeding on Gull Island belong to the subspecies *U.a. aalge* which occupies a wide geographic range streching from eastern North America across the North Atlantic to Great Britain. Intergradation of this subspecies with others occurs at Vesteraalen with *U.a. hyperborea*, in Scotland with *U.a. albionis*, and at Shetland with *U.a. spiloptera* (Tuck, 1960).

"Nest Sites"

Common Murres nest on a variety of ledge surfaces which include flattened outcrops, beneath overhangs and even under boulders (Belopol'skii, 1957). On Gull Island they nest in a diversity of ledge locations.

In site 9b (figure 3; plate 1) murres were found nesting in a very protected crevice which was approximately one half meter wide. The ledge in this case was overhung by a large rock formation and eggs were cradled protectively in the seam. Below this ledge the cliff fell inwards so that the entire ledge formed an overhang, making it hard to imagine a more secure place for a bird to raise its young.

Conditions were very much different in site 5 (figure 3; plate 2). Here a very broad gentle slope (approximately 65^0) ran two thirds the way down to the sea and then dropped a distance of 15 meters to a jumble of sea-washed rocks below. Here birds, eggs and chicks were very exposed.

Lying somewhere between these two extremes were most of the other nesting sites on the island. In sites 7 and 2 (figure 3; plates 3 & 4) the murres were nesting adjacent to the turf and in the former site a newly exposed ledge was being used mainly as a resting platform. This platform still retains a covering of topsoil although the turf has been lost. The

Plate 1

Site 9b showing the sloping ledge and overhang above. Birds on the extreme left of the photograph are leaning out from the crevice. A murre in the center foreground has a fish in its beak.

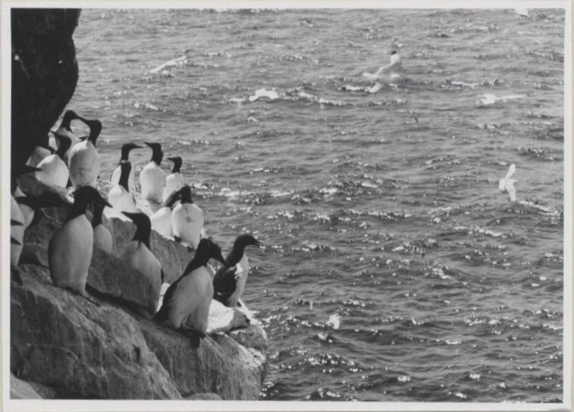


Plate 2

Site 5 showing the broad sloping ledge and the sea-washed rocks below. The crevice noted in the center foreground and extending three quarters the way up the slope was frequently followed by young murres on their way to sea at fledging.

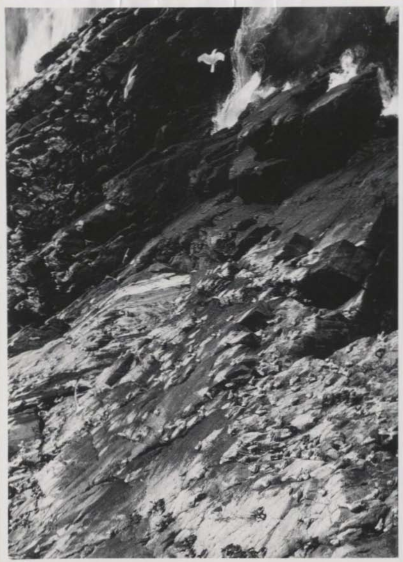


Plate 3

Site 7 showing how the murre (and Kittiwake) nesting ledge extends up to the "puffin slopes" above. The turf platform referred to is the upper dark band noted running longitudinally across the ledge.

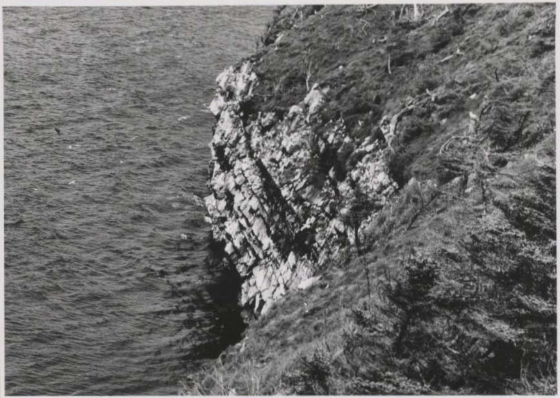


Plate 4

Site 2 in close up showing a ledge in more detail. Note the "step-like" aspect to the ledge which is important in influencing density and incubation position of breeding birds. Chick in the upper right-hand corner is approximately 15 days of age.

nesting of murres on topsoil or even turf has been previously reported (Tuck, 1960).

Eventually this topsoil will be eroded through natural processes and the scraping and wing beating of the resident murres. The end result will be a typical (and new) breeding ledge. Murres are one of the few species which "create" their own habitat in such fashion.

Egg laying

In 1977 laying commenced on 14 May and continued until 29 June; the 1978 season differed slightly from this with initiation and termination dates of 21 May and 4 July respectively. Table 2 compares these dates with those obtained for the species in various other localities. In 1969 Haycock (1973), during an ecological study of the island, noted the first murre egg on 30 May with laying continuing until 17 July. Such protracted laying periods are certainly the results of relayings and the delayed arrival of first time breeders (Tuck, 1960). Figure 11 shows the distribution of layings for sites 2, 3, 4, and 5 over the course of the breeding season on Gull Island.

The chronology of laying was very different in 1977 and 1978. In the first year laying was generally intense from 16 May until approximately 10 June (85 % of total egg production) while 1978 showed a very restricted and intense burst of laying from 28 May until 5 June (46 % of total egg production). While it is difficult to account for any phenomenon influenced by so many factors, slight differences in weather in the early parts of both seasons may well have been one of the contributing factors. Table 3 gives values for some relevant meteorological parameters for the month of May in 1977 and 1978. The differences between the two years do

Table 2: Nesting phenology of the Common Murre (after Tuck, 1960)

	Egg Date	Sea-going Date	Source
Eastern Atlantic			
Shetland Islands	-	July 12, 1946	Perry (1948)
Farne Islands	3rd week in May	-	Watt (1951)
Faeroe Islands	May 15	-	Salomonsen (1935)
St. Kilda	May 15	-	Witherby *et. al.* (1941)
Wales (Skomer I.)	-	July 11, 1946	Keighley & Lockley (1947)
Yorkshire	May 14	-	Witherby *et sl.* (1941)
Channel Islands	1st week in May	-	Dobson (1952)
France (Toulinguet)	May 19, 1926	-	Berhet (1947)
Western Atlantic			
Labrador	-	August 3, 1953	Tuck
Gulf of St. Lawrence	May 20	July 27, 1930	Bent (1919), H.F. Lewis (in litt.)
Newfoundland	May 22, 1952	July 14, 1952	Tuck
Newfoundland	May 14, 1977	July 11, 1977	Mahoney
Newfoundland	May 21, 1978	July 20, 1978	Mahoney

Table 3

Weather Parameters For The Month of May 1977 and 1978

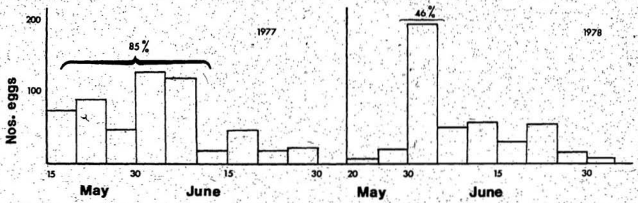
Parameter	1977	1978
Mean Max. Temperature	8.7°C	9.2°C
Mean Min. Temperature	0.6°C	0.2°C
Mean Wind Direction and Speed	WSW/19.6Km/h	WSW/22.1Km/h
Total Precipitation (Rainfall)	76.0 mm	40.7 mm
Total Precipitation (Snowfall)	2.1 mm	4.9 mm
Min. Temperature	-4.4°C	-6.1°C
Mean Temperature	4.7°C	4.7°C
Date of Min. Temperature	May 2	May 7 *

* Departure Date From Gull Island in 1978

Figure 11

Chronologies of egg-laying at sites 2, 3, 4 and 5 for 1977 and 1978.

Note: These figures do not represent total egg production for these ledges.


Nos. eggs
200
100
85 %
1977
46 %
1978
15
30
15
30
20
30
15
30
May
June
May
June

not appear significant and yet a phenomenon observed on Gull Island in 1978 indicates that perhaps enough difference existed to meaningfully affect the population.

On 7 May, 1978 the murres (and puffins) deserted Gull Island. Observation of Green Island indicated that very few birds were present there either. Although admittedly circumstantial, it is interesting that this exodus occurred on the day of the month (and of the entire breeding season) with the lowest temperature (-6.1^{0}C) and followed two days of very cold northerly winds. The murres had most definitely been active on the ledges previous to this and had been involved in courtship activity. Possibly this one very cold day and night and the two previous cold days with northerly winds drove the birds from the island. Conceivably this departure and disruption of breeding site contact, might have retarded follicular development and resulted in later laying dates. This could easily be seen to differentially affect the population so that essentially only those birds which would have laid early would be affected. The overall result therefore, would be to compress the layings by having early layers (affected) and later layers (unaffected) all lay at the later dates. Uspenski (1956) has provided evidence that murres are subject to rapid gonad recrudescence and that at the beginning of the breeding season their gonads are not fully developed. Given this fact, and the tight schedule of murre breeding activity, the two day absence from Gull Island (May 7 & 8) could seriously effect the entire cycle.

Certainly other interpretations are possible. For example, it is well known that the tie to land is gradually developed in murres (Tuck, 1960). It is quite possible that the murres had initially returned to the island at a later date in 1978 than in 1977 and had therefore been much more easily driven from the ledges. Such a situation would automatically have led to a later beginning to the laying period.

It is also possible that the intense synchrony of laying in the second season (albeit belated) meant that fewer eggs were lost and replaced because of greater assiduousness of incubation. This difference could have expressed itself in the critical first few days of incubation when most eggs are lost, and after which, eggs, when lost, may not be replaced.

The postponement of laying in 1978 had other ramifications. Total egg production was less for the sites examined in 1978 than in 1977. This was most probably a reflection of there being less time over which to lose and then relay eggs. In social species, where density works to affect various aspects of the breeding cycle through social facilitation (Wilson, 1975), the collapsed time frame evident in 1978 could have reduced the likelihood of relayings as the season progressed.

The loss of eggs in a murre colony is substantial and breeding success would be very much lower than it is if these birds were not capable of replacement laying. Table 4 presents data from three intensively studied ledges. In 1977 the mean percentage of relayings for all three ledges was 84 per cent, a figure greater than Uspenski's (1956) value of 77.3 per cent but less than Kaftanovski's (1951) of 100 per cent.

The values recorded for 1978 are very much lower and can be related to those factors previously discussed regarding egg-laying chronology.

Eggs laid as replacements are smaller than initial layings; the mean weight of replacement eggs (N= 30) was 10.43 g less than that of the first eggs laid. The mean time between disappearance of one egg and the

Table 4

Numbers of pairs laying replacement clutches (%)

Site Number	% of Pairs Laying Second Egg		Mean %	
	1977	1978	1977	1978
2	92%	50%		
3	81%	48%	84%	41%
4	78%	26%		

laying of a replacement was 15.54 days (range 14-18), a figure in general agreement with that of Uspenski (15-22 days).

Factors influencing relaying and the duration of intervals between successive clutches include food conditions in a particular year or area, the age composition of the colony in question, and the length of incubation of lost eggs (Slepstov, 1948; Tuck, 1960).

Regarding this last factor, Kraftanowskii (1951) reported that eggs incubated for twelve to fifteen days were not usually replaced, if lost. On Gull Island however, eggs incubated for sixteen days and more were frequently replaced.

In reference to the first factors one can only say that the age composition of Gull Island, being (presumably) an overflow population, would be expected to show a high proportion of inexperienced breeders. Prey species appeared to be abundant during both years although Capelin (*Mallotus villosus* Müller) did not enter Witless Bay in as great a number in 1978 as in 1977. Without detailed information on the latter factor it is difficult to suggest causal relationships.

Eggs

Two hundred and eighty-seven eggs were weighed and measured during the 1977 field season. Analysis revealed a mean weight of 108.39 g (S.D. 9.24) with maximum length and breadth having means of 82.67 mm (S.D. 3.58) and 50.87 mm (S.D. 2.16) respectively. The figure quoted for mean weight underscores the large size of this egg representing as it does eleven per cent of the adult female body weight. These figures are very similar to those quoted by numerous other researchers for this species. Thus Uspenski (1958) stated mean lengths and breadths of forty-four murre (*U.a. hperborea*) eggs in Novaya Zemlya as being 84.1 mm and 51.4 mm respectively. This same author noted a mean egg weight of 111.7 g representing 10.6 per cent of the mean adult body weight for *U.a. hyperborea*. Mean dimensions given by Tuck (1960) for eggs of four *Uria aalge* subspecies are also quite similar to those recorded for Gull Island birds with mean length having a value of 82.94 mm (S.D. 1.76) and mean width of 50.86 mm (S.D. 1.07). Table 5 compares measurements of Gull Island eggs with those from other areas.

Eggs collected on Gull Island demonstrated the characteristic murre shape having one very blunt end and one very tapered one. Nevertheless, as plate 5 demonstrates considerable variation exists regarding the exact outline of the egg perimeters with the long pyriform and long oval designations of Palmer (1962) being the most frequently encountered. The classic murre egg is represented by the former appellation.

Methods for describing in a precise manner the shapes of bird's eggs have been the subjects of considerable investigation. Kaftanovski (1941) described the egg forms of all auk groups according to index F, i.e. the length of the pointed half in proportion to the length of the broad half. The results of this indexing proved Common Murre eggs to have the highest mean values of F or, in other words, were examples of the typical pyriform egg being most removed (of all auks) from the more normal elliptically-shaped egg.

Preston (1953) developed a more rigorous method for determining the shape of any egg which employs parametric equations and the determination of values for three variables (C_1, C_2, C_3). The first two variables (C_1, C_2) are general expressions of how far removed the egg contours are from a sphere or, more exactly, how closely they resemble the simple ovoid. More

Table 5

Comparative Measurements (mm) of Common Murre eggs
(after Tuck, 1960)

Subspecies	Number in sample	Mean Dimensions	Source
aalge	64	81.0 x 50.3	Bent (1919)
	287	82.7 x 50.9	This study
	100	81.7 x 50.0	Witherby *et al.* (1941)
albionis	100	81.5 x 49.7	Witherby *et al.* (1941)
californica	74	82.2 x 50.2	Bent (1919)
hyperborea	44	84.1 x 51.4	Uspenski (1956)
	29	84.5 x 52.5	Le Roi (1911)
	21	85.6 x 51.9	

specifically the C_1 term is an expression of how much the broad end contour of the egg is removed from the simple oval— as C_1 increases the broad end of the egg becomes more expansive. C_2 is also called the Biconical Term and indicates the tendency of both ends of the egg to be slightly more conical than in the Simple Ovoid shape. According to the jargon developed by Preston (1953) the Standard Avian Egg Shape refers to eggs which possess significant values for only these first two terms with C_3 being usually zero or negligible.

C_3, where it is expressed, emphasizes the attenuation, of one end of the egg and the blunting of the other. Preston discerned sizeable values of C_3 only in murres and their allies and called an ovoid in which C_3 is important an Alcid Ovoid. Thus using Preston's scheme murre eggs have a very high C_1 term (have a broad upper end), a very small C_2 term and a high C_3 value.

The shape of a bird's egg is probably acquired while it is in the magnum of the oviduct (Welty, 1962). The diameter of the oviduct, muscular tension of its walls, the packing of visceral organs and the shape of the pelvic bones, have all been implicated as factors in its particular geometry (Welty, 1962). The shape of the murre pelvis which is very shallow indeed agrees with Rensch's (1947) correlation of the deeper the pelvis the rounder the egg.

Other aspects of the eggs investigated and their determined values are as follows. Mean area of the eggs was 107.53 cm^2 with egg density averaging 1.067 g cm^{-3}. Average shell weight was 9.697 g and shell density was determined to average 2.076 g cm^{-3}. All of these values were calculated using the equations of Paganelli *et al.* (1974) (Table 6a).

Table 6a

Allometric Equations For Determination of Egg Characteristics (Excluding Volume)

Characteristic	Equation
Area (A, cm^2)	$A = 4.835\ W^{0.662}$
Egg Density (P_e, gcm^{-3})	$P_e = 1.038\ W^{0.006}$
Shell Weight (W_{sh}, g)	$W_{sh} = 4.82 \times 10^{-2}\ W^{1.132}$
Shell Density (P_{sh}, gcm^{-3})	$P_{sh} = 1.945\ W^{0.014}$

Table 6b

Murre Egg Volume Calculations: Methods and Sources

Method	Source
$V = 0.445\ LB^2$	Bergtold, (1929)
$V = {}^{11}/_{21}\ LB^2$	Preston, (1974)
$\log V = \frac{\log A - \log 4.951}{0.666}$	Paganelli *et al.*, (1974)
Volumetric Displacement	Groebbels, (1927)

Legend Table b: V= volume, L= length, B= breadth (max.), A= area

Egg volumes were calculated employing a number of methods (Table 6b). Results ranged from 95.19 cm^3 (Bergtold) to 111.885 cm^3 (Preston) with the Paganelli *et al.* equation yielding a value of 100 cm^3. The actual volume as determined by water displacement experiments (N= 10) was 95.88 ml (cm^3) (S.D. 11.37). Presumably, for murres at least, the Bergtold equation most accurately determines volume. It should be pointed out, however, that eggs chosen for the water displacement experiments were selected as representing the widest range of murre egg shapes. This fact, together with the small sample size, could result in a non-representative mean. If this is the case, personal observation suggests that the mean would in fact be greater than that calculated, with the Paganelli value being a likely correct figure.

