ASPECTS OF THE BEHAVIOUR AND ECOLOGY OF BLACK-LEGGED KITTIWAKES, *RISSA TRIDACTYLA*, BREEDING AT TWO SITES IN NEWFOUNDLAND, 1990-1991

JOSEPHINE ANN NEUMAN

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

ASPECTS OF THE BEHAVIOUR AND ECOLOGY OF BLACK-LEGGED KITTIWAKES, *Rissa tridactyla*, BREEDING AT TWO SITES IN NEWFOUNDLAND, 1990-1991.

A thesis submitted to the School of Graduate
Studies in partial fulfillment of the
Requirements for the degree of
Master of Science

Biopsychology Program
Departments of Psychology and Biology
Memorial University of Newfoundland
May 1993

St. John's Newfoundland Canada

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

THE AUTHOR HAS GRANTED AN IRREVOCABLE NON-EXCLUSIVE LICENCE ALLOWING THE NATIONAL LIBRARY OF CANADA TO REPRODUCE, LOAN, DISTRIBUTE OR SELL COPIES OF HIS/HER THESIS BY ANY MEANS AND IN ANY FORM OR FORMAT, MAKING THIS THESIS AVAILABLE TO INTERESTED PERSONS.

L'AUTEUR A ACCORDE UNE LICENCE IRREVOCABLE ET NON EXCLUSIVE PERMETTANT A LA BIBLIOTHEQUE NATIONALE DU CANADA DE REPRODUIRE, PRETER, DISTRIBUER OU VENDRE DES COPIES DE SA THESE DE QUELQUE MANIERE ET SOUS QUELQUE FORME QUE CE SOIT POUR METTRE DES EXEMPLAIRES DE CETTE THESE A LA DISPOSITION DES PERSONNE INTERESSEES.

THE AUTHOR RETAINS OWNERSHIP OF THE COPYRIGHT IN HIS/HER THESIS. NEITHER THE THESIS NOR SUBSTANTIAL EXTRACTS FROM IT MAY BE PRINTED OR OTHERWISE REPRODUCED WITHOUT HIS/HER PERMISSION.

L'AUTEUR CONSERVE LA PROPRIETE DU DROIT D'AUTEUR QUI PROTEGE SA THESE. NI LA THESE NI DES EXTRAITS SUBSTANTIELS DE CELLE-CI NE DOIVENT ETRE IMPRIMES OU AUTREMENT REPRODUITS SANS SON AUTORISATION.

ISBN 0-315-96087-6

Canada

GENERAL ABSTRACT

An examination of variability in the breeding success of Black-legged Kittiwakes, Rissa tridactyla, was the focus of this research. An attempt was made to relate this variability to ecological conditions, in particular food availability. Apparent food shortages in 1991 provided a natural experiment as data were collected from two Newfoundland colonies, Cape St. Mary's and Gull Island in Witless Bay, in 1990 and 1991. Comparisons were also made with previous Newfoundland studies.

At both colonies, timing of breeding was later, there was a greater amount of non-breeding, and clutch sizes were smaller in 1991, the year with the most apparent food shortages. Observer access to the nests was only possible on Gull Island and there egg volumes were smaller, and chick survivorship and growth rates were lower in 1991. The behavioural evidence for food shortages on Gull Island in 1991 was also compelling. Chicks begged more intensely and had fewer successful begging bouts in 1991, but chick feeding rates in the two years were similar. As the few chick growth rates obtained in 1991 clearly showed that chicks were starving, future studies should incorporate estimates of bolus size and food type in addition to determining feeding rates. Chicks were seldom left unattended in 1990 (for all ages combined, less than 3% of the time), and in 1991 they were not seen left alone at all. Adults may have been responding to increased predation by Herring Gulls, Larus argentatus.

Courtship feeding, a significant event in the pre-laying period, was the subject of special emphasis at Cape St. Mary's in 1990. One of the hypothesized functions of courtship feeding is its nutritional significance, providing the female with extra food prior to egg laying. The phenology of courtship feeding in relation to egg laying, and the substantial amount fed (at the peak, 8 boluses per pair per day) circumstantially confirmed the nutritional importance of courtship feeding. Courtship feeding rate was not significantly correlated with timing of breeding, clutch size, hatching success or fledging success.

An examination of inter-observer reliability was made in the context of the courtship feeding study. Two of the seven variables were scored reliably, while the remaining variables were affected by either systematic error or random error and influenced conclusions differently depending on the questions asked. The difficulties inherent in obtaining adequate observer agreement in field studies of animal behaviour indicate that an assessment of inter-observer reliability should be a part of every behavioural study.

In general, seabirds represent extreme "K-selected" species and this pattern was clearly exemplified by Black-legged Kittiwakes in a year of apparent food shortages, as they attempted to maximize adult survival rates by reducing their investment in reproduction.

IN MEMORY OF ELSA AND TYBEE

ACKNOWLEDGEMENTS

Science is a collaborative effort and I have many people to thank for their support in the successful conclusion of this research project.

Firstly, I would like to thank my supervisors, Dr. Julie Porter with Fisheries and Oceans, St. Andrews, New Brunswick and Dr. John Chardine with the Canadian Wildlife Service, St. John's, Newfoundland, for their good advice, patience and steadying influence over the last few years.

Thanks also to my field assistants, Andrea McCharles in 1990 and Ulrike Mulroney in 1991, for their companionship and for their endurance and diligence in the long hours spent watching and recording kittiwake behaviour. They maintained their good humour and enthusiasm throughout all difficulties.

Members of my committee, Dr. Anne Storey and Dr. Bill Montevecchi, have improved this research with their good advice in the planning stage and with their helpful comments on an earlier draft of this thesis.

The chapter on inter-observer reliability benefited greatly from lengthy discussions with Dr. Deanne Renouf and with my former employer, Dr. Susan Goldberg, at the Hospital for Sick Children in Toronto. Both read and commented on an early draft of that chapter.

Bay Roberts and Scott Hatch, with the U.S. Fish and Wildlife Service in Alaska, sent me a copy of a paper they had written on kittiwake behaviour in a failing colony and the approach I then adopted to the presentation of the behavioural data on parental attendance, and chick begging and feeding in Chapter 2 owes a debt to their work.

I wish to thank Joe and Loyola O'Brien of Bird Island Charters in Bay Bulls for providing transportation to Gull Island and for their concern for our safety. Thanks also to Chip Weseloh and Christine Bishop of the Canadian Wildlife Service in Burlington, Ontario for allowing me to use their laser printer for the final drafts of this thesis.

This study would not have been possible without generous financial support from Dr. Julie Porter through NSERC Operating Grant (No. 3-31876). A grant from Sigma-Xi in 1991 also helped defray costs.

Last, but not least, I would like to thank the people who looked after my cats while I was in the field, and set my heart at ease with their attentive care and affection for them. These people are: Frank Chopin, Julie Huntington, Rosie Seton, Pam Jones and Irene Cole.

Thanks everyone.

TABLE OF CONTENTS

Page

General Abstract.......................... ii

Dedication................................ iv

Acknowledgements.......................... v

Table of Contents......................... vi

List of Tables............................ ix

List of Figures........................... xi

List of Plates............................ xvi

List of Appendices........................ xvii

Chapter 1 **Introduction**............................ 1

1.1 References............................ 7

Chapter 2 **Breeding Biology of Black-legged Kittiwakes at Cape St. Mary's and Gull Island in 1990 and 1991**

2.1 Abstract............................. 10
2.2 Introduction......................... 12
    2.2.1 Timing of Breeding.............. 14
    2.2.2 Clutch Size..................... 16
    2.2.3 Egg Size and Survivorship....... 18
    2.2.4 Incubation Period............... 20
    2.2.5 Nestling Period................. 21

2.3 Methods

    2.3.1 Study Sites..................... 23
    2.3.2 Collection of Breeding Biology Data........................... 28
    2.3.3 Collection of Behavioural Data.. 30
    2.3.4 Data Analyses................... 32

2.4 Results

    2.4.1 Timing of Breeding.............. 34
    2.4.2 Clutch Size..................... 36
    2.4.3 Egg Size and Survivorship....... 38

Page

2.4.4 Incubation Period.............. 41
2.4.5 Nestling Period................ 43
2.5 Discussion........................ 47
2.5.1 Timing of Breeding............. 50
2.5.2 Clutch Size.................... 51
2.5.3 Egg Size and Survivorship....... 53
2.5.4 Incubation Period.............. 56
2.5.5 Nestling Period................ 57
2.6 References........................ 91

Chapter 3 **Inter-observer Reliability**

3.1 Abstract.......................... 101
3.2 Introduction...................... 102
3.3 Methods
3.3.1 Study Site..................... 109
3.3.2 Collection of Data
3.3.2.1 Schedule of Observations and Sampling Effort..... 110
3.3.2.2 Behavioural Observations. 111
3.3.3 Analyses of Data............... 112
3.4 Results........................... 115
3.5 Discussion........................ 120
3.6 References........................ 146