It has long been appreciated that during incubation an egg loses weight, and that this weight loss can be ascribed almost exclusively to the loss of water vapor (Drent, 1973). The average weight loss recorded for fifty murre eggs on Gull Island was 20.53 per cent (S.D. 2.83). Tuck (1960) stated that the egg loses approximately 20 per cent of its weight during embryogenesis. Similar figures have been recorded for other species as well with Barth (1953) obtaining a figure of 21.8 per cent for the Mew Gull (*Larus canus* L.). Indeed recent investigations into various aspects of egg weight loss (Drent, 1973, Ar *et al.*, 1974) indicate incubation time for a given egg weight to be inversely proportional to the water vapor conductance of the egg shell, with all eggs, regardless of size, losing approximately 18 per cent of their initial weight during incubation.

Water vapor conductance for murre eggs in this study was found to be 16.62 $mg.H_2o.day^{-1}\ torr^{-1}\ H_2o$ as calculated from the following equation:

$$G_{H_2o} = 0.43\ W^{0.78}$$

where G_{H_2O}= water vapor conductance of the egg (mg $H_2o.day^{-1}.torr^{-1}H_2o$) and W= initial weight of the egg (Rahn and Ar, 1974). The water vapor conductance of the egg is in turn set by the pore area and thickness of the shell with mean values of 3.01 mm^2 and .43 mm respectively being derived for murres on Gull Island. These values were determined using the following equations:

$$L= 5.126 \times 10^{-3}.W^{0.456}$$

where L= thickness of the egg shell (mm) and W= the initial weight of the eggs (g) and

$$Ap= 92.10^{-5}.W^{1.236}$$

where Ap= total functional pore area (mm) and W= initial weight of the egg (g). Both equations are from Ar *et al.* (1974).

The predicted incubation time for murres based on the equation of Rahn and Ar (1974) where incubation time (I) is equal to 5.2 times the quotient of initial weight of the egg (W) divided by the water vapor conductance of the egg (G H_2o) is 33.9 days. This figure is quite close to the 32 day actual value determined during the present study.

It is unknown whether the increase in pore area with weight is achieved by increasing the number of pores or their diameter but Tyler (1969) suggests a tendency of increasing complexity in pore structure with egg size. Both Tuck (1960) and Belopol'skii (1957) have commented on the significance of the egg shell thickness and porosity. Tuck (1960) has pointed out that the egg shell thickness reaches a maximum of 0.6-0.8 mm at those places where the egg comes into contact with the rock surface. The thinner portion of the shell located at the large end of the egg has a thickness of 0.4-0.6 mm (Uspenskii, 1958) a figure close to that determined for the Gull Island birds using the Ar *et al.* (1974) equation.

Kaftanovskii (1941) and Krasovskii (1937) both commented on the great porosity of murre eggs. According to the former author the average number of pores in the egg shells of murres is 1½-2 times as large as that found in shells of the Herring Gull (*Larus argentatus* Pont.) and Black Guillemot (*Cepphus grylle* L.). Undoubtedly this great porosity facilitates embryonic respiration under situations where the egg is covered with a slimy coating of excrement or is half submerged in a pool of water and bird droppings-conditions which are more the rule than the exception on murre ledges. Kaftanovskii (1941), in support of this statement, emphasized the fact that eggs of Puffins (*Fratercula arctica* L.) and Black Guillemots maintain a normal porosity as do those of seabirds whose eggs are deposited in separate nests which are kept relatively clean. As will be discussed later this high porosity is complimented by certain behaviors which also perform adaptively to ensure development of the embryo under the normally extreme conditions of murre incubation.

Tremendous variation exists in the colors and patterns found in murre eggs. As plate 5 demonstrates background color can vary from white (Munsell notation N 9.5) to an intense blue-green (5BG 8/4) with pale yellows (10Y 9/1) and pale greens (5G 9/1) also occurring. To compliment this background the entire egg surface is most frequently strewn with streaks and blotches of disparate shapes and sizes. Such markings are often concentrated at the blunt end of the egg, a not uncommon phenomenon in birds eggs generally (Welty, 1962). The colors of these surface markings range from black (N 2.0) through medium brown (5YR 4/4) to very dark brown (10YR 2/1).

Belopol'skii (1961), commenting on the varying colors and patterns found

Plate 5

Eggs of murres on Gull Island showing the great variation in background color, size and surface markings.

in the eggs of seabirds, stated that while the bright ground colors of murre eggs could not be considered cryptic the patterns of streaks and blotches certainly could be. Uspenski (1958), on the other hand, maintained that "it is possible to explain such variability in colour of eggs...by the fact that this characteristic has little or no significance for the species, not being firmly linked to natural selection." This same author maintained that the eggs were in fact made conspicuous by their surface appearance and that the assiduous incubation typical of the murre species was to be given a further measure of significance as a preventative means of keeping such arrestive morsels out of the sight of predators.

Experiments conducted by Tuck (1960) on egg selection by the Greater Black-backed Gull (*Larus marinus* L.) demonstrated that for 77 per cent of the trials (N= 9) this species selected a plain white puffin egg in preference to a coloured murre's egg. While this evidence certainly is not definitive it does suggest that the variations of colour and markings lend some survival value to the individual.

With this degree of variation it is surprising that murres do not appear capable of distinguishing their own eggs. While numerous authors have commented on this fact (Tuck, 1960; Uspenski, 1958) only one has provided evidence to the contrary. Tschanz (1959) stated that members of a pair behave selectively toward their own egg on the basis of colour and pattern. However, in the same study birds were seen to adapt to eggs of a new colour and pattern if the appearance of the egg was changed gradually. Tschanz (1959) also stated that there was a combined affect of area and egg, the two factors performing mutually to produce the strongest inhibitions against incubating a foreign egg.

During the present study eggs were substituted in five separate incidents. In all cases the eggs exchanged varied a great deal in shape, color and size and, in all cases, the murres involved unhesitatingly incubated the new egg. In one of these instances the exchange involved a Herring Gull egg which was incubated and successfully hatched by the murre foster parent.

While it is difficult to explain the singularity of Tschanz's findings certainly his comment concerning the affect of area on the acceptance of a strange egg is agreed with. Occupying, as they do, a very small area of ledge amongst a dense group of conspecifics, murres have strong inhibitions toward trespassing. This will be discussed at length later in this thesis.

Embryology

For the present study weights and measurements of twenty-six embryos were taken from the 6th day after laying, until 28 days or just before hatching. Embryo weight attained 50 per cent of the embryonic maximum at 25 days (approximately 6 days before hatching). As demonstrated in figure 13 weight increase up until day 20 was quite gradual ($b= .320$) as compared with the increase shown for days 21-28 ($b= 3.66$, $p<.05$). The general shape of the weight gain curve compares favorably with those obtained by Haycock (1973) for Herring Gulls and Maunder (1971) for Kittiwakes (*Rissa tridactyla* L.). The average rate of weight increase recorded in this study, 1.9 g per day, is very close to that obtained by Harris (1964) and Haycock (1973) for Herring Gulls, their values being 2.0 g and 1.9 g per day respectively.

Embryos at 6 days (plate 6a) showed very pronounced cerebral development with the mesencephalon being much exaggerated. The prosencephalon and rhombencephalon were easily discerned, as were the front and hind limbs. While the digits had not yet begun to differentiate the distal portions of

Figure 12

Weights of murre embryos over the course of their development.

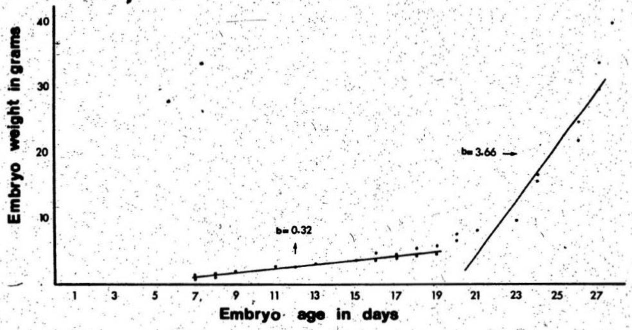

Embryo weight in grams
40
30
20
10
b= 0.32
b= 3.66
1
3
5
7
9
11
13
15
17
19
21
23
25
27
Embryo age in days

Plate 6

Murre embryos at various stages of development

b- 17 days
a- 6days c- 21 days e- 28 days
d- 25 days


METRIC 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

the limbs had broadened. The eye at this stage was pigmented and manifested a well-defined lens. As is typical of avian embryos (Hamilton, 1965), the head at this stage was the most prominent section of the body with the beak just beginning to differentiate from the general head mass.

By eleven days the midbrain had begun to lose its prominence and the general contour of the brain had taken on a more equable form. While pterylae remained undeveloped, tiny protuberances could be discerned over the general body surface, marking the sites of future follicular eruptions. Digits had now begun to differentiate on the forelimb with the pollex being particularly noticeable. The beak had further lengthened with the egg tooth having appeared as a tiny white protuberance encircled by a fascia of pigment granulations. The eyelid had increased to cover approximately 50 per cent of the eye. All three digits of the hindlimb had become distinguishable with their distal ends having become flattened foreshadowing the appearance of claws.

The small protuberances first noted on day 11 had further developed by day 17 (plate 6b) and had extended to regions where previously they had been absent; such regions included the eyelid and head region generally and the extremeties of both hand and tarsus. Along the humeral, alar, spinal and femoral tracts feather eruption had taken place and, due to the increase in eyelid dimensions, the eyes had begun to close. Nails could easily be discerned on all three toes as projections beyond the perimeters of the webbed feet. The bill had increased in length reaching 50 per cent of the embryonic maximum with the white centrum of the egg tooth having expanded to dilute the pigment circle so prominent on day 11. Further, the upper manible had taken on a decidedly hooked appearance, a somewhat surprising development considering the very straight lines of the adult beak. Shoulder to tail and arm dimensions had also attained 50 per cent of the embryonic maximum.

Further changes in the bill had appeared by day 21 (plate 6c) with the distal portion of the lower mandible showing a slight swelling. The hook on the upper mandible had become much more prominent as had the egg tooth. These developments and the hardening of the entire bill structure all indicated preparedness for emergence from the egg. The eyes were completely closed by now and feathers had appeared on all body regions. Large blood vessels were quite noticeable at this stage particularly in regions lacking general integumentary pigmentation or feathering - e.g. tarsi, feet, lower jaw. Ear openings were clearly visible. Claws had further developed, having taken on a definite white coloration. The tarsus had now increased beyond 50 per cent of the embryonic maximum and a thin strip of webbing had developed on its undersurface. This webbing is retained in adults of this species whose members do not possess a hallux.

By day 25 (plate 6d) the entire body surface was covered with down feathers of approximately 10 mm in length. These neossoptiles were dark on the dorsum, light on the belly and showed a gradation of shades along the sides. The "silvering" evident in newly-hatched chicks (page 65) was observed at this point with numerous dark down feathers having a lighter aspect along their surface. The distal portions of all claws were turning darker as was the most distal one third of the upper mandible. Pigmentation was just appearing in the lower mandible which had seen a reduction in the swelling noticeable on day 21. The lower mandible contour had now developed with a drooping at the extreme distal end over which fitted the hook of the upper mandible. Scaling on the tarsus was apparent at this stage with the anterior scutellate and posterior reticulate patterns being clearly defined.

The tarsus and foot had taken on the characteristic greyish hue and the tarsal scaling had been completed by day 28 (plate 6e). The bill had turned darker than in earlier stages and the egg tooth appeared much as it does in newly-hatched chicks. The hook on the upper mandible was still present but the lower mandible now appeared of very even contour. The neossoptile covering was noticeably more dense than was the case on day 25 and the length of the down feathers had increased to approximately 16 mm.

Figure 13 presents growth measurements for the various embryo regions recorded during this study.

Incubation

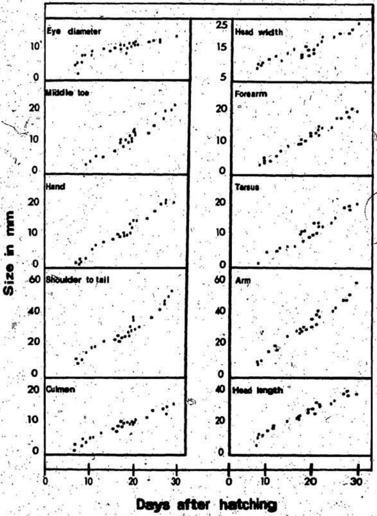
Murres are assiduous incubators and commence "sitting" on their eggs immediately after laying. Such early incubation results in the precariously placed egg being offered immediate protection from the weather, predators and rolling from the ledge surface. On Gull Island, as in other areas, site tenacity increased markedly with the onset of laying and even newly-laid eggs were seldom left unattended.

The duration of the incubation period is quite variable and undoubtedly the ledge microclimate plays a key role in its determination (Tuck, 1960). The shortest period recorded for the species is 28 days with the longest being 35 days. Individual periods recorded for Gull Island ran from 29 to 35 days in 1977 (N= 50) with a mean of 31.9 and from 29 to 33 days with a mean of 30 in 1978 (N= 40).

Incubation period in this study (and in those previous) was the time

Figure 13

Growth measurements of the various embryo regions recorded for this study.


Eye diameter
Head width
Middle toe
Forearm
Hand
Tarsus
Shoulder to tail
Arm
Culmen
Head length
Size in mm
Days after hatching
0
10
20
30
0
10
20
30
25
15
5
60
40
20
0

interval between laying of the egg and emergence of the chick (Heinroth, 1922). This definition has limited accuracy for murres as much of the variation reported for incubation periods is attributable to the variation in pipping times. If incubation period was defined as terminating with appearance of the first pipping hole, reported incubation times would certainly be a good deal less variable. If this is done for the 1977 season on Gull Island the incubation period range decreases by 3 days (to become 29 to 32 days) while the mean incubation period decreases by more than 0.5 of a day (to become 31.3 days).

Besides the ledge microclimate (noted above) individual differences between birds must also be considered to affect the range of incubation periods. As well, it should be noted that eggs used for the incubation analysis were not differentiated as first layings or re-layings. Conceivably this could affect incubation time because of egg weight/incubation relationships noted earlier. Furthermore, there may well be a behavioral change in the adult associated with a replacement clutch. Uspenski (1958) noted that losses of eggs and chicks from a second laying were much higher than from a first.

As incubation proceeds the site (egg) tenacity expressed by murres becomes more and more pronounced. On numerous occasions this author was allowed to approach incubating murres to within less than 1 m. Indeed, while eggs were being weighed and measured, some incubating murres remained with their charges for up to half an hour. In these situations the greatest agitation was shown when the observer stood erect or attempted to move behind the birds. Such observations indicate that caution in approaching the nesting ledges can effectively reduce disturbance in colonies. Thus, when this observer approached with his body flattened against the rock face, the murres conscious of his presence would back slowly off their eggs, turn and face the sea, and eventually depart. Infrequently birds having moved away from their eggs would return and settle down on them again without ever leaving the ledge.

When approaching their eggs the murres would often spread their wings slightly so as to protect the egg if it started to roll. Once settled on the egg they would fold their wings and pocket them. When backing away from their eggs they often adopted a similar posture.

Murres often incubated eggs for lengthy periods of time without being relieved. Continuous observation at site 5 on 25 June revealed that seven murres remained on their eggs for periods in excess of twelve hours. Such lengthy periods of inactivity were broken only by stretching movements; infrequently the bird would stand erect, strech out its neck and point its bill towards the vertical, shake its head with its gape distended, and rapidly flutter its wings. After this process was completed the bird would again settle on the egg. The only other activity noted during incubation was preening. Self-preening was usually carried out shortly after incubation commenced. The bird involved would be only shortly returned from the sea and the preening would serve to arrange the feathers and to waterproof them. The latter function was carried out by first rubbing the bill under the tail and presumably contacting the uropygial gland and then rubbing the bill over the feathers. Allopreening (the preening of one bird by another) was also occasionally observed during incubation. This sometimes involved two incubating birds or more usually two members of a mated pair, one of which would not be incubating. In over ninety per cent of the cases observed (n= 325) it was the latter which preened its incubating partner. Reciprocal allopreening (= Mutal preening) was sometimes observed between members of a mated pair, one of which was incubating.

While one murre was incubating the egg its partner was usually at sea but often the two could be seen together on the ledge. Changeovers of incubation duties were usually casual affairs with the incubating murre rising and moving aside as its mate moved to take charge of the egg. The elaborate ceremony described by Uspenski (1958) as "usual" where the egg is transferred from foot to foot (in this species the egg is not incubated on the rock but is held on the webbing of the feet) between the adults was seldom observed on Gull Island. It may be that in very crowded, sloping ledges this manoever reduces loss of eggs. The fact that these conditions are rare on Gull Island probably explains the low frequency of this behavior.

In certain instances the incubating murre did not appear inclined to leave its charge and was in such cases literally forced off the egg. In one such situation the relieving murre, after several times placing its bill beneath the incubating bird, placed its upper body beneath its mate's neck and forced upward displacing the incubating bird. The newcomer then assumed incubation. After being relieved most birds flew out to sea within a few minutes. Some relieved birds did remain on the ledge in excess of one hour, but this occurred for less than five per cent of the observations.

Incubation position varied for Gull Island birds with both the prone and upright stances being frequently observed. Tuck (1960) stated that the prone position was more characteristic of Thick-billed Murres while the Common Murre most frequently adopts the upright position, the latter being an adaptation to crowding. Evidence from this study supports the suggested association between incubation position and nesting densities. Murres nesting on Gull Island do so at densities far below those found in many larger colonies. Because of this birds can incubate in the prone position without interfering with the bird nearby. Furthermore, the broad ledges which form many of the Gull Island sites (e.g. 4, 5, and 2) are sloping and indented so that they are actually step-like. Such formations are conducive to occupancy by single rows of birds with enough space available for prone incubation. Observations at sites where the ledges differ from the above (e.g. 1 and 9b) and where densities are higher indicated a much higher percentage of birds incubating in the upright position (75% vs. 25% at site 4). Apparently Common Murres can adopt whichever incubation posture ledge conditions dictate. In situations where space is available the prone position will be favoured.

Murres do not appear capable of differentiating between fertile and infertile eggs. On ten occasions at site 4 alone murres were observed incubating eggs which were infertile or which, because of their position, could not possibly hatch; seven of these eggs were incubated for periods of time in excess of the normal incubation period. Four of the eggs were positioned in crevices and therefore were not being successfully brought into contact with the brood patch; three of these were abandoned after approximately two weeks but one was incubated for thirty-six days. Why birds would continue to incubate such eggs is difficult to understand - such wastage of energy is seldom tolerated in nature. Presumably the low percentage of such occurrences would mean that no strong selection against it is in operation. However, as Drent's (1973) and other exhaustive studies have indicated, a very narrow zone of optimal temperature exists for proper embryonic development. This indicates that the incubating bird possesses adaptations enabling the embryos to be maintained under these optimal conditions. Furthermore, the embryo itself produces heat which should act as a feed-back mechanism to assure the parent bird that its efforts aren't being wasted. For the Herring Gull Drent (1973) showed that embryonic heat production begins to exceed evaporative heat loss at about ten days of age. If a similar time frame operates for murres then the abandonments noted above at approximately two weeks could represent responses to negative signs (lack of heat) from the eggs at this stage. The percentage of birds abandoning should not be considered indicative of the number which recognize and leave infertile eggs. Numerous infertile eggs could possibly be included in those lost through breakage and predation. Tuck (1960) similarly noted murres incubating eggs which could not possibly hatch.

On two occasions incubating murres were observed to brood chicks which had wandered over to them. The significance of such altruistic activities will be discussed elsewhere in this thesis.

Hatching

Hatching in murres can be a long process with mean pipping time for Gull Island birds being 2.7 days (S.D. 1.21). Table 7 shows the various durations of pipping (from the first puncture of the shell to emergence of the chick) and the numbers of eggs in each group. Clearly there is much variation in pipping time and presumably there is no strong selection pressure favouring rapid departure from the egg. The situation is much different in many charadriiform (and other) species where synchronous hatching of entire broods occurs within a few hours (Vince, 1969).

Hairline fractures, so frequently reported by researchers for other

Table 7

Numbers of eggs recorded for the various pipping times on Gull Island

Duration (Days)	Number of Eggs	Per cent of total
1	8	15%
2	17	32%
3	12	22%
4	11	21%
5	5	10%

N= 53

$\bar{X}$= 2.7 days
S.D.= 1.21

species (Maunder, 1973; Drent, 1973) as preceding the formation of the pipping hole, were not observed for the murres during the present study. Their "absence" may have been a mechanical factor due to the thickness of the shell or it simply may have been that the colours of the eggs made these fractures difficult to observe. Other researchers have also failed to report their presence.

Of sixty eggs observed only in a single instance was the pipping hole discovered on the undersurface of the egg; in all others it appeared on the upper surface of the blunt end. This compares favorably with observations on birds generally and this consistent pattern of appearance of the pipping hole in the most advantageous position has led to speculation as to the methods responsible. Tinbergen (1953) considered the dual roles of parent and chick, observing that the former must for some reason cease turning the egg after a pipping hole has appeared and that the chick must initially select the uppermost portion of the egg to pierce. Regarding the parent's behavior, Tinbergen discovered, through the means of egg "dummies" that it was not the sight of the pipping hole itself that was the influencing factor but rather it was the "peeping" vocalizations of the chick. The chick's ability represented a normal response to gravity.

Drent (1973), in his substantial work on Herring Gull incubation, demonstrated that weight displacement in the egg is responsible for the embryo, which has assumed a relatively static and characteristic position a few days before hatching, pecking a hole in the upper surface of the egg. Furthermore, for the Herring Gull at least, the embryo does not rotate on its axis within the egg to eventually sever it in two. For this and certain other species the separation of the shell into halves is accomplished via

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head rotations only with the circular cutting patterns being essentially dictated by embryo position. The cut thus made is usually about 120 degrees only.

Personal observations and those of Tschanz (1968) demonstrate that murre embryos do move through a complete 360 degree turn while hatching. A similar pattern has been observed in the Turnstone (*Arenaria interpres* L.) (Bergman, 1946) while the Black-tailed Godwit's (*Limosa limosa* L.) strategy resembles that of the Herring Gull (*vide* Drent, 1973). Presumably no fixed pattern has been determined for this phenomenon in the charadriiformes.

Regarding modification of parental behavior Tschanz (1968) stated that "the calls and bill activity of the chick (in the egg) stimulate the adult to rise frequently, roll the egg, utter an 'egg acceptance' call and to 'feed' the egg." In the establishment of a parent-chick bond these last few days of incubation are, then, of extreme importance - in such a nesting situation where numbers are dense and territories are small the mutual recognition of parent and chick is of much significance. The ability to find one's own chick (parent) through vocal means (imprinting which occurs while the chick is still in the egg) remains important throughout the pre-fledging and fledging periods. It attains acute significance in situations where the chick has wandered away from its hatching area (which sometimes occurs after the first few days) and at the time of seagoing. Vince (1969) has also reported on the significance of pre-hatching vocalizations, stating that the coordination shown by many species during synchronous hatching of entire clutches is achieved via sound signals exchanged by chicks while still in the egg.

The chronologies of hatching for the breeding seasons on Gull Island are illustrated in figure 14. As would be expected from the laying chronology outlined earlier (figure 11) the 1977 season showed an earlier beginning to hatching. In this first season sixty-six per cent of all chicks emerged within the first week of hatching with smaller numbers appearing late into the season. The last recorded hatching was July 16. In 1978 eighty per cent of all chicks appeared within one five day period with fewer chicks being recorded over the total hatching period than in 1977. Both of these latter results (which of course are themselves interrelated) are expressions of the reduced number of relayings recorded in the 1978 season.

Eggs hatched at all times of the day with there being no indication that weather was a modifying influence. Maunder (1973) gave evidence that weather might have a modifying affect on hatching dates of individual eggs for Kittiwakes.

The hatching itself was typical, with chick activity patterns being of varying duration and alternating with periods of rest. Chicks were quite vocal throughout the entire hatching period and are presumably afforded this extravagance by the intense incubation of the parent bird and the advantages which accrue to both chick and adult as a result of pre-hatching vocalizations.

Parental assistance of hatching chicks, as reported by Tuck (1960) and Belopol'skii (1957), was not observed during this study.

Chicks

Chicks emerged from the egg with remnants of the yolk sac still attached and relied on these nutrients for the first two days. The chicks were ptilopaedic, hatching with a complete covering of down, with a mean hatching length of 8 mm on the head and 11 mm on the back (N= 30). Chicks hatching

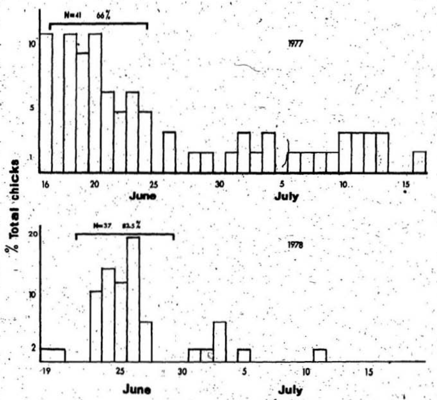

N=41 66%
1977
10
5
1
16
20
25
30
5
10
15
June
July
% Total chicks
N=37 82.5%
1978
20
10
2
19
25
30
5
10
15
June
July

Figure 14

Chronologies of hatching at sites 4 and 5 for 1977 and 1978.

Note: these figures do not represent total chick production for these ledges.

Plate 7a

A two day old murre chick showing the characteristic prone position. Chicks of this age are unable to maintain an upright stance. The silver-tipped feathers of the head and neck region are clearly visible.

on Gull Island were consistently charcoal-grey on the dorsum with a white ventral aspect and suffusions of tan appearing in the neck region. The belly white extended as an inverted "V" into the darker throat region and the egg tooth was very prominent at this stage. The head feathers had a silver-tipped appearance which extended to the neck and throat region (plate 7 a, b).

By day 6 neossoptiles had disappeared from large portions of the wing (and other body regions) and contour feathers were emerging over the general body surface. By this time the egg tooth had faded and the yolk sac was completely resorbed.

The development of the "mesoptile" plumage (Bedard, 1969) continued and at about twelve days of age contour feathers were well developed everywhere, except on the head and neck. In the latter area the tawny band of neossoptiles remained. Plate 8 shows a chick at approximately this stage of development with the original neossoptile plumage being pushed outwards by the developing contour feathers.

At approximately fifteen days of age advanced development of the mesophile plumage was noted with the white of the belly being almost continuous with the more recently developed white of the throat and cheek regions. A sparse band of dark neossoptiles usually remained in the throat region at this stage. Feathering-in of the culmen and eye regions had been completed and in many chicks a prominent black stripe could be observed running from the culmen, through the eye and into the dark plumage at the back of the head and neck. This stripe was very conspicuous as it ran between the white area along the cheek and the grey area on the head (plate 9a, b). The egg tooth, when present, had become very scale-like and often rubbing the "tooth"

Plate 7b

A three day old murre chick. Note the prominent egg-tooth and the silver-tipped head and throat feathers and how the feathers in these areas resemble hairs.

Plate 8

A twelve day old murre chick showing how the neossoptiles are being pushed out by the developing mesophile plumage.

Plate 9a

A fifteen day old murre chick showing the alert, upright stance and the well developed mesoptile plumage.

Plate 9b

A fifteen day old murre chick showing detail of the head area and the prominent black stripe running through and back from the eye.

would cause it to flake off. Major plumage developments had all been completed by this time and from this point until fledging energy allotted to plumage was presumably invested only in growth of the feathers (and possibly conditioning them for continuous immersion in water).

Murres have been shown to feed on a number of prey species (Pearson, 1968; Cody, 1973; Uspenski, 1956) with the diet of particular populations reflecting local abundances. Thus Birkhead (1976) and Pearson (1968) report high percentages of Clupeidae (Herrings) and Ammodytidae (Sand Eels) respectively in the diet of murre chicks in Great Britain while in the western United States Engraulidae (Anchovies) are the most important item fed to the young (Scott, 1972; Cody, 1973).

Food items returned to the breeding ledges by adult murres on Gull Island and the percentages of each are shown in table 8. As the table indicates chick diet was very similar over both seasons with Capelin (*Mallotus villosus* Muller) representing ninety-four per cent of the total food consumed. Of the remaining food items only Sand Lance (*Ammodytes americanus*) was observed being eaten. Short-finned Squid (*Illex illecebrosus* (Leseur)) although infrequently brought to the ledge by adults were consistently refused by the chicks. Presumably the latter species was brought to the chick when other prey items were difficult to procure and/or squid were very abundant. Experience with a captive-reared chick also indicated preference for certain food items. In the early (less than seven days) stages of its development the chick had difficulty manipulating items of certain texture and, although hungry, would be unable to pick up, or even in some cases, swallow, morsels which had a greasy surface. This particular handicap resulted in an observed preference in this one captive bird for cocktail sausages over canned Sardines or regurgitated and/or partially decomposed Capelin. For chicks on the ledges however, the refusal of squid was probably a mechanical function, this food item being simply too large for their gullets. The preponderance of Capelin in the diet is easily explained by the fact that during the period the chicks are on the ledge this superabundant species is usually close inshore for its annual spawning (Winters, 1966).

Birkhead (1976) found evidence, on Skomer Island, Wales, that adult birds were selecting fish of a certain size to feed their chicks. On Gull Island a similar phenomenon was recorded in a somewhat exaggerated form where adult murres were observed with Capelin which they had severed before returning to the ledge. The frequency of this occurrence was appreciable, representing approximately ten per cent of all returns with fish. On Skomer the proportions of fish species involved in fish-presentation differed significantly from that fed to chicks. Fish-presentation is an inter-mate behavioral phenomenon to be discussed later. For this study the selection of fish species was similar for both chick diet and fish-presentation although squid were never recorded for the latter.

On two occasions observations of chick feeding activity were conducted over fourteen hour periods (figure 15). On both days feeding activity gradually increased in the early morning and tailed off in the late evening, peaking between mid-morning and late afternoon. Comparison of this figure with number 10 shows how more and more birds leave the ledge to feed (themselves and the chicks) as the morning proceeds and then begin to return to the ledges in the evening to roost overnight. The difference in total numbers of fish brought to the ledge on the two days may reflect a decreased rate of feeding for older chicks. Birkhead (1976) observed that older chicks

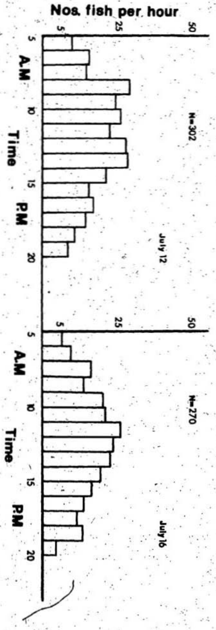
Table 8

Food items returned to the ledges by adult murres on Gull Island 1977 and 1978

Year	Species			
	Mallotus villosus	*Ammodytes americanus*	*Illex illecebrosus*	Total
	N % total	N % total	N % total	
1977	170 (92.9%)	4 (2.2%)	9 (4.9%)	183
1978	350 (94.1%)	11 (2.95%)	11 (2.9%)	372
Totals	520 (93.7%)	15 (2.7%)	20 (3.6%)	555

Figure 15

Chick feeding activity for sites 4 and 5 recorded over 14 hour periods on July 12 and 16, 1978.


Nos. fish per hour
5
25
50
5
A.M
10
Time
15
P.M
20
N=302
July 12
5
25
50
5
A.M
10
Time
15
P.M
20
N=270
July 16

were fed less often on Skomer. This same author discovered a small peak of chick feeding soon after first light with there being a significant (t=3.74 18df $p<0.002$) difference between feeding rate in the morning, 0.257 feeds per chick per hour, and in the afternoon, 0.193 feeds per chick per hour.

Mean feeding rates were determined from the continuous observations on the 6 and 12 July (referred to above) and from observations conducted over shorter periods of time on five different occasions.Table 9 outlines the duration and timing of each of these observation periods and records the individual mean feeding rates per hour and per day (actual or extrapolated) as well as overall hourly and daily averages of feeding activity. All observations on which analyses were performed were conducted at site 5; supportive observations were made at site 4.

The data gathered over these periods indicated a mean hourly feeding rate for forty chicks (aged 1-2 weeks) of 0.231 feeds per chick per hour. Food consumption over the entire daylight period (taken as fourteen hours) was calculated to be 3.25 feeds per chick per day (S.D. 0.806).This figure is thought to be a little too high and its exaggeration results from overstated mean hourly feeding rates determined for the shorter observation periods and the dependent (extrapolated) estimations of daily feeding intensity. A more accurate figure would be in the order of 3.00 feeds per chick per day.

Birkhead (1976) found the food consumption of a total of sixty chicks (average age 9.9 days; range 1-20) over the entire daylight period (eighteen hours) to average 3.23 feeds per chick per day (S.D. 1.42) with a mean hourly feeding rate of 0.23 feeds per chick per hour.

Table 9

Rate of Food Consumption (Nos. fish) of Chicks recorded over varying periods of Time in 1978

Date	Period (hrs.)	# Chicks	# Fish/Chick	Fish/Hr./Chick	Fish/Day/Chick
July 6	6:00-20:00	17	3	.214	2.99
July 6	6:00-20:00	8	2	.142	1.98
July 6	6:00-20:00	12	4	.285	3.99
July 11	7:00-15:00	1	3	.375	5.25
July 11	7:00-15:00	3	2	.250	3.50
July 10	10:00-14:00	4	1	.250	3.50
July 10	10:00-14:00	1	2	.500	7.00
July 9	12:00-15:40	3	1	.384	5.38
July 8	7:00-17:00	4	2	.200	2.80
July 7	11:00-21:00	1	2	.200	2.80
July 12	6:00-20:00	30	3	.214	2.99
July 12	6:00-20:00	2	4	.285	3.99
				$\overline{X}$= .231 SD= .057 N= 89	$\overline{X}$= 3.25 SD= .806 N= 89

Notes: (1) Day= 14 hrs.