Chapter 4 **The Functional Significance of Courtship Feeding in Black-legged Kittiwakes**

4.1 Abstract.......................... 148
4.2 Introduction...................... 150
4.3 Methods
4.3.1 Study Site..................... 155
4.3.2 Collection of Data
4.3.2.1 Schedule of Observations and Sampling Effort..... 156
4.3.2.2 Collection of Breeding Success Data........... 157
4.3.2.3 Behavioural Observations. 158
4.3.2.4 Inter-observer Reliability............ 160
4.3.3 Analyses of Data............... 161
4.4 Results
4.4.1 Inter-observer Reliability...... 163
4.4.2 Seasonality of Courtship Displays....................... 164

Page

4.4.3 Courtship Feeding Rate as a Predictor of Reproductive Success........................ 166
4.4.4 Courtship Feeding Rate as a Predictor of Copulation Success........................ 166
4.5 Discussion
4.5.1 Inter-observer Reliability...... 167
4.5.2 The Nutritional Importance of Courtship Feeding............... 169
4.5.3 Courtship Feeding Facilitates Copulation...................... 171
4.6 References........................... 189

Chapter 5 **General Discussion**....................... 191

5.1 References........................... 197

Appendices............................... 198

LIST OF TABLES

Page

Table 2-1 Schedule of visits to study colonies in 1990 and 1991 and sample sizes of nests studied.................................. 66

Table 2-2 Sampling effort for behavioural data at Gull Island in 1990 and 1991.............. 67

Table 2-3 The timing of breeding of Black-legged Kittiwakes at Cape St. Mary's (CSM) and Gull Island (GI), Newfoundland in five years between 1969 and 1991............... 68

Table 2-4 Black-legged Kittiwake clutch size composition at Cape St. Mary's (CSM) and Gull Island (GI) in 1969, 1970, 1988, 1990 and 1991........................... 69

Table 2-5 Seasonal trends in Black-legged Kittiwake clutch size in 1990 and 1991 in early, middle and late laid eggs................ 70

Table 2-6 Changes in the proportions of occupied nests with eggs for Black-legged Kittiwakes at Cape St. Mary's (CSM) and Gull Island (GI) in 1969/1970, 1988, 1990 and 1991.... 71

Table 2-7 Seasonal trends in Black-legged Kittiwake egg volumes on Gull Island in 1990 and 1991 in early, middle and late laid eggs.. 72

Table 2-8 Comparisons of Black-legged Kittiwake egg volumes from Gull Island, and their relationship to hatching and fledging success................................. 73

Table 2-9 Black-legged Kittiwake egg fates from Gull Island in 1990 and 1991................... 74

Table 2-10 An inter-colony and inter-year comparison of hatching success at Cape St. Mary's (CSM) and Gull Island (GI) in 1969, 1970, 1990 and 1991............................ 75

Page

Table 2-11 An inter-colony and inter-year comparison of fledging success in Black-legged Kittiwakes at Cape St. Mary's (CSM) and Gull Island (GI) in 1969, 1970, 1990 and 1991.................................... 76

Table 2-12 Black-legged Kittiwake parental attendance patterns during chick rearing, Gull Island, 1990 and 1991........................... 77

Table 2-13 The rate of Black-legged Kittiwake chick begging bouts and the percent that resulted in a feed on Gull Island in 1990 and 1991................................ 78

Table 2-14 The feeding rate (number of boluses per hour) of Black-legged Kittiwake chicks according to age on Gull Island in 1990 and 1991................................ 79

Table 3-1 A summary of the results of the analyses of inter-observer reliability in the study of courtship feeding in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 128

Table 4-1 The number of nests and number of hours of observation in relation to the date of egg laying................................. 175

Table 4-2 Food boluses (per pair per hour) correlated with food solicitation, copulation and measures of reproductive success in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 176

Table 4-3 The effect of prior feeding on the likelihood of copulation success during the 14 days preceding egg-laying in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 177

LIST OF FIGURES

Page

Figure 2-1 Locations of Cape St. Mary's and Gull Island seabird colonies.................. 80

Figure 2-2 Number of hours of behavioural observation in relation to time of day on Gull Island in 1990 (18/6 - 23/6, 9/7 - 1/8) and 1991 (24/6 - 30/6, 3/7 - 17/7)................ 81