The mean weight of Capelin in the Newfoundland area is 26.5 g (Winters, 1966). As this species constitutes greater than ninety per cent of all food items brought to chicks the mean daily feeding rate of chicks aged 1-2 weeks translates into approximately 79.5 g of fish per chick per day. On Skomer, Sprats (*Clupea sprattus* L.) formed 95.4 per cent of the total prey items and, with a mean weight of 8.8 g, resulted in a daily food intake of 28.4 g of fish per chick per day (Birkhead, 1976). The prey dimensions on Skomer agree with those reported by Pearson (1968) and Scott (1973) for the Farne Islands and Yaquina Head, Oregon respectively, but are smaller than Uspenski's reported 15 g mean weight for Novaya Zemlya birds and the 25 g figure quoted by Tuck and Squires (1955) for Thick-billed Murres on Akpatok Island. This last figure is very close to the 26.5 g figure obtained for the present study although the prey species were different with Polar Cod (*Boreogadus saida* (Lepechin)) representing 34.5 per cent of all food items brought to chicks on Akpatok.

Chick growth was calculated using the following equation (Banks, 1959):

$$R = 2.3\ \frac{\log W_2 - \log W_1}{t_2 - t_1}$$

where W= weight and t_2-t_1 equals the time interval in days; 2.3 is a factor used to convert logarithms to the base 10. Data were combined into two-day periods so as to allow for better comparison with Birkhead's (1976) data. The overall R is therefore a summary (mean) R for the entire "Nestling" period. For the Gull Island chicks R was calculated as 0.063 (S.D. 0.056) in 1977 and 0.062 (S.D. 0.049) in 1978.

Table 10 gives a comparison of patterns of weight increase for three populations, namely: Gull Island, Newfoundland, (this study); Skomer Island, Great Britain (Birkhead, 1976) and the Farne Islands (Pearson, 1968). While

Table 10

Weight (Wt) increments per 48 hours of murre chicks at different localities

	Locality								
	Gull Island			Skomer Island			Farne Islands		
Age	Mean Wt.(g)	Wt. change (% adult Wt.)	R	Mean Wt.(g)	Wt. change (% adult Wt.)	R	Mean Wt.(g)	Wt. change (% adult Wt.)	R
1	74.5	- -	-	67.3	- -	-	55.5	- -	-
3	92.1	17.6 (1.7)	0.105	91.0	23.7 (2.7)	0.118	83.2	27.7 (3.0)	0.202
5	112.0	19.8 (1.9)	0.097	104.8	13.8 (1.5)	0.108	129.5	46.2 (4.9)	0.220
7	149.0	37.0 (3.7)	0.142	135.7	30.9 (3.5)	0.112	148.0	18.5 (2.0)	0.066
9	153.0	4.0 (0.4)	0.014	155.8	20.1 (2.3)	0.071	166.5	18.5 (2.0)	0.058
11	195.0	42.0 (4.2)	0.119	179.4	23.6 (2.7)	0.069	185.0	18.5 (2.0)	0.054
13	193.3	-1.7 (-0.1)	0.004	208.0	28.6 (3.2)	0.042	203.5	18.5 (2.0)	0.047
15	215.7	22.4 (2.2)	0.054	200.6	-7.4 (-0.8)	0.008	212.7	9.2 (0.9)	0.022
17	223.0	7.3 (0.7)	0.016	217.3	16.7 (1.9)	0.047	220.0	9.3 (1.0)	0.016
19	236.0	13.0 (1.3)	0.028	216.7	-0.6 (-0.0)	-0.001	249.7	27.7 (2.9)	0.061
21	247.0	11.0 (1.1)	0.022	217.4	0.6 (0.0)	0.006	-	- -	-
23	260.5	13.5 (1.3)	0.049	-	- -	-	-	- -	-

Gull Island Mean R= 0.062 Skomer Island Mean R= 0.058 Farne Islands Mean R= 0.[illegible]41

Note:

(1) Adult Weights: (a) Gull Island= 992.5 g (b) Skomer Island= 875.0 g (c) Farne Islands= 925.0 g
(2) Data for Skomer is from Birkhead (1976); that for Farne Islands is from Pearson (1968)

Table 11

Nesting Densities of Murres at various sites on Gull Island

Site #	Density 1	Density 2	Density 3
1			X
2		X	
3	X		
4		X	
5			X
**6		X	
7			X
8			
9a		X	
9b			X
10		X	
11	X		

Notes:

1= Sparse	2-3 prs./m^2
2= Medium	3-4 prs./m^2
3= High	4-5 prs./m^2

** Site deserted both seasons

different patterns of weight increase are indicated for the three groups during particular days, the overall growth rates (R) are not significantly different ($t = .65$ df$= 7$ $p < 0.05$). The different patterns of weight increments probably reflect day to day variations in chick feeding rates which may be influenced by weather and/or prey distribution in the different areas. Birkhead (1976) showed a significant negative relationship between feeding rate and sea conditions ($r = 0.563$; $p < 0.01$) which accounted for thirty-two per cent of the variation in provisioning rate. The provisioning rate of chicks was highest during calm sea conditions when, supposedly, the ability of adult murres to capture food is greatest.

It should be noted at this point that all chicks for which growth data **are** presented were from ledges in sites 4 and 5. Coulson (1968) has suggested there may be differences in the quality of birds nesting in "central" and "peripheral" sites. Both of the above areas have shown continued increase in bird numbers over the past ten years and at present represent two of the largest on the island. Furthermore, the breeding success (table 17) for both these ledges compares favorably with others on the island; their populations being more productive than the majority. Nesting densities for areas 4 and 5 (especially) were among the highest for the island (table 11) but this did not appear to affect breeding success in any consistent manner. Thus for the Gull Island situation at least, an exact distinction between "central" and "peripheral" sites, and the connotations these terms carry, remain undefined. Considering breeding success to be a good indicator of habitat quality it can safely be assumed that chicks used in growth analysis for Gull Island were from areas more "central" than "peripheral". The possibility that human disturbance affected growth rates is considered slight;

Birkhead (1976) found little difference in development of chicks visited regularly and those visited only once or twice during the "nestling" period.

Between days 1 and 16 chicks increased approximately 144 g giving an average increase of 8.78 g per day. With a daily food intake of 75.5 g of fish this gives a conversion rate of 11.6 per cent; 8.59 grams of fish were required to build one gram of body weight. Chicks on Skomer (Birkhead, 1976) averaged an increase of 9.25 g per day, showed a conversion rate of 31.3 per cent and required 3.2 g of fish to produce one gram of body weight.

The development of various body regions for sixty-five murre chicks is depicted in figure 16. The graphs differ from those recorded by previous researchers in that definite asymptotes and/or pre-fledging weight recessions are not present. This is in part a result of combining the 1977 and 1978 data; figure 17 shows how the 1977 and 1978 growth curves differ and for 1977 weight and tarsus asymptotes (but not pre-fledging weight recessions) can be seen.

For the six body regions presented in figure 16 a pronounced division is immediately apparent between the development of the foot (= foot and tarsus) region generally and all other body areas. Tarsus, middle toe and claw lengths all have a mean value at hatching of greater than forty per cent of their mean adult values. Culmen length, weight and wing chord, on the other hand, do not attain forty per cent of adult values even at fledging. By the time chicks are ready to go to sea the tarsus, middle toe and claw are all in excess of seventy-five per cent of their adult dimensions.

Such non-uniform allottment of energy is found in many species of diverse phylogenetic position. Ground-nesting altricial passerines, for

Figure 16

Development of various body regions of 65 murre chicks expressed as % adult size in 1977 and 1978.

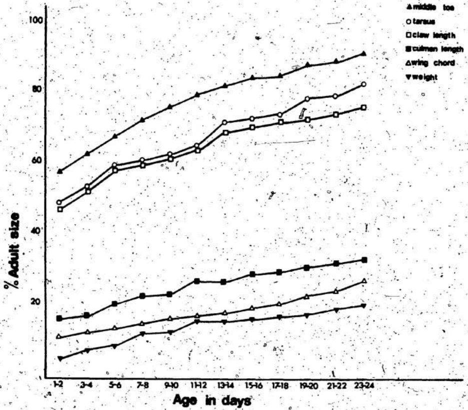

▲middle toe
○tarsus
□claw length
■culmen length
△wing chord
▼weight
% Adult size
100
80
60
40
20
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-16
17-18
19-20
21-22
23-24
Age in days

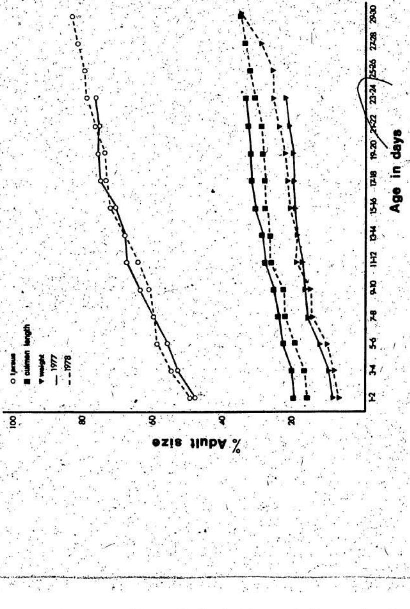
Figure 17

Individual 1977 and 1978 growth curves for developing murre chicks expressed as % adult value. Note the weight and tarsus asymptotes.

example, also show marked differential growth of body parts with strong selection for early development of the feet (Maher, 1972). Clearly those attributes which afford the greatest survival value to the developing organism are selected for and, at this critical stage, rather than evenly distribute its energy, the organism allows for rapid growth of those essential body parts and functions which allow for continued development of the chick under less hazardous conditions.

For murres the feet not only provide stability while on the ledge but also are required by the chick to swim away from the colony at the time of fledging. As murre chicks, like the adults, rest on their tarsi, all three "foot" parameters are intensely selected for with the middle toe indicating how fast the foot generally is developing and the claws being advantageous for climbing about the ledges and maintaining a hold under slippery conditions.

The large size at hatching of these three body regions suggest their confering immediate survival value to the hatchling i.e. while it is on the ledge. Certainly for the claw it is difficult to imagine what advantage this structure would offer birds while in the water; selection in this case must be seen to operate almost totally for survival on the ledge. The tarsus certainly is of great value while the chick is on the ledge and is also important at sea. The length of the tarsus should control the length of the foot stroke during swimming and thus exert much control over the power of the forward thrust. Furthermore, the length of the tarsus may be important for the leap from the cliffs at the time of fledging. At this time the chick must leap outwards and away from the cliff face and, although aided by the small wings once airborne, the initial force during leaping comes


○ tarsus
■ culmen length
▼ weight
— 1977
- - 1978
% Adult size
100
80
60
40
20
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-16
17-18
19-20
21-22
23-24
25-26
27-28
29-30
Age in days

from the leg and foot regions. Increased leverage at this point would certainly be desireable.

The broad flat surface of the foot webbing offers much stability to the chick while it is on the ledge. In the water, the propulsive force of the swimming stroke would be dependant on the cross-sectional area of the foot surface (and tarsal length). Thus strong selection for development of the tarsus and foot probably occurs for life on the ledge as well as in the water while claw dimensions express functional significance only while the chick is on the ledge.

The percentage of adult dimension that each of these parameters attained by the time of seagoing is illustrated in table 12 (data are combined for 1977 and 1978). In order of increasing percentage of adult size are the claw (72.3%), tarsus (78.4%) and middle toe (91.8%). The latter is taken as indicative of how the foot webbing is developing. Obviously those parameters most important for life at sea have reached greater relative (per cent adult) size at fledging than those which are either more important while on the ledge (e.g. claw) or are not immediately essential to the survival of the fledgling (wing and beak dimensions). After fledging the chick is accompanied to sea by a single adult which cares for it over a period of time probably exceeding two months (Keighley and Lockley, 1947). This period of continued chick dependancy and adult care allows the chick time to develop bill and wing lengths sufficient for the underwater pursuit and capture of prey.

In many species of bird the weight of growing young increases to a peak above normal adult weight and then decreases before fledging. Ricklef's (1968) intensive work on growth in birds indicates that such weight recession

Table 12

Fledging and adult values of growth parameters for Gull Island Murres

Parameter	W	H	F	WL	T	MT	C	CL	CD
Adult	992.5	88.8	174.7	481	39.6	45.2	11.2	43.3	14.2
Fledging	240.5	26.6	31.5	135.2	31.3	41.5	8.1	14.6	9.3
% Adult	24.2	29.9	18.0	28.1	78.4	91.8	72.3	33.8	65.8

Notes: W= Body Weight
H= Hand
F= Forearm
WL= Wing Length
T= Tarsus
MT= Middle Toe
C= Claw (on Middle toe)
CL= Culmen length
CD= Culmen depth

Summary values (% ± 1 S.D.):
(a) For all wing parameters: 25.3 ± 6.4
(b) For all Tarsus and Foot parameters: 80.8 ± 9.97
(c) For all bill parameters: 49.8 ± 22.62

is restricted primarily to oceanic species and to the Hirudinidae (swallows) and Apodidae (swifts). Sealy (1973) in his review of post-hatching developmental patterns in the alcids found that "supra-adult" body weights were not usually achieved by alcid nestlings. This same author stated that a pronounced pre-fledging weight recession was exhibited by the semi-precocial alcids and even in the Razorbills and murres.

The first weight increase figures for murres were published by Johnson (1944) and certainly are not detailed enough to indicate any general trends. Neither Cody (1973) nor Belopolski (1957) reported any weight loss prior to fledging and Birkhead (1976) found that the difference between peak weight and fledging weight amounted to less than two per cent. While Tuck (1960) reported a pre-fledging weight loss of seventeen per cent for Common Murres, his data is an interpretation of Johnson's (1944) figures. For the present study no weight recession before fledging was observed (figures 17 and 18). Thus it appears that a pre-fledging weight loss is not consistently expressed in this species.

Lack (1968) has attempted to explain the diversity of growth rates in birds by arguing that growth rate per se is flexible and directly responsive to selective pressures. From this perspective growth rate is seen to have a direct influence on reproductive success; growth requires energy and its rate thus affects the number of offspring that can be raised. In short, the number of surviving offspring is limited by the amount of energy the parents are capable of supplying as food.

In contrast to Lack's view Ricklefs (1968, 1969) has suggested that the growth rate of a species is determined, within narrow limits, by adult body size and the precocity of development. Under this hypothesis growth rate is driven to a physiological maximum rather than adjusted to some ecological optimum, with nestling mortality being the driving selective force. Cody (1971, 1973) has also considered predation to be an important factor in the evolution of short nestling periods. Sealy (1973) disagreed with this pointing to the fact that seabirds generally colonize islands which lack at least terrestrial predators. The latter author further noted that predation on nestlings of the "open-nesting" murres and Razorbills is low with mortality being largely restricted to the egg stage. Thus the departure of young of these two species when only one-fifth grown is because both young and adults can then forage over greater areas offshore than would be possible if the young remain in the nest and are fed by the parents until fully grown.

Birkhead (1976) concluded from foraging and energetics data that if a murre chick was to remain at the nest site until it attained adult weight, its food requirements would rapidly exceed that which its parents could transport. Thus, as Lack (1968) and Sealy (1973) have suggested, the short nestling period and low fledging weight, do enable the adult to take the chick to feeding areas where it can continue its development. Birkhead (1976) also considered it likely that one parent murre remains with the chick, at the nest-site, to guard it from predation. This effectively means that only one adult at any given time can forage for the chick. The nestling period in murres may well be affected by both predation pressure and the ability of the adults to feed their chicks.

The energetics data presented for Gull Island and Skomer show a marked difference between the daily food intake and conversion rates of chicks in the two localities. Two possible explanations of the mechanism involved present themselves. Firstly, as Ricklefs (1969) has suggested, internal constraints set by the design of the growing organism, may be limiting the rate at which the young grow. Such a modus would explain the R values of the two groups which are quite similar despite the disparity in the amounts of food delivered daily to the chicks and in the conversion rates for the two groups. Ricklefs (1968) has discovered for a number of passerine species that while poor nutrition reduced the magnitude of growth there was no evidence that the rate of growth was similarly affected.

The second explanation has to do with the relative energy requirements for maintenance and growth of chicks in different geographical locations. Certainly most maintenance requirements should be constant regardless of where a chick is but the cost of thermoregulation can reasonably be expected to change with location and ambient air temperatures. Energy drains due to thermoregulatory processes can be quite substantial. Royama (1966) noted that daily maintenance costs for Great Tits (*Parus major*) chicks more than doubled over a two day period when rapid development of the chicks' thermoregulatory mechanism was occurring. Tuck (1960) considered increased demands for thermoregulation to be responsible for the smaller size of fledgling murres at Cape Hay as compared to those at Akpatok Island farther south.

Comparisons of air temperatures at Skomer and Gull Island for June and July are shown in table 13. These data indicate substantial differences between the two localities for the month of June especially, with mean temperatures and mean minimum temperatures being approximately 4°C and 5°C (respectively) warmer on Skomer than on Gull Island. The majority of chicks hatching on Gull Island emerged during the last two weeks of June

Table 13

Comparison of air temperatures for June and July at Gull Island and Skomer

	Gull Island	Skomer
Mean Temp. (June)	10.4°C	14.2°C
Mean Minimum Temp. (June)	5.5°C	10.5°C
Mean Temp. (July)	15.3°C	15.5°C
Mean Minimum Temp. (July)	10.4°C	12.7°C

(figure 14) and it was not until the end of their first week of life (see below) that their thermoregulatory mechanism had become established. It is therefore quite probable that Gull Island chicks expended greater amounts of energy in thermoregulation than was the case for birds on Skomer.

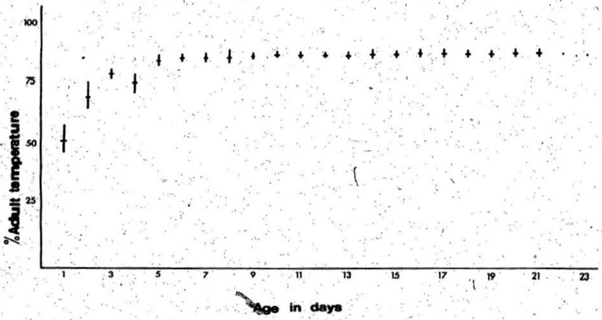
Which of the above hypotheses best explains the differences between the two populations it is difficult to say. Intuitively, intrinsic constraints on chick growth seem logical and would explain why greater food intake did not result in a higher R for Gull Island birds. Increased energy demands for thermoregulation (at lower temperatures) is also an acceptable postulate. Detailed experiments on energetics of this species are clearly needed to resolve the question. Certainly it may well be an interaction of both factors which surfaces as the underlying cause.

The body temperatures recorded for developing murre chicks on Gull Island are graphed in figure 18. The pattern indicates that from ten days of age onward these chicks were maintaining body temperatures of greater than ninety per cent of the mean adult value. Adult body temperature was considered to be the same as that recorded by Iversen and Krog (1947) for *U.a. californica* (range 40.7°C - 42.5°C, mean 41.7°C).

Chick temperatures and the ages at which they were recorded are seen in table 14. Temperatures of chicks were taken over a variety of ambient temperatures and therefore selecting the age at which homeothermy actually developed was a subjective decision. Nevertheless the appearance of an asymptote at approximately day 10 and the conspicuous reduction in deviations about the mean for chicks of this age and older both indicate that at this stage chicks are exerting a great deal of control over their body temperatures. These data show marked similarity with those of Johnson and West (1975) who

Figure 18

Recorded body temperatures expressed as % adult value for developing murre chicks. Note the asymptote at approximately day 10 and reduction in the deviations about the mean after this date.



%Adult temperature
100
75
50
25
1
3
5
7
9
11
13
15
17
19
21
23
Age in days

Table 14

Rectal temperatures of developing murre chicks on Gull Island 1978

Chick Age (Days)	Mean Temperature (%)	% Adult temperature	S.D.	N
1	22.7	54.5	17.0	9
2	29.7	71.2	9.1	26
3	33.1	79.4	5.4	7
4	31.9	76.5	7.7	12
5	36.1	86.5	4.5	8
6	37.0	88.8	3.2	12
7	36.5	87.6	2.7	12
8	36.7	88.1	2.2	26
9	37.5	90.1	1.9	9
10	37.8	90.7	1.4	10
11	37.7	90.5	1.5	12
12	37.8	90.7	0.6	6
13	37.8	90.7	0.6	6
14	37.9	90.8	1.5	8
15	38.6	92.6	1.5	5
16	38.2	91.8	0.6	10
17	38.5	92.5	1.5	7
18	38.4	92.3	1.6	8
19	38.4	92.1	0.9	6
20	38.4	92.1	1.0	10
21	38.7	93.0	1.6	4
22	38.9	93.5	-	1
23	38.9	93.5	-	1

Note:
S.D.= Standard Deviation
N= Number of observations
Temperatures in °C.

discovered via much more stringent experimentation that sustained homeothermy developed in *U.a. inornata* at between six and eight days of age. Tuck (1960) suggested that complete homeothermy in murre chicks was not attained until nearly sea-going. Rolnik (1948) reported that the "setting in" of thermoregulation for *U. aalge* chicks occurred at three days of age but he did not mention when the shift was completed.

Fledging

Young murres leave the nesting ledges while still incapable of sustained flight. Usually this activity occurs at dusk and is in a very real sense a culmination to the breeding season, the phenomenon witnessed being one of intense energy and excitement involving chicks as well as adults.

In 1977 fledging commenced on 6 July and continued until 20 July with peak numbers of chicks leaving in the first few days of the sea-going and numbers falling off as the fledging period progressed. Eighty-five per cent of all chicks had departed the island by 20 July. The mean stay of chicks on the ledges was 20.2 days (S.D. 2.27) which is precisely one day earlier than that recorded by Birkhead (1976) for birds on Skomer. Table 15 shows the number of chicks fledging per date in 1977 while the ages at fledging of forty chicks are presented in table 16. The mean fledging weight of chicks (N= 40) in this first season was 216.32 g (S.D. 10.13) which is greater than the 179.9 g datum of Swartz (1966) for Alaskan birds (*U.a. inornata*) but considerably less than Belopol'skii's (1957) 274 g figure recorded for murres (*U.a. hyperborea*) in the Barents Sea region. Birkhead (1977) noted a mean fledging weight of 214.9 g for murres on Skomer.

The delayed initiations of laying and hatching in the second season resulted in a delayed onset of fledging as well. Thus in 1978 fledging

Table 15

Numbers of Chicks Fledging per day in 1977 at site 5

Date	Nos. Chicks	% of total
July 6	3	7.5%
7	7	17.5%
8	9	22.5%
9	6	15.0%
12	5	12.5%
15	4	10.0%
16	2	5.0%
19	2	5.0%
20	2	5.0%

Note: N= 40= total number of fledgings observed commenced on 10 July and by 18 July (nine day interval) sixty per cent of all chicks had fledged. This compares with 1977 when 61.5 per cent of all chicks had departed the island in the first four days of fledging i.e. by 9 July. This observation underscores the fact that the fledging period of 1978 showed no real peak for numbers of chicks leaving the island; instead chicks departed in twos and threes (per evening) and in general remained on the ledges for longer periods (mean stay on the ledge was 26.7 days S.D. 3.21). As well, 1978 chicks attained greater weights than did chicks of the preceding year with a mean fledging weight for fifteen chicks being 260 g while five chicks, aged thirty days, were all in excess of 300 g.

As to why chicks experienced a protracted sea-going in 1978 it is difficult to say. Certainly, in terms of development, many of these second season's chicks were at the time of fledging considerably more advanced than had been the chicks of 1977 (figure 17). Furthermore the greater synchrony of hatching in 1978 (figure 14) meant that staggered hatching of chicks, which could conceivably have affected the length of the sea-going period, was not a factor. Given these observations and that the ledge microclimate at the time of fledging was similar over both seasons (table 3) it appears likely that water temperatures might well have been the factor responsible for the observed differences between the two seasons. Certainly this is not meant to imply that the chicks in any way "knew" what the water temperatures were in this second (or any other) season. However the adult birds are very much involved with the sea-going and complex behavioral interactions between adults and chicks occur during this time which result in a heightened activity level for entire ledge populations

Table 16

Fledging Ages of Murre Chicks at sites 4 and 5 in 1977

Chick Age (Days)	Nos. Chicks	% total
16	3	7.5%
17	0	0.0%
18	6	15.0%
19	6	15.0%
20	9	22.5%
21	6	15.0%
22	4	10.0%
23	3	7.5%
24	1	2.5%
25	1	2.5%
26	1	2.5%

(see below). This synchronous excitement of both adults and chicks is believed to be of much importance in stimulating chicks to fledge. Conceivably, therefore, water temperatures may affect adult behavior and thus the sea-going itself.

Comparison of water temperatures for both years indicated a difference of 1.5°C (18.75%) at the beginning of July with 1978 being the year of colder water temperatures. By the middle of the month this difference had reduced to 1°C and by the end of the month temperatures were the same (11°C). Whether or not this degree of difference could result in the disparate fledging schedules noted above is impossible to state with any certainty. As Greenwood (1964) has noted, however, weather can affect the sea-going in murres but whether or not local populations have adapted to very narrow ranges for any climatic variables we simply do not know. Greenwood (1964) has observed high winds (and heavy seas) as preventing the fledging of murres but these conditions were not in evidence on Gull Island during the sea-going period.

While quantitative data are lacking, personal observations indicated lower numbers of Capelin in Witless Bay in 1978. Whether prey abundance and distribution in the immediate vicinity of the colony, and hence the distances chick and adult must move after fledging, may affect sea-going remains unspecified. As will be discussed later adult behavior is significantly altered and its intensity level much heightened during the sea-going. The stimuli which trigger this behavioral change remain unknown but food and water temperatures may well form part of the complex of interacting forces which is responsible. Further observations on the exigencies of this particular species are essential to elucidate this and other aspects of its ecology and behavior.

On Gull Island fledging, with three exceptions, commenced at approximately 20.00 hours and terminated at darkness or about 22.00 hours. This timing is in general agreement with the majority of previous observations on this phenomenon (Greenwood, 1964; Kay, 1947; Norrevang, 1958: Storer, 1952; Tschanz, 1959; Tuck, 1960) with Pennycuick's (1956) observation of fledging throughout the day on Spitsbergen and Williams' (1975) report of 17.15 - 05.00 hours as a fledging time on Bear Island being somewhat unusual. All night observations were not carried out on Gull Island but watches were continued until 23.00 hours and certainly the characteristic calls associated with fledging were not heard after darkness fell. It therefore seems unlikely that chicks fledged after this time. Furthermore, early morning counts of chicks at the various sites failed to reveal any disparity between the numbers of chicks present then and on the preceeding evenings.

The few exceptions to this timing occurred at midday and no good reason is offered for this observation. Such anomalous fledgings were also reported on Lundy Island, southwest England (Greenwood, 1964).

Numerous authors (Tuck, 1960; Perry, 1944; Birkhead, 1977) have commented on the predation of murre fledglings at the time of sea-going, suggesting that the fledging of murre chicks at twilight has definite survival value as it affords protection from predators (and marauding gulls especially). Greenwood (1964) working at Lundy, England and Handa, Scotland, recorded three out of eight chicks which fledged before 21.20 being taken by predators whereas all twenty-two which fledged after that time survived. He attributed this to the poorer light conditions at the later time interfering with the depradations of the gulls. This same author suggested that the synchronization of fledging was an adaptation to "swamp" predators with an overwhelming number of prey. Data gathered on Bear Island (Williams, 1975), suggesting that the chance of a predation attempt being made on a fledgling was greater before or after the peak fledging period, supported this premise.

On Gull Island predation on murre chicks at fledging was never actually observed. Three murre chicks were however found at the nest sites of two pairs of Greater Black-backed Gulls after fledging had commenced in 1977. These observations suggest that predation of newly-fledged murres on Gull Island occurs infrequently. This was further suggested when in 1977 an unaccompanied murre chick was observed in the water near site 5 for over three hours (13.00 - 16.30) without it once suffering the attention of numerous gulls in the vicinity. During the entire observation the chick was calling loudly; in fact, it was the vocalizing of the chick which initially caught the observer's attention.

Greater Black-backed Gulls also prey on adult murres on Gull Island. Threlfall (pers. comm.) has on three separate occasions observed single adult murres at the nest-sites of these birds and in all instances a gaping hole had been torn in the abdominal region thus yielding access to the viscera.

Accounts of the intensity of predation on fledgling murres suggest considerable variation with locality. Tuck (1960) reported a near doubling of the numbers of predators at Akpatok Island between the early portion of the breeding season and sea-going stating that there was 'great danger' to fledglings from gulls. Swartz (1966) however, in describing murre fledging in Alaska, did not mention predation as a cause of fledging failure. Greenwood (1964) worked on two separate populations and presented data for

Razorbills, Common Murres and 'unspecified' auks of one or the other species. As his results showed no major differences between the two species, the data presented represent his combined totals per colony. At Lundy three out of forty-seven fledgling auks were killed by predators while at Handa not a single predation attempt was noted for 384 chicks which attempted fledging. At Bear Island, Williams (1975) recorded fifty-seven chicks out of a total of 326 attempting fledging being killed by predators.

Two factors present themselves as possible explanations of why the incidence of predation varies so much between different colonies. The first of these is the proportion of *Larus* gulls to murres at the various colonies. Greenwood (1964) considered this to be the underlying cause of the striking difference between the predation-rates on Handa and Lundy - on the latter island the ratio was about 2.5:1, whereas on Handa it was at least 70:1. Following this line of reasoning he stated that food for the gulls was far more abundant throughout the season on Handa and therefore the need to use the resource provided by fledging chicks was not so great there as on Lundy. Terrain, the second factor, was considered by Williams (1975) to be the major reason for the difference in predation levels between the British colonies and the one on Bear Island. In the former colonies chicks could leap directly into the sea and were thus provided the safest situation for fledging. The cliffs on Bear Island were skirted by exposed rocks or beach and such places were favoured by gulls, the main predators, as resting and watching places. Furthermore 43 of 57 (75.4%) fledglings killed were caught on the rocks, beach or immediately after entering the water. In all these cases predation was probably facilitated by the suitability of the terrain for the predators. Excluding these terrain-facilitated predations only six chicks of 267 (2.2%)

(1960) cited strong evidence that chicks are rarely, if at all, accompanied to sea by one of their parents. His experiments at Cape Hay and at Funk Island with color-marked birds revealed color-banded adults returning alone to the nesting sites as long as two weeks after the sea-going and unmarked adults swimming at sea with color-banded chicks.

On Gull Island chicks were always accompanied to sea by at least one of their parents but sometimes three birds were observed accompanying a chick to sea. This observation and those noted above suggest a considerable inconsistency in the behavior of these birds at the very crucial period of the sea-going. While further investigation is essential it may well be that the sheer number of birds involved has considerable bearing on whether or not adults other than parents accompany chicks to sea. It appears that in instances where this has been reported the colonies studied have been large ones (Tuck for the Funks (500,000 pairs) and Cape Hay (400,000 pairs); Perry for Isle of Puffins (19,000 pairs)). Furthermore, Greenwood (1964) noted that on Lundy chicks fledging *alone* were never joined by adults and, they soon lost all sense of direction and got washed towards the rocks. On Handa (the much larger colony) however, any lone chick became the object of attention from individuals among the rafts of adults awaiting at the base of the cliffs. The latter author did point out that in no case was such a chick seen to become permanently linked with an adult other than with the one that descended with it from the cliff (its parent). Birkhead (1976) recorded only parents taking chicks to sea on Skomer and stated that it is the male which accompanies the chick to sea. The latter observation supports that of Scott (1973) who collected single adult and chick groups at sea (N= 17) and found that all adults were males. It may reaching the sea were killed by predators. This figure is very similar to those recorded for the British colonies. Swartz (1966) also noted the importance of terrain stating that it influenced the failure rate of chicks attempting to unite with their parents and hence affected the incidence of abortive fledging.

On Gull Island the ratio of *Larus* gulls to murres was 3.6:1 and because of the general topography of the island few gulls nested in the immediate vicinity of murre ledges. Certainly for gulls on this island food availability presented little problem as both a fish plant and a fish-meal plant at Witless Bay provided vast amounts of easily procured offal. The situation was therefore similar to that on Handa and murre fledglings simply did not constitute any significant food resource. However, if there had not been a surplus of food available to the gulls, predation of murre fledglings would very likely have been significant. This fact stems from the terrain of the seaward-facing (east side) nesting ledges which was sloping and, like those of Bear Island gave way to rocks and broken contours below.

Swartz (1966) stated that the major causes of abortive fledging of murres in Alaska was failure of the chick to unite with its parent and injury to the chick during its descent. Greenwood (1964) similarly reported that at Lundy eight and at Handa forty-two chicks did not fledge successfully because they failed to unite with their parents. These observations and those of Perry (1944) and Tuck (1960) are at odds regarding whether or not murre chicks do unite with their parents before swimming out to sea. The former author stated that a chick, once fledged, moved quickly out to sea while one and sometimes both its parents continued to return to the nesting ledge as long as a fortnight after departure of the young bird. Tuck be that the female uses this time to regain any vitality that laying of the egg(s) has drained away.

Thus, regarding this most interesting question of whether "non-parent" adults accompany chicks to sea (and care for them while at sea for some period of time probably not exceeding two months) it is impossible, at this juncture, to make any generally applicable statements. Certainly however, the significance of such a behavior, if evolved, would be immediately obvious when one considers the improbability of parent and chick uniting at huge colonies such as those at Digges Sound where a chick may alight on the water amidst 10,000 milling adults. Even the auditory cues which have repeatedly been referred to as being crucial in uniting the adult and chick (Tschanz, 1959; Greenwood, 1964) at this time, must be considered deficient in their purpose with the clamor raised by this many birds. Furthermore, and this is an important supplementary, such altruistic acts are *not* alien to the behavioral repertoire of the species - the brooding of foster chicks by incubating adults has already been noted and observations of a single murre brooding two, three or even four chicks were recorded for this and other studies (Tuck, 1960).

One further point associated with chicks failing to unite with their parents is the premature fledging of chicks which are still incapable of thermoregulating. Tuck (1960) reported observations in which such chicks went to sea and then attempted to regain the land where they eventually perished during the night. Swartz (1966) describes the behavior of many chicks which "failed to unite with their parents" and stated that many of these returned to the shore in a weakened condition or died in the water. From such descriptions it appears that many of the chicks which perish due to failure to unite with the parent may in fact have gone to sea prematurely. Intensive work with color-banded chicks and adults (at large and small colonies) would go a long way towards resolving this question. On Gull Island no chicks were observed entering the water before they were sufficiently thermoregulated.

The fledging of murre chicks on Gull Island was preceeded by a marked increase in activity amongst both adults and chicks. The latter, which for several days prior to fledging had been brooded much less frequently than during the first week or ten days after hatching, were clearly visible on the ledges and were observed to frequently strech upwards and wing flutter in a manner very similar to the streching movements of the adults. Chicks were also seen to scramble about the ledge. Such movements initially suggested a lack of direction (frequently chicks would scramble short distances up the ledge) but eventually the chick would settle on a course either following or being followed by the parent and would leave the ledge, leaping into the sea. Other activities of the chick included bobbing and bowing motions and utterance of a 'peep-peep' call. These various activities were sometimes interspersed with short bouts of brooding.