Figure 2-3 Laying date (date first eggs laid) distribution for Black-legged Kittiwakes on Gull Island in 1990 and 1991........... 82

Figure 2-4 Laying date (date first eggs laid) distribution for Black-legged Kittiwakes at Cape St. Mary's in 1990................ 83

Figure 2-5 Black-legged Kittiwake egg volumes on Gull Island in 1969, 1988, 1990, and 1991...... 84

Figure 2-6 Seasonal trends in Black-legged Kittiwake egg volumes on Gull Island in 1990 and 1991 in early, middle or late laid eggs... 85

Figure 2-7 Black-legged Kittiwake egg survivorship curves on Gull Island in 1991............. 86

Figure 2-8 Chick survivorship curves for Black-legged Kittiwakes on Gull Island in 1990 and 1991................................. 87

Figure 2-9 Growth rates of Black-legged Kittiwake chicks during the period of linear growth (6 - 20 days) on Gull Island in 1990...... 88

Figure 2-10 Black-legged Kittiwake chick masses on Gull Island in 1990 and 1991.............. 89

Figure 3-1 Correlation between observer 1 and observer 2 in returns to the nest (mean per pair per hour) in adult Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 129

Page

Figure 3-2 Correlation between observer 1 and observer 2 in food solicitation bouts (mean per pair per hour) in adult Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 130

Figure 3-3 Seasonal changes in food solicitation bouts (mean per pair per hour) in adult Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990................ 131

Figure 3-4 Correlation between observer 1 and observer 2 in courtship feeding bouts (mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 132

Figure 3-5 Seasonal changes in courtship feeding bouts (mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 133

Figure 3-6 Correlation between observer 1 and observer 2 in courtship feeds (mean boluses per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 134

Figure 3-7 Seasonal changes in courtship feeds (mean boluses per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 135

Figure 3-8 Correlation between observer 1 and observer 2 in boluses per courtship feeding bout (mean number) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 136

Figure 3-9 Seasonal changes in boluses per courtship feeding bout (mean number) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 137

Page

Figure 3-10 Correlation between observer 1 and observer 2 in successful copulations (mount with cloacal contact - mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.... 138

Figure 3-11 Correlation between observer 1 and observer 2 in total copulations (successes + attempts - mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990................ 139

Figure 3-12 Correlation between observer 1 and observer 2 in copulation attempts (mount, no cloacal contact - mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990............ 140

Figure 3-13 Seasonal changes in attempts to copulate (mount, no cloacal contact - mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....... 141

Figure 3-14 Correlation between observer 1 and observer 2 in cloacal contacts per mount (mean number) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.... 142

Figure 3-15 Seasonal changes in cloacal contacts per mount (mean number) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 143

Figure 3-16 Frequency plots of the different courtship behaviours in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....... 144

Figure 4-1 Number of hours of observation in relation to time of day, Cape St. Mary's, Newfoundland, 1990....................... 178

Figure 4-2 Seasonal changes in adult returns to the nest (mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990....................... 179

Page

Figure 4-3 Seasonal changes in bouts of courtship feeding, food solicitation and copulations (mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990........................ 180

Figure 4-4 Seasonal changes in the proportion of bouts of food solicitation followed by courtship feeding in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990........................ 181

Figure 4-5 Seasonal changes in courtship feeding bouts (mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990........................ 182

Figure 4-6 Seasonal changes in the mean number of boluses per feeding bout in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990........................ 183

Figure 4-7 Seasonal changes in courtship feeds (mean boluses per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990........................ 184

Figure 4-8 Seasonal changes in successful copulations (cloacal contact), attempts to copulate (mount, no cloacal contact), and total copulations (successes + attempts) (mean per pair per hour) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990........................ 185

Figure 4-9 Seasonal changes in the proportion of all copulations involving cloacal contact in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990................ 186

Figure 4-10 Seasonal changes in cloacal contacts per mount (mean number) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990........................ 187

Page

Figure 4-11 The influence of multiple boluses on the success of subsequent copulations in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990................ 188

Figure C-1 Greeting ceremony in the Black-legged Kittiwake (Cramp 1983).................... 205

Figure C-2 Head-tossing in the Black-legged Kittiwake (Paludan 1955).................. 206

Figure C-3 Food begging in the Black-legged Kittiwake (Paludan 1955).................. 206

Figure C-4 Courtship feeding in the Black-legged Kittiwake (Paludan 1955).................. 207

Figure C-5 Copulation in the Black-legged Kittiwake (Cramp 1983)............................. 208