Deep bowing movements of the whole body were frequent in the adult. These bows were most often made in the direction of the sea and this was particularly true after the activity had been ongoing for sometime. When the adult led the chick to a particular position on the ledge prior to fledging (see below) it often adopted and maintained a deep bowed position and shuffled along in a manner reminiscent of penguin movement (Stonehouse, 1975). The adult frequently uttered a low, gargling call.

These pre-flight behaviors displayed marked social facilitation

(Greenwood (1964) has described them as contagious). Thus, at first just a few birds were involved but eventually large portions of a given ledge would become caught in the excitement until the entire ledge was one maze of movement, noise and general activity. At this point even adults without chicks often became involved. If the "swamping" of predators at this time (Greenwood, 1964) does in fact occur then certainly this synchronization of pre-fledging activity through mutual stimulation could be of great importance.

Sometimes chicks which appeared intent on fledging were forced by adults into the brooding position. In such situations the adults would continually change position, with their wings drooping and slightly splayed, so as to position themselves between the chick and the open sea. On Gull Island this was observed on four separate occasions.

In situations where adults were not observed preventing chicks from going to sea there was usually intense exchange and seemingly, reciprocal stimulation between the young bird and its parent. Thus billing and mutual preening were very frequent activities; such behaviors are probably important in strengthening of the pair-bond between members of a mated pair and between chicks and parents as well.

Where chicks moved to a particular position on the ledge from which to jump they would often cross the territories of several pairs of murres. In such instances the adult would sometimes lead the way but at other times the chick would take the initiative and move off first, with the adult trailing behind. While moving across the ledge the young bird was often surrounded by several adult birds. Usually upon entering a new territory the chick was greeted by the resident adult which gave a deep bow and uttered the gargling call. Often the adult would peck at the bill of the chick and nudge at its posterior. Such peckings were never intense although confrontations between the parent accompanying the chick and the adults whose territories were being trespassed upon were often quite heated. Significantly, the chick was never confronted with a threat posture (to be described later), such as frequently occurred between adults.

Upon reaching the point from which it would leave the chick often gave several very deep bobs and/or bows before leaping into the sea. On Gull Island all chicks either lept from the ledge accompanied by the parent or shortly after the parent had flown down to the sea. In the latter instance the adult would call from the water or rocks at the base of the cliff, enticing the chick to depart from the ledge.

The following excerpt from the field notes for 12 July, 1978 describes the fledging of a murre chick on Gull Island:

"At 20:30 an adult murre flew down from the ledge and alighting in the water at the base of the cliff began calling loudly and swmming back and forth. After five minutes of this activity its chick moved away from the other parent and began to move towards the brink of the ledge. At this point the parent in the water moved up onto the rocks at the cliff-base and continued uttering the low, gargling call. At 20:32 an irruption of Kittiwakes frightened the chick which retreated back to its original position where it was brooded by its parent. The other parent (on the rocks) returned to the ledge as well.

At 20:42 the chick, apparently taking the initiative, started to move away from its parents. It soon found itself amongst a group of several murres through whose territories the young bird and *one* of its parents were then moving. These "resident" murres gaped, gave the gargling call and pecked lightly at the chick. The accompanying parent pecked at these birds. The other parent remained at the "nest-site".

By 20:50 the chick had moved a distance of approximately 5 m; its progress was quite slow as it frequently stopped, bowed, wing fluttered and stretched. The accompanying parent at such times pecked lightly at its bill, nuzzled it and preened it. Its progress was further slowed by confrontations with other adults.

The chick eventually (21:10) reached a crevice located approximately 10 m north of its original position. Both it and its parent moved down the crevice until arriving at the brink of the ledge. At this point an adult Kittiwake which was brooding two chicks pecked at the adult bird and forced it from the ledge. After its parent had departed the chick moved slightly closer to the edge (and the Kittiwake). The Kittiwake then grabbed the chick at the back of the neck and, after flying a short distance seaward, dropped the young murre onto the rocks below. The chick, unaffected by this fall of approximately 10 m, scrambled from the rocks and swam out to sea. As it swam the young bird continually uttered the 'peep-peep' call while its parent uttered the gargling call and swam towards it. Parent and chick quickly came together and then proceeded out to sea. The other parent remained on the ledge."

Certainly many of the fledging behaviors of adults and chicks are of considerable functional significance. The vocalizations in particular can be important at smaller colonies (like Gull Island) in guiding the chick and the adult towards each other once at sea. The exchange between the birds while on the ledge is also largely of a vocal nature. The importance of the vocalizations in uniting the birds at sea was reported by Tschanz (1959) and agreed with by Greenwood (1964) who noted that chicks ceased to call when joined by the adult. Norrevang (1958) described the bow of the adult as a flight-intention movement and Greenwood (1964) agreed with this assessment but noted the fact of its ritualized form. The latter author similarly interpreted the chick's bobbing as a jumping-intention movement. The significance of the billing and preening behaviors between the chicks and their parents have been already mentioned.

Frequently during fledging adults other than parents would be at the base of the cliff calling. Similar observations have been reported by Greenwood (1964) and Tuck (1960) although the former author noted that on Lundy, "due to the small size of the colonies there", no such congregations of murres were seen. Small numbers of such birds were observed during fledgings on Gull Island although the intense interactions described for larger colonies (harassment of the parent-chick pair, mock attacks etc.) were not recorded.

Breeding Success

Breeding success data, expressed as the percentage of adults successfully fledging a chick, is presented in table 17. The ledges mentioned therein were chosen because most other sites did not offer vantage points from which accurate assessment of chick numbers could be made. These sites represent both medium and high density nesting conditions and in this, and in their relatively open ledge position, were representative of the usual murre nesting situation. Breeding success values for the other ledges are not presented beyond the stating of estimates obtained from indirect evidence and/or infrequent (and difficult to obtain) counts of chick numbers.

Representing as it does the quantified expression of the culmination of all previous aspects of the breeding cycle and their interactions, it is not surprising that a great many factors have been demonstrated to affect breeding success. These may be split into intrinsic and extrinsic factors with the former representing characteristics of the reproducing organism such as age, genetic make-up and physical condition and the latter involving environmental parameters such as food availability, predation, competition, habitat quality and meteorological factors (Coulson, 1971; Horn, 1968; Perrins, 1970; Tenaza, 1971; Tuck, 1960). Further determinants which are expressions peculiar to colonial species include position within the colony, colony size and nesting density (Coulson, 1971; Belopol'skii, 1957; Kaftanovski, 1938). Quantification of all these parameters would represent a major study in itself and was beyond the scope of the present effort. However, because predation was directly observed and was such a significant factor in the ecology of the Gull Island population during the incubation period its impact is discussed below.

The total absence of chicks from sites 2 and 3 is primarily a result of Herring Gull predation. These ledges were particularly susceptible in this regard as the broken terrain immediately above them offered numerous platforms which served as Herring Gull nesting and resting sites. Consequently murre abandonment of the ledges for any reason was immediately noted by gulls in these areas and exposed eggs were quickly picked up and consumed. Predation was also facilitated by the Kittiwakes nesting in the area. These were much given to irruptions which were at times a response to the approach of the observer and at times occurred without apparent cause. Almost invariably such irruptions would result in the murres hastily departing

Table 17
Breeding Success

Site #	Nos. Prs.		Nos. Chicks fledging		% pairs fledging a chick		Average Success
	1977	1978	1977	1978	1977	1978	
2	27	30	2	0	7.4	0	3.7
3	27	35	0	0	0	0	0
4	95	110	53	44	55.7	40	47.85
5	130	165	67	53	51.5	32.2	41.85

the ledges leaving their eggs exposed. At site number 2 one such incident resulted in two Herring Gulls consuming seventeen murre eggs - all the eggs on the ledge at that time.

Murres were also absent from the ledges when the researcher was occupied in weighing and measuring eggs and/or chicks and the birds did not return immediately after the observer had departed. In the iterim, between departure of the researcher and return of the murres, heavy losses of murre eggs to gulls often occurred.

These observations are not meant to imply that all gulls or even a large percentage of gulls were actively engaged in the predation of murre eggs on Gull Island. In actual fact, of the approximately 3000 pairs of Herring Gulls breeding on the island only six or seven pairs were seen to specialize in this occupation.

The intensely opportunistic nature of this predation was well illustrated when during observation one very warm day an incubating murre was seen to leave the ledge, dive into the water and return to the ledge after an absence of fifty seconds. During this time two Herring Gulls swooped down and devoured its egg. Most frequently eggs were removed from the ledge and taken to a particular "feeding-site" where they were consumed. Such feeding-sites were often littered with the shells of five, or more, eggs.

In over ninety per cent of the observed predation attempts (N= 26) gulls sought to take (or took) exposed eggs, but on two occasions incubating murres were approached by gulls which attempted to dislodge them from their egg. In such situations the murre jabbed at the gull and continually turned to face the would-be predator as the gull attempted to get behind it. In one such instance (at site 6) the gull departed the ledge after one and one half hours of trying (unsuccessfully) to dislodge the incubating murre. While in this same instance other murres, including the harassed bird's mate, paid little if any attention to the gull. On another occasion (at site 4) a number of incubating murres were observed to jab and thrust their bills towards a Herring Gull attempting to take an abandoned egg from their midst. Interestingly, during almost all predation attempts vacant Kittiwake nests were present in the immediate vicinity but these (and their eggs) did not attract the attention of the gulls. The well developed mobbing tactics in this species may have been a strong deterrent to gulls preying on their eggs. Furthermore in some, but not all, situations the topography of the Kittiwake nesting areas was such that it would have been difficult for a Herring Gull to land to retrieve an egg.

Birkhead (1976) reported even more intense interactions between gulls and murres on Skomer. At this colony gulls were seen to actually grab murres and drag at them until the egg (or chick) was exposed and could be snatched up. On Gull Island such encounters were not observed and it seems likely that gulls here have not "specialized" in the robbing of murre eggs and chicks to quite such an extent as have the birds on Skomer. The abundance of food available to Herring Gulls on Gull Island probably means that only those eggs and chicks which can be obtained with a very minimal expenditure of energy are sought and taken. Furthermore, the majority of gulls involved in this activity (the actual removal of incubating birds from their eggs) on Skomer were Greater Black-backed Gulls with Herring Gulls being much less adept at this and doing so only infrequently. Greater Black-backed Gulls were not observed preying upon murre eggs on Gull Island and their predation of murre chicks, as noted previously, was considered minimal and restricted to the fledging period.

Ravens (*Corvus corax* L.) have been reported to steal murre eggs (Tschanz, 1959; Tuck, 1960) but this was not observed on Gull Island. It is of course possible that predation did occur but simply was not observed; this possibility was suggested by the fact that Ravens did nest on the island and were frequently observed flying along the edges of the cliff-tops.

The smaller ledge populations suffered the highest losses of eggs and basically two reasons are suggested for this. Firstly, birds nesting in these situations were much more restless at all times during the breeding season and were therefore much more easily driven from the ledges. Consequently their eggs were more frequently exposed to marauding gulls. Storer (1952) made a similar observation stating that group size was proportional to the amount of disturbance necessary to make the birds leave the ledges. This idea was stated somewhat differently by Johnson (1938) who noted that birds were dependant on their neighbours for assurance; thus birds in smaller ledges could reasonably be expected to show considerably more "alertness" (= nervousness) than those in larger groups simply because of the difference in the number of individuals capable of warning their neighbours of danger. This "assurance" hypothesis was supported by observations on Gull Island where bowings (which are considered suspicion or alarm reactions) by a single bird were often seen to spread across a ledge giving a communal warning of a potentially dangerous situation. On smaller ledges (e.g. 2 and 3) once this posturing was begun by one bird it invariably induced a similar reaction in the entire ledge population while on larger ledges this was not consistently the case and where this did occur it was usually restricted to early in the breeding season when all birds showed a high level of uneasiness.

Birkhead (1976), in an effort to determine whether the greater uneasiness of birds in low density areas was due to the simple lack of near neighbours or vulnerability to predation, noted the amounts of time spent bowing and sleeping in two low density groups one of which was not vulnerable to gull predation and the other of which was. The results indicated a significant difference ($X^2 = 77.8$ df= 1 $P<0.001$) in the amounts of time spent in these activities by the two groups, with the birds in the group vulnerable to predation spending more time bowing and less time sleeping than the "predation-free" area. This observation coupled with the fact that a comparison between the low density "predation-free" site and a high density one revealed no difference between the amounts of time spent bowing suggested that a murre's nervousness in sparse groups was a result of potential vulnerability and not the lack of conspecific proximity *per se*.

Earlier workers have apparently not considered the lunging behavior of murres to be an effective anti-predator strategy, however observations made during this study and that of Birkhead (1976) suggest that dense groups of breeding murres can be quite effective in preventing loss of eggs and chicks to marauding gulls. In both these studies gull predation was restricted to areas of low density. On Gull Island, for example, unattended eggs were very quickly taken from low density sites and the presence of incubating murres did not result in the eggs being saved from the gulls. However, at site 5 (high density) during one continuous twelve hour observation two abandoned eggs were seen and, although clearly visible, neither was taken by gulls. Similar observations (of shorter duration) were made at this site on a number of different occasions and, while it may simply have been that specialist feeders were lacking in this vicinity at these particular times, the possibility that the presence of large numbers of murres and their potential anti-predator strategy acted as a deterrent to any would-be predator cannot be overlooked. Certainly in the instance previously noted, where murres lunged at the gull attempting to steal an egg from their midst, the gull was most careful to avoid the murres' beaks. That murres can be accountable adversaries was indicated by Tuck (1960) who stated that "even an injured murre is not easy prey for (even) a peregrine or a gyrfalcon. I (Tuck) have observed falcon and murre cartwheeling along the beach in a welter of blood and feathers for nearly a mile before the murre was subdued. More often than not the murre reached the water and escaped."

Terrain was an important factor influencing breeding success. It affected both the incidence of predation and the accidental loss of eggs and chicks due to their being knocked from the ledge by adult murres. Thus site 2, which was exposed and offered an adequate and easily approachable landing platform for gulls, suffered high predation while site 9b suffered little if any. At the latter site chicks and eggs were protected in a crevice out of the sight of gulls and an overhang immediately above the ledge made approach and landing difficult. Similarly, the accidental loss of eggs and chicks was observed only for the open, sloping sites such as 2, 3, 4 and 5, whereas the loss of progeny in this manner would have been next to impossible at site 9b and was thought to never occur there. Only fifteen observations of such accidental losses were recorded for Gull Island (eleven eggs, four chicks) but this almost certainly occurred much more frequently as the numerous egg shells noted on the rocks below the nesting ledges previous to the commencement of hatching indicated. Accidental mortality also occurred as a result of eggs being knocked into puddles of excrement and water where they eventually rotted. Only eggs which had been moved very short distances were retrieved by murres on Gull Island and the loss of eggs at site 4 due to their moving greater distances and/or suffering mechanical damage as a result of their jostling was estimated to be approximately twenty per cent.

Regarding the influence of terrain (which is of course one very important aspect of habitat quality) Birkhead (1976), during his investigations into density and breeding success, also concluded that small numbers of birds nesting on open ledges were more vulnerable to predation than those nesting in dense groups. Birkhead (1976) related breeding success to the synchrony of laying and discussed the relationship between the variables by stating that "in dense groups where the spread of laying is short (social facilitation) the chance that two or more birds may lay on the same day are increased (thereby effectively increasing the likelihood of greater anti-predation forces - non-incubating murres are not likely to threaten or attack a marauding gull). A further advantage of synchrony is that it means that most chicks fledge over a short period of time, and the chances that a single bird guarding a chick will be left on the ledge at the end of the season (a situation showing a high incidence of predation on Skomer) are reduced." While fully detailed observations of laying synchrony and nesting density were not established for the Gull Island population the data that were gathered did suggest a wider spread of laying for the lower density ledges. However, as with breeding success itself (as table 17 indicates), the relationship was not without exception. Furthermore, this whole question is a fairly complex one since the lower numbers of birds at the "smaller" sites means that regardless of density there will have to be absolutely fewer numbers of birds coinciding at any point in the breeding season and there will always be fewer birds to ward off predators. Consequently there is a question of numbers of breeding birds as well as one of density to be considered here. The implication remains however that the protective abilities of nesting murres increase with numbers.

Considering breeding success for the entire island, observations suggest that while density was certainly a factor, high density did not consistently result in high breeding success. Certainly birds were more successful at the larger sites (e.g. 4 and 5) and at sites like 9b, where ledge conditions were extremely safe, than birds on the smaller more exposed ledges. In no way was a truly linear relationship between density and breeding success noted for Gull Island. Thus there did not appear to be a graduation in breeding success from high through medium to low density areas. Furthermore, certain ledges, for example number 7, showed high density breeding conditions but were quite unproductive. While it was difficult to assess the actual number of birds bringing fish to the ledge observations indicated that probably not more than four chicks were hatched there in 1978 giving a breeding success estimate of thirteen per cent. On Gull Island where presumably the population represents one of less experienced birds it may well be that at recently established sites, such as number 7, high densities cannot 'compensate' for inexperience.

The combined breeding success for ledges four and five was 44.85 per cent which was lower than that recorded by Birkhead (1977) for birds on

Skomer which bred at medium (5.5 birds/m^2) and high (10 birds/m^2) densities (74% and 88% respectively) but higher than the 30 per cent figure he obtained for birds nesting in sparse groupings (2.5 birds/m^2). The datum for Gull Island is very similar to that recorded by Tuck (1960) for Thick-billed Murres at Cape Hay (41%). Certainly part of the difference between the figures established for Skomer and Gull Island is attributable to the human disturbance caused in the latter colony by the researcher during the weighing and measuring of chicks and eggs. Similar work at other colonies has resulted in appreciable egg and chick losses (Tuck, 1960; Belopolskii, 1957). This was strongly suggested when in 1978 four chicks fledged from a small portion of site 9b which in 1977 had failed to produce a single egg. In the first year the ledge had been visited every two days while in 1978 it was visited only twice. The population on this portion of the ledge was the same in both years.

Thus predation, at times facilitated by the human presence, was a most significant factor influencing the breeding success of murres on Gull Island. "Optimum density" was not really a workable definition for the Gull Island situation because of the colony's origins and the extremely variable nest-site conditions (habitat quality). However, observations for the entire island did indicate birds to be most successful in larger, long-established groups and where ledge conditions were safest. Smaller sites offered easiest access to marauding gulls. Birds nesting in these conditions left their eggs more frequently exposed and, as a group, offered the least resistance to predators on the ledge.

Part II

Behavior

Introduction

Murres exhibit a definite predilection for colonial nesting and characteristically breed at densities unattained by any other bird species. The extreme of this tendency is seen when nesting murres are in physical contact with their neighbours. Such intraspecific proximity at breeding is somewhat surprising since once away from the breeding sites murres are a "distance species" (Williams, 1972) and each bird maintains an area around itself within which the approach of another conspecific causes an attack or avoidance (Hediger *in* Crook, 1964). This 'individual distance' is lost once murres are in position on the breeding ledges and the expected result is a preponderance of attack or escape tendencies which do not, however, occur. Given that the spacing of members of any named species is to a considerable degree regulated by conspecific response (Brown and Orians, 1970), the considerable change in murre spacing with the onset of breeding suggests that normal (= non-breeding) behavioral sequences are replaced with different systems once at the breeding site, which allow for extreme crowding through inhibition of the expected tendencies for intense aggression and escape responses.

Most bird species maintain territories (Hinde, 1956), with certain essential behaviour systems being operative, and identifying, for any truly territorial species (Tinbergen, 1964). These systems include selection of and conditioning to the territory, a tendency to attack conspecifics intruding upon this territory and a tendency to flee from other territory owners once outside one's own territory. For these systems to operate effectively territories are usually large enough that overtly aggressive contact between two potentially competetive conspecifics can be allayed via long distance and/or highly mobile warning and/or threat displays. Furthermore, the sizes and spatial distribution of most bird territories usually mean that approach of one's own territory does not necessitate direct movement through another bird's territory or face-to-face encounters with other territory owners.

In murres however only a very small area (approximately one square foot) around the egg is actually defended (territory type c; Hinde, 1956) and thus long distance displays, and 'non-confrontative' access to one's territory are obviated. Given this fact, and that proximity of conspecifics has been shown to be an important factor in determining levels of aggression (Hinde, 1974), the tendencies to attack and flee could be expected to operate with very high frequencies. Strong inhibitions against such tendencies should, however, be operating simultaneously. Thus overt aggression (e.g. attack) is wasteful and potentially injurious and could conceivably lead to extremely high mortality of eggs and chicks. Escape behaviour, in its turn, would only result in further aggressive encounters given the distribution and proximity of neighbouring territories. The tension between all of these conflicting tendencies and inhibitions has been succinctly described by Williams (1972) as representing an agonistic impasse which may express itself to the human observer as a form of conspecific tolerance.

The problems presented by this highly stressful situation have been well defined by Birkhead (1977) and include enforced trespassing of neighbouring territories, promiscuity due to proximity of conspecifics (Norrevang, 1958; MacRoberts, 1973), and preclusion of 'long-distance' or highly mobile displays. Other problems include the forcing of mates to exist in close proximity for extended periods of time (under the intense conditions of close conspecific proximity) and the potentially severe nest-site competition which probably results in increased efforts for site maintenance and fidelity.

More or less general comments on murre behaviour have been made by numerous researchers (Johnson, 1944; Norrevang, 1958; Perry, 1940; Storer, 1952; Tschanz, 1959, 1968) but undoubtedly the two most intensive studies have been those of Williams (1972) and Birkhead (1978). Of these two studies, the former stands out as an extensive appraisal of the forms and origins of the behaviours while the latter represents the lone quantitative analysis of the subject. The present investigations were carried out to add to our knowledge of these basic parameters in a northwest Atlantic population (Williams and Birkhead worked in the northeast Atlantic) and to determine whether differences in the behaviour in a new and small colony could be detected.

The latter endeavor concentrated on aggression as this factor was thought to most likely be affected by the status and breeding densities of birds in this "overflow" population.

The figures to follow illustrate the most frequently encountered behaviors observed during the present study. The titles of these figures are with the exception of "foot-looking" those used by Birkhead (1976). The lone exception was adopted from Williams (1972) and was considered a more accurate description of this behavior for the Gull Island context.

Figure 19

Threat

Birds in this posture stood with feet widely splayed. One foot was usually stretched in the direction of the opponent while the other was variously positioned but usually it was nearly perpendicular to the first. Such a wide-legged stance provided support. Birds were usually standing side to side rather than face to face and were separated by an approximate 30 cm distance. The neck was stretched upwards and the bill was slightly above the horizontal.

The wings were held out from the body but were not outstretched. As jabs were delivered the wings were flicked simultaneously. Jabbing at this stage was more ritualized than actual and was centered on the bill tip of the opponent. Sometimes threats were terminated by the birds stretching forward until their bill tips were almost touching and then breaking off the encounter by "head-shaking" and/or "side-preening."

Threat postures probably serve to reduce high intensity aggression as "level 3" encounters (see Aggression) very seldom developed from the threat situation. More usually extreme aggression resulted from a very spontaneous and initially intense encounter. The threat display may therefore serve the functions of aggression while obviating the essentiality of highly injurious confrontations.

Threat was often accompanied by a low gargling call.

Figure 20

Rape

During rape attempts the bird being mounted remained upright and did not adopt the prone position usual during copulation. The rapist, confronted by this upright stance, attempted to hook his head and neck around the breast of the other bird and thereby maintain his position. Rape attempts were usually aborted by (1) the resistance of the bird being mounted which turned and jabbed the more persistent rapists and (2) the male partner vigorously attacking the rapist.

Rape attempts regularly occurred on Gull Island and such promiscuity is probably a result of dense nesting. Often attempts would follow a fight on the ledge and in such situations rape appeared to be almost an outlet activity where non-combatants became excited by the fracas and hopped on the back of either a bird nearby or one of the anatgonists. In these instances males were sometimes mounted by other males and infrequently three birds were involved.

Sometimes birds returning from the sea would fly right onto the back of a bird on the ledge and attempt copulation.

Figure 21

Strech-away and Turn-away

Both these gestures were frequently recorded appeasement displays. The bird in the background is showing "strech-away" which was performed almost exclusively by incubating or brooding birds. The movement consisted of fully extending the head and neck away from (but in line with) the body. Essentially this posture gave the bird a pronounced horizontal aspect while removing its (more conspicuous ?) vertical one. Usually the neck was maintained in this position until the event which triggered the response had ended. Such events included being pecked by a conspecific and the occurrence of a fight on the ledge close by.

"Turn-away" (the bird in the foreground) was a similar behavior but was more characteristic of non-incubating birds and most frequently occurred after the bird had been pecked or simply threatened by another bird. It very seldom occurred in response to movement on the ledge and it bears a striking similarity to the posture performed by canids in similar situations (Fox, 1974).

Figure 22

Side-preening

This was the most frequent appeasement display recorded during this study. In this posture a murre would turn its head backward and down and ostensibly preen the scapular region. This display consistently occurred (1) when a bird returned to its site and (2) after aggressive encounters. By removing the bill from a potentially aggressive position this display presumably indicated in (1) a lack of aggressive intent and in (2) a submission or stoppage of hostile activity.

In over ninety per cent of the potential and actual aggressive encounters where this display was given (further) hostility did not materialize.

Figure 23

Post-landing Display

This appeasement display was assumed by birds immediately after landing. During this display the wings were held outstretched and backward and the head was tilted well above the horizontal. The tarsi were held above the ledge surface. The posture was usually maintained for two or three seconds after landing and occurred in over ninety per cent of the instances where birds landed within one meter of conspecifics. Murres infrequently performed this display even in the absence of other birds.

A slightly modified version of this display was usually performed when a murre returned to its site and walked *through* a dense group of birds.

Figure 24

Ritualized-Walking (1)

During this appeasement display murres held the wings outstretched and backward. The neck was outstretched and the bill was in the horizontal position or slightly downturned. In sixty-five per cent of the observations both the "wings-up-and-back" and "head-down" components were expressed but frequently (35%) the "wing-up" component was abandoned. On Gull Island this display occurred only when conspecifics were within approximately a two meter distance and where a bird was forced to walk *past* a group of birds.

Figure 25

Ritualized-Walking (11)

This display was adopted in eighty per cent of the cases where a bird moved *through* a group of conspecifics. It was very similar to the "post-landing display" except that in thirty-seven per cent of the recorded instances the "wings-up-and-back" component of the posture was absent.

Aggression directed towards birds which had assumed this posture was infrequent and where it did occur was relieved by "exaggeration" of the display (figure 26).

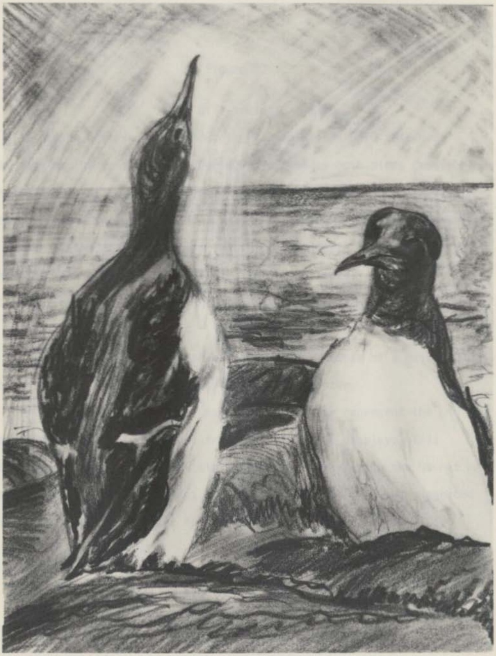


Figure 26

Exaggerated Ritualized-Walking (11)

Where murres adopted "ritualized-walking (11)" and were threatened or attacked they would stretch the neck upwards until it ran as an almost vertical line from the body to the tip of the bill. This posture always appeased further hostility.

Figure 27.

Bill-arring

Bill-arring occurred throughout the season when a bird returned to its mate at the "nest-site". During this display both birds gaped and exposed the yellow mouth lining. A gargling call was usually given by both birds and the bill clashing that ensued made it appear as though each member of the pair was attempting to grab its mate's bill while at the same time preventing having its own bill gripped. This display usually continued for five to fifteen seconds and usually terminated with "allopreening."

Bill-arring was frequently observed after one member of a pair had been involved in a "level 2" or "level 3" encounter.

This display, in both of the above contexts, may represent the rechanelling of aggression into a friendly inter-mate display. This has been postulated for the very similar fencing behavior in the Gannet (Nelson, 1966). The similarities of this display with fighting suggested to Norrevang (1958) that mates fought each time they met at the site.

Figure 28

Allopreening

This was the most frequently encountered inter-mate activity over the entire breeding season and infrequently it was observed between non-mated birds. In the latter instance all birds were incubating at the time of preening. This activity was usually restricted to the head and neck regions and the bird being preened frequently turned its neck in such a way as to ruffle its feathers in the target area.

"Allopreening" is a very common activity among bird species which nest in high densities (and have restricted breeding sites) (Cullen and Ashmole, 1963). Between mates the activity is seen to function in strengthening the pair-bond and probably reduction intra-pair aggression (Birkhead, 1976; Nelson, 1965). Its conspicuous occurrence among only incubating neighbours (non-mate conspecifics) implies (Birkhead, 1976) that in this instance too aggression avoidance is the primary function.

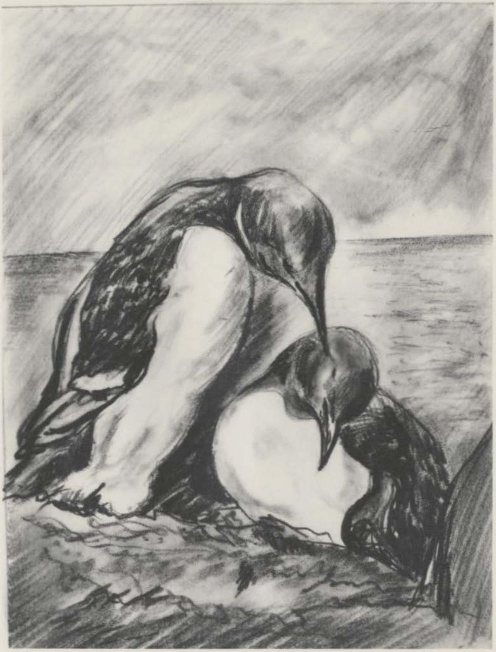


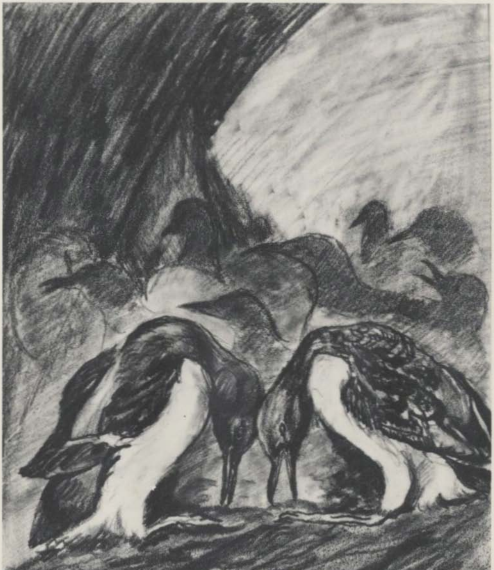
Figure 29

Foot-looking

This display occurred between members of a pair and was restricted to the period before egg-laying and during incubation. It involved one or both birds bending forward and picking up small pebbles or pieces of grass. Sometimes birds would bite one another's feet while in this position and frequently both birds would place their bills down between the feet of one of them. This position was often maintained for several seconds.

Bowing movements comparable to "foot-looking" in murres are a widespread phenomenon among many different bird species. Van Tets (1965) has suggested similar behavior in the Pelecaniformes to have been derived from nest-building movements and Tinbergen (1959) has suggested that the choking display in larids is derived from pecking at nest material or from nest-building. That bowing movements might represent an aggressive activity was suggested by Nelson (1970) for Gannets.

In murres these movements may represent vestigial nest-building tendencies (supported also by observation of incubating murres placing small pebbles beside the egg during "foot-looking"); certainly any aggressive components that might once have been influential in the evolution of this display have disappeared.



Agonistic Behavior

Pettingill's (1970) definition of agonistic encounters as all hostile activities from overt attack to overt escape is the one used here. Such encounters are discussed separately as aggression and appeasement.

Aggression

While numerous specific responses have evolved in murres to reduce the frequency of overt agonistic encounters, the breeding densities characteristic of this species inevitably result in hostile confrontations.

The most frequent expression of overt aggression recorded for this and previous studies was jabbing. This involved one bird thrusting its bill towards a nearby conspecific, sometimes with definite intent to make contact and sometimes in a more ritualized form. In the initial stages of any confrontation such jabs were directed only at the head and bill of the opponent, but as the intensity of the confrontation increased, so too did the viciousness, frequency and placement of jabs.

Contact aggression ("level 2" - see below) was usually preceeded by threat display (figure 19). Here birds usually stood about one foot apart facing the cliff and thus with their shoulders facing. The head was turned sideways to the body with the neck slightly outstretched and curved towards the opponent and with the bill held a few degrees above the horizontal. Essentially this posture maximized the distance between the two birds but still allowed the behavior to retain functional potential; the posture (and spacing) minimized, for low key aggressive encounters at least, the likelihood of serious injury but maintained the birds within a range where actual physical contact could occur. Once an encounter intensified beyond this point this "critical distance" was broken down and highly intense aggression might ensue. This distance appeared well defined as observation of threat posturings between any two birds greater than one half meter apart was recorded in only 3 (1.5%) of 200 threat displays observed. In 76 (38%) of these observations threat was accompanied by utterance of a low, gargling call. Threat displays seldom developed into 'level 3' aggression; only in 4 (2%) of 200 threat displays did such intense aggression follow. This represented thirteen per cent of the total "level 3" encounters observed (N= 30).

Various intensity levels were identified for aggressive encounters. In the first level (level 1) jabs were directed at the opponent's bill but contact was not actually made. Once level 1 intensity had been surpassed, actual contact was observed (level 2) with the target area having expanded to include the head and neck. Up to this point birds kept their mandibles closed during thrusts. The most intense (level 3) aggression involved birds jabbing with half-open beaks, locking bills and then head twisting and beating one another with their wings. Such extreme encounters were rare, only 30 such observations were recorded for both seasons on Gull Island, Birkhead's (1976) record of 200 "level 3" encounters over four years suggest that very intense aggression is more frequent on Skomer than Gull Island.

One fight on Gull Island lasted for over seventeen minutes and resulted in blood appearing on the breasts of both birds and on the underwing of one of them. The duration of this encounter was unusual however as fights rarely exceeded two minutes in length. During longer bouts birds often became fatigued and would cease struggling for brief intervals, often resting with their beaks still entwined. Infrequently one bird would manage to grip its opponent by the back of the neck and invariably this led to cessation of struggling. Such behavior could be of considerable value as Birkhead (1976) reported a similar encounter on Skomer which resulted in the severing of a major blood vessel in the pinned bird.