LIST OF PLATES

Page

Plate 2-1 Representative study and control plots on Gull Island: Upper - study plot F, Lower - control plot I.................... 90

LIST OF APPENDICES

		Page
Appendix A	Common and scientific names of species mentioned in the text	198
Appendix B	Personal communications	200
Appendix C	Black-legged Kittiwake courtship displays (from Paludan 1955)	201

Chapter 1

INTRODUCTION

The ways in which animals allocate resources to the potentially conflicting demands of survival and reproduction are referred to as life-history strategies. One concept which has been particularly influential in the search for life-history patterns is the concept of r and K selection, originally propounded by MacArthur and Wilson (1967) and elaborated by Pianka (1970). Some species have a comparatively high reproductive rate and short lifespan (r-selected - represented by the parameter r, the intrinsic rate of natural increase, in equations of population growth), while others reproduce at a much lower rate, provide those few young with more parental care, and have higher adult survivorship (K-selected - represented by the parameter K, carrying capacity, in equations of population growth).

For the most part, seabirds represent extreme K-selected species. Within this general pattern there is some variability in the way different seabird species allocate resources to survival and reproduction. Several authors (Lack 1968, Ashmole 1971, Nelson 1983) have tried to relate this variability among species to ecological conditions, in particular food availability. An examination of within-species variability in breeding success caused by ecological conditions is the central aim of this research. Adult Black-legged Kittiwakes (common and scientific names listed in Appendix A) were observed during courtship in 1990 and chick rearing in 1990 and 1991, and fluctuations in food supplies were the hypothesized cause of inter-year and inter-colony differences in courtship feeding rate, timing of breeding, clutch size, brood size and chick growth and parental care.

This study also exemplifies a central subject area of behavioural ecology, that is, an examination of the survival value of different behaviour patterns. The optimal behaviour for an individual, in balancing the competing demands of survival and reproduction, will depend on the ecological circumstances it encounters (Krebs and Davies 1981).

In general, the conditions for recording behaviour in the field are rarely ideal and high quality data are not easy to collect (Aldrich-Blake 1970). As behavioural observations may sometimes involve subjective judgements on the part of the observers, inter-observer reliability was assessed in the behavioural data collected during the courtship period. Inter-observer reliability measures the extent to which two or more observers obtain similar results when measuring the same behaviour on the same occasion. Factors which can influence the consistency with which a behaviour pattern is recorded are the frequency at which it occurs, observer experience, observer fatigue, and how well each behaviour pattern is defined. Awareness of this possible methodological difficulty is important, for despite the sometimes difficult conditions of a field study, it provides unique opportunities for observing important aspects of a species' behaviour and biology.

Observations began in 1990 with the courtship period. Courtship behaviour has been the subject of a wide variety of studies of differing approaches. Ethologists have described courtship displays and focused on the analysis of their derivation (Huxley 1923, Tinbergen 1952, Blest 1961) and motivation (Moynihan 1955a,b 1958, Bastock 1967). These authors have shown that displays have been ritualized for communication through evolution, and have generally been derived from activities that previously served functions unrelated to courtship. Analyses of motivation suggest that many of the displays associated with courtship result from conflicting tendencies of fear, aggression and mating (Bastock 1967).

An alternative approach is to ask questions about the function or survival value of courtship. Many species of seabird have elaborate and lengthy courtship ceremonies which must therefore entail some cost (Nelson 1977, Daly 1978), as well as benefits. Although courtship feeding in birds has a number of hypothesized functions or benefits (Lack 1940, Brown [illegible]7, Nisbet 1973, Tasker and Mills 1981), one function may be to increase a female's fitness by providing her with extra food (Royama 1966, Nisbet 1973,1977, Tasker and Mills 1981, Morris 1986). Supplementary food is particularly important in the Laridae, where females lay a clutch with a total mass representing almost one third of their body weight (Hunt 1980). Before egg laying, courtship feeding can also serve to increase male fitness by contributing to the quality of the eggs before they are fertilized. In monogamous species, such as Black-legged Kittiwakes, this contribution to egg quality could well be a major function of courtship feeding. The size and type of food items available to males for courtship feeding, as well as the feeding rate, can affect the fitness of their mates through differences in clutch size, egg size and laying date (Nisbet 1977).