The low frequency of these very intense confrontations suggest strong inhibitions against them. Such inhibitions, coupled with the gradations in the intensity of these encounters, work effectively in performance of the essential functions of aggression (protection of site, mate and self) while at the same time precluding the need to engage in the highly wasteful and injurious "level 3" interactions.

During "level 3" confrontations antagonists would seemingly lose all inhibitions towards the crossing of territories and would scramble about the ledge, often with their beaks entwined, hitting other birds and generally interfering with them. Incubating birds were never seen to respond to these intrusions even though at times they were repeatedly struck by the wings of the fighting birds. Even non-incubating birds were seen to retaliate only twice (6.6% of the occasions). This absence of retaliation by incubating (and brooding) birds prevents the endangering of chicks and eggs which their involvement in such encounters could incur.

Differences in levels of aggression between different categories of birds were also noted by Birkhead (1976) and Williams (1972). Both these authors noted findings similar to those above. On Gull Island this was also noted for trespassing birds; birds passing the nest-sites of conspecifies seldom responded to attacks by territory-owners. Williams (1972) similarly noted that birds with no adjacent site usually fled from agonistic encounters whereas site-owners on or near their sites retaliated or challenged.

During challenge the bird faced its opponent with an alert posture with the neck outstretched and the bill 5-10 degrees above the horizontal. Such a challenge was usually ended by the "ambiguous headshake" (Williams, 1972) which simply consisted of rapid lateral movements of the head. For both this study and that of Williams (1972) the head was lowered as head-shaking occurred until eventually it touched the breast or shoulder at which point preening (an appeasement posture) commenced. Thus head-shaking was employed as an interim gesture which connected the alert challenge posture of potential aggression with the appeasement gesture signifying passivity.

Birkhead (1976) made some interesting observations on head-shaking and found that the frequency of expression for this behavior was similar for both the winners and losers of aggressive encounters. However, both this and William's (1972) study indicated that this display was usually performed before confrontations reached the stage where a "winner" and "loser" could be defined. Birkhead (1976) thought that this might be a comfort movement and cited the work of Ainley (1974) who showed that increased salt secretion in Adelie Penguins accompanied "head-shaking" during territorial disputes. Thus the high frequency of "head-shaking" during agonistic encounters might be indicative of hypersecretion of salt during such situations.

Observations on Gull Island indicated that this gesture occurred very frequently in non-agonistic situations as well. It was usually associated with gape distension in resting or incubating birds and in this situation was interpreted as a comfort movement. Certainly this may well be another example of a behavior which originally served a maintenance function having been ritualized (in much the way preening has been) into a display. Body maintenance behaviors would seem likely candidates for ritualized appeasement gestures as they contain no threat components.

Both Williams (1972) and Birkhead (1976) have commented on the seasonal aspects of murre aggression behavior. The former author stated that especially during the incubation and fledging periods murres had a tendency to turn and jab neighboring birds without apparent reason. After doing this these birds almost immediately began appeasement posturing so that when the bird that had been attacked turned to retaliate it confronted a bird in an appeasement posture. Similar observations (N= 63) were noted for Gull Island. The latter author reported that levels of aggression and appeasement were significantly lower in the pre-laying period than at other times and this too agrees with data gathered on Gull Island. This same author noted higher levels of aggression during the winter period when birds first returned to the ledges on Skomer. He interpreted this as a reflection of competition associated with re-establishment of site ownership. Such an interpretation was in keeping with his earlier noted conjecture that one function of such early return to the breeding ledges was maintenance of the nest-site under the highly competitive conditions suggested to operate in that area. If a similar situation operated on Gull Island then higher levels of aggression would be expected in the pre-laying period and this was not the case. Thus varying levels of aggression with first contact of the land represents a further difference between the British and Newfoundland (Gull Island) situation.

The vast majority of aggressive encounters were associated with defense of the nest site or mate; the latter was observed during rape attempts. Such attempts consistently resulted in resistence by the female and an aggressive attack by her mate on the rapist. The latter was never seen to retaliate in forty-two such observations.

Aggressive encounters between mates were rare - only two such observations were made and both of these followed copulation attempts where the female jabbed at the male. Birkhead (1976) noted a similarly low level of intra-pair aggression on Skomer.

Appeasement

Elements of fear are associated with aggression in many species (Hinde, 1966) and this was certainly true of the murres on Gull Island. Frequently aggressive gestures (e.g. jabs) would abruptly give way to appeasement and as noted previously actual fights ("level 3" encounters) were seldom preceeded by threat displays which in the majority of cases prevented highly intense aggression. Obviously if strategies had not evolved for the mitigation of aggression, coloniality could never have become a successful reproductive design. While threat is itself a form of aggression it represents a successful trade-off as a lesser of two evils. Going one step further are the non-aggressive displays which function to bridle potential aggression. Such displays are of course appeasement gestures and while not one hundred per cent successful they result in a surprisingly low level of high intensity aggression in murre colonies.

Appeasement can operate in either of two ways - it can prevent the onset of aggression or it can terminate aggression once it is started. Birkhead (1976) has consisely dichotomized murre appeasement displays along these lines and describes the former as "passive appeasement" and the latter as "active appeasement". Certain displays can, in different contexts, function as either active or passive appeasement.

Side-preening, the most frequently encountered appeasement posture (figure 22) occurred regularly in two situations. It consistently followed the return of a bird to its site and either took place almost immediately if its mate was absent or followed bill-arring (figure 27) if its mate was present. Side-preening also occurred at the end of fights and sometimes in the middle of "level 2" encounters as well as ending threat-only confrontations. The latter observation underscores the fact that appeasement displays do not always work and that once "level 3" aggression begins appeasement displays do not usually take place until the encounter has definitely ended(i.e. there is a clear winner). This once again (as did the previously noted loss of inhibitions towards trespassing) points out the total involvement of fighting murres once "level 3" aggression is reached.

Williams (1972) suggested that there was a directional component to side-preening and that this was related to dominance. Thus in situations where both birds side-preened the dominant individual (the winner of an encounter) would preen its side nearest the opponent whereas the less dominant bird (the loser) would preen its far side. Birkhead(1976) however, found that no such directional component was detectable for birds on Skomer. While specific investigation of this phenomenon was not part of this study,observations that were made agreed with those of Birkhead (1976).

The "preening" executed during the side-preening display was often of a token manner, emphasizing the ritualization of the posture. The latter is important as sudden movements (such as landing) elicit aggression from birds nearby (this study; Birkhead, 1976; Williams, 1972). The effectiveness of such displays was manifest on Gull Island when threats against returning birds were initiated and then abandoned once the post-landing display and/or side-preening were carried out. In fact for 340 observed returns to site in 311 (91%) birds sidepreened immediately or just after bill-arring with their mates. Of these returns with appeasement 167 (54%) saw nearby conspecifics adopt a challenge or threat posture and in 42 (25%) of the cases actual jabbing of the new arrival occurred. In all but 7 (17%) of the latter instances aggression terminated with the appeasement posture. This means that of 311 returns to the site, which were accompanied by appeasement, only in 7 (2%) instances did post-appeasement aggression occur. Potentially all 311 returns could have elicited aggression.

In the nine per cent of the returns to site where side-preening was not recorded all birds did go through bill-arring. For birds returning to an unoccupied site (mate absent) side-preening was always expressed. This evidence certainly suggests non-mate conspecifics to be the prime eliciters of side-preening during site returns.

Strech-away and turn-away (figure 21) appeasement occurred after an aggressive encounter (involving the bird showing appeasement or in response to a nearby "level 2" or "level 3" encounter) and in response to the movement of nearby birds. Stretch-away was performed mainly as passive appeasement (88% of all observations N= 86) and was only performed by incubating birds. During active appeasement the neck extension would sometimes be maintained even while the bird suffered jabs from its opponent. This prolonged display was referred to by Birkhead (1976) as the "prolonged stretch-away."

Turn away was observed very infrequently as passive appeasement and in 95% (N= 127) of the observations it occurred immediately after an aggressive "level 2" or "level 3" confrontation but only in 3% of the cases did it follow threat encounters. In five "level 2" encounters where turn-away was used to terminate aggression the initial jabs were a response to the stretch-away posture which had been ellicited by the movement of a bird nearby. Parodoxically in this situation one appeasement gesture had elicited aggression and thereby necessitated a further and different appeasement display. These observations (once again) underline the high tension inherent in murre breeding associations and support the earlier-noted observation of how sudden movements often elicit conspecific aggression.

The post-landing display (figure 23) was a totally passive appeasement display and it occurred in ninety per cent of the observed landings where birds alighted within a meter of conspecifics and/or followed landing by movement through the colony (N= 360). Murres landing on the periphery and remaining there seldom performed a post-landing display. The latter observation disagrees with that of Williams (1972) who stated that birds returning to the ledge performed this display whether or not conspecifics were nearby. Birkhead (1976) found that birds were more likely to perform post-landing displays in the proximity of other birds.

The origin of the display is probably a combination of the recovery after landing and the preparedness for a number of antagonistic tendencies including attack, defense or fleeing. Van Tets (1965) has suggested a similar origin for the post-landing display of various of the Pelecaniformes. Williams (1972) has commented on the balance (= recovery) aspect of the murre post-landing posture and has also considered the bringing of fish to chicks to have been an influencing factor. In this situation murres hold the fish in their beaks and have their neck outstretched to the fullest with the bill above the horizontal. The posture is essentially the ritualized-walk (11) (figure 25) posture and presumably aids in prevention of fish stealing. Certainly this factor could influence the "head-up" component of the display and possibly the "wings-up-and-back" component could represent the recovery aspect.

Post-landing displays function as appeasement and may partly accomplish this by allowing conspecifics to recognize the alighting bird before it enters their midst en route to its site. Lorenz (1934) claimed this to be the case for the post-landing posture of the Black-crowned Night Heron (*Nycticorax nycticorax* (L.)) stating that such habituation reduced conflict; Dorward (1962) considered the post-landing display of sulids to inhibit molestation via a similar modus.

Once having landed murres face the problem of reaching their "nest-site" which may be a considerable distance away. To get there they must cross the territories of a number of potentially aggressive conspecifics. Essentially two different contexts are possible here - either the bird can move past a group of other murres or through the group. On Gull Island if the bird could walk *past* the group at a distance of approximately two meters or greater no posture was assumed. However, if the bird was forced to walk *by* the group at less than this distance it usually (78% of 207 observations) adopted the ritualized-walking (1) (figure 24) posture which consisted of the "head-down", "wings-up-and-back" components. Where one component was abandoned it was always the "wings-up-and-back" and this occurred for 35 per cent of the observations. This suggests that the "head-down" aspect is the most essential postion of the display and certainly if, as Birkhead (1976) suggests, the wing component functions to draw attention to the moving bird, then it may well be that the post-landing display which has preceeded the "ritualized-walking" has accomplished this end already.

When a murre was forced to move *through* a dense group of nesting birds it adopted the ritualized-walking (11) (figure 25) posture which was practically identical to the "post-landing" display except that in 37 per cent of the instances (N= 63) the "wings-up-and-back" component of the landing posture was absent. This usually occurred in dense nesting groups where possibly the "wings-up-and-back" aspect might have elicited aggression from birds struck by the wings. The appeasement function of this display was demonstrated by two different sets of observations. Firstly, of fifteen situations where birds did not adopt this posture while moving through a group of birds, fourteen (93%) resulted in their being threatened and/or engaged in "level 2" encounters by conspecifics. Secondly in eight of these situations (57%) birds once threatened or attacked stretched the neck higher and positioned the bill almost in a vertical plane (figure 26). If the attacker was on their side or behind them the birds would hurry out of range but if their path was blocked by the aggressor then they would stop and often accept several jabs without retaliation. Aggression was always aleviated by the "exaggeration" of the basic posture outlined above and "level 3" encounters never developed in this context.

Murres are aggressively colonial (Nelson, 1970) and each breeding pair may encounter strong resistance in seeking a territory close to other conspecifics. This compression of territory and inter-pair distances means that intense agonistic behavior should characterize murre breeding strategies as the use of long-range threat is precluded and because territory trespassing is, of necessity, frequent.

However the very fact that murres do nest in such high densities indicates that highly intense (e.g. "level 3" aggression cannot be prevalent as such a situation would have led to a spacing-out of birds (Williams, 1972)). Observations indicate that low intensity aggression ("levels 1 and 2") is commonplace while "level 3" encounters are expressed less often in murres than in other colonial species (e.g. sulids (Nelson, 1970)). The open nesting habits of murres have undoubtedly been a strong selection favoring low levels of high intensity aggression.

Murres have, in effect, achieved an equilibrium for aggression, maintaining it largely in an essentially ritualized form (threat) for the protection of nest-site and mate and preventing it via appeasement gestures which thereby inhibit injury to self.

The breeding situations characteristic of murres necessitate unambiguous displays which clearly define the intentions of the displaying bird. However, the antagonistic tendencies that operate simultaneously in colonial situations are responsible for the frequent expression of conflict behaviors. Such behavior often leads to aggression being directed at objects other than the one which elicited the aggression. Thus in murres many of the attributes of overt aggression such as jabbing, bill-gripping and head twisting are seen in the bill-arring between mates suggesting that a behavior which presumably now functions in strengthening of the pair-bond has been derived from overt aggression. Allo-preening, another display important in pair-bond maintenance, has similarly been suggested to represent redirected aggression (Harrisson, 1965). Restriction of the breeding site has led to the appearance of both these behaviors, allopreening and a protracted greeting ceremony, in numerous, and taxonomically quite distinct, species (Cullen and Ashmole, 1963; Nelson, 1967).

The behaviors illustrated and discussed in the foregoing section do not represent all the displays which have been identified for Common Murres. Birkhead (1976) noted fifteen displays for this species on Skomer. However, the behaviors discussed herein have all been ones strongly influenced by aggression.

The behaviors observed on Gull Island were also recorded by Birkhead (1976) with one possible exception. The "exaggerated ritualized-walking (11)" display noted on Gull Island bears a strong resemblance to what Birkhead (1976) called the "head-vertical" posture and which he recorded as occurring almost exclusively in clubs. He interpreted this display as a male advertising posture performed by non-territorial (non-mated) males. The posture illustrated in the Birkhead (1976) study is apparently identical to that observed on Gull Island and it may well be that the posture functions in both contexts - those of male advertising and active appeasement, both situations being ones requiring conspicuously non-aggressive intent. As detailed observations of club birds were not made on Gull Island any differences which might be expressed in the different contexts (breeding ledge vs. clubs) await further study.

Indications from this study are that ("level 3") aggression occurred less frequently on Gull Island than on Skomer. This is probably a reflection of the status of birds on Gull Island and the availability of unoccupied habitat that exists there.

Final Discussion

The adaptive strategy of any species represents an evolutionary end-product, a balanced strategy for survival which has been shaped by a multiplicity of interacting, and species-specific, selection pressures. The interaction of all these factors means that effects on any one aspect of a species' biology are seldom isolated and usually input at any point along the continuum of organism-environment exchange results in a rebalancing of all associated parameters.

The Common Murre is a species adapted for life in two very different environments and strategies operational in one situation are often, of necessity, mitigated in the other. Thus during the non-breeding season this species ranges over the coastal and inshore waters and exploits a vast foraging area where direct contact between conspecifics is prevented. This situation changes abruptly once breeding starts and high density nesting conditions develop.

Both the density of breeding birds and the lack of any actual nest have influenced, and been influenced by, predation, clutch size and breeding success. The density of breeding birds leads to vastly increased conspecific contact and the tendency to maintain "individual distances" during the non-breeding season translates into territorial responses at breeding time which result in frequent expression of aggression behaviour. Such aggression has been a dominant force in the evolution of murre social behaviour.

Birkhead (1976) has similarly noted the complexity of adaption in this species and considered body size and the morphological adaptations for diving to have been major influences on the general breeding strategy of murres. He noted that because of their specialization for life at sea, murres are awkward on land. One consequence of this awkwardness is that murres are unable to take off from a flat surface and therefore must move to the edge of a cliff before flying out to sea. As noted earlier, such situations elicit aggression from nesting birds and therefore have associated with them well-defined appeasement displays. This awkwardness on land has also affected the abilities of murres to defend their eggs and chicks as it precludes the use of any mobile defence such as the dive-bombing tactics that gulls and terns employ. Thus a single factor, morphology, has influenced a range of responses in murres to such varied factors as predation, territoriality and social behaviour.

The high nesting densities of murres are probably an adaptation to predation; certainly large, dense groups of murres can represent an effective anti-predator device. These high densities are adaptive also in that they function to synchronize ledge populations and thereby allow for maximum numbers of chicks to be fledged and of course fledging itself takes place just before dark when presumably a predator's chances of taking a chick are reduced. The eggs too, while exposed, are given a large measure of protection by the assiduosness characteristic of murre incubation. Similar attention is shown to the chick and this places constraints on the amount of food that can be brought to the young bird. This problem is gotten around by reducing the fledging period and allowing the chick to leave the ledge at an early age. Differential growth patterns for various body parts means that the chick is capable of following the adult to sea.

Murres as a group have been very successful in their exploitation of the marine environment and essentially come to land only to lay their eggs and raise their chicks. Their adaptation to this way of life has been complete, to the extent that on land they are awkward and have, of necessity, evolved complex behaviour patterns which function to reduce those problems which this awkwardness and their high-density nesting have created.

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