The courtship feeding study was originally undertaken to gain additional experience before beginning what was to be the main part of the research, a study of the "brood reduction" hypothesis of hatching asynchrony in Black-legged Kittiwakes (Lack 1954, Mock 1984). The courtship feeding study was successful, but massive breeding failure at Gull Island in 1991 prevented the brood reduction study from being completed. This breeding failure in 1991 proved fortuitous however as it indicated a difference in ecological conditions from the previous year, providing a natural experiment to test how environmental differences affect breeding success.

It was hypothesized (post hoc) that variation in reproductive success in Black-legged Kittiwakes was caused by fluctuations in food supplies. Productivity was examined at several stages from egg laying to fledging to determine when birds are most sensitive to decreased food supplies. Although no direct sampling of fish stocks was conducted in this study, it was predicted that behavioural and biological indices alone would provide a convincing demonstration of food shortages. Behavioural differences between reproductively successful and unsuccessful pairs will demonstrate that ecology influences reproductive success through behaviour, a central theme of behavioural ecology.

If the reproductive success of a population is limited by food availability, then this population is placed at risk by environmental changes and fisheries which may lower prey populations. Thus studies of seabird behaviour and breeding biology such as this are important for predicting the ways in which populations will respond to human exploitation and environmental disasters. Because seabirds tend to feed in the upper trophic levels of marine food webs and are numerous and conspicuous, they are excellent indicators of the marine environment. For example, dietary changes in seabirds can be used to predict local fishery collapses and to provide information about fish stocks that are not commercially exploited (Anderson and Gress 1984, Ricklefs et al. 1984, Montevecchi et al. 1988).

The following three chapters constitute the main body of the thesis and while general conclusions are drawn in Chapter 5, each chapter has been written to stand on its own. Chapter 2 documents the breeding success during the study at Gull Island and Cape St. Mary's and includes comparative data from previous years. Basic information on timing of breeding, clutch size, incubation period, egg volume, hatching and fledging success and chick growth rates are presented to confirm interpretations of kittiwake behaviour patterns surrounding courtship feeding and chick rearing. Evidence is presented to show that decreases in food supply have a negative effect on the breeding success of kittiwakes. (Henceforth "kittiwakes" will refer to Black-legged Kittiwakes, as distinguished from Red-legged Kittiwakes.)

Chapter 3 focuses on inter-observer reliability, a crucial methodological issue in the collection of behavioural data. This examination of inter-observer reliability was carried out in conjunction with the study of the functional significance of courtship feeding (Chapter 4), which provides further evidence about the importance of food for reproductive success.

1.1 REFERENCES

Aldrich-Blake, F.P.G. (1970). Problems of social structure in forest monkeys. In: Social Behaviour in Birds and Mammals. Essays on the Social Ethology of Animals and Man (ed. by J.H. Crook), pp. 79-101. Academic Press: London.

Anderson, D.W. and F. Gress. (1984). Brown pelicans and the anchovy fishery off southern California. In: Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships (ed. by D.N. Nettleship, G.A. Sanger and P.F. Springer), pp. 128-135. Canadian Wildlife Service: Ottawa.

Ashmole, N.P. (1971). Seabird ecology and the marine environment. In: Avian Biology, Vol. 1 (ed. by D.S. Farner, J.K. King and K.C. Parkes), pp. 224-286. Academic Press: New York.

Bastock, M. (1967). Courtship: An Ethological Study. Aldine: Chicago.

Blest, A.D. (1961). The concept of ritualization. In: Current Problems in Animal Behavior (ed. by W.H. Thorpe and O.L. Zangwill), pp. 102-124. Cambridge University Press: Cambridge, England.

Brown, R.G.B. (1967). Courtship behaviour in the Lesser Black-backed Gull, Larus fuscus. Behaviour, 29, 122-153.

Daly, M. (1978). The cost of mating. American Naturalist, 112, 771-774.

Hunt, G.L. Jr. (1980). Mate selection and mating systems in seabirds. In: Behaviour of Marine Animals, Vol. 4 (ed. by J. Burger, B. Olla and H. Winn), pp. 113 - 151. Plenum Press: New York.

Huxley, J.S. (1923). Courtship activities in the Red-throated Diver (Columbus stellatus Pontopp); together with a discussion on the evolution of courtship in birds. Journal of the Linnean Society of London, 25, 253.

Krebs, J.R. and N.B. Davies. (1981). *An Introduction to Behavioural Ecology*. Blackwell Scientific Publications: Oxford.

Lack, D. (1940). Courtship feeding in birds. *Auk*, *57*, 169-178.

Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Oxford University Press: Oxford.

Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. Methuen: London.

MacArthur, R.H. and E.O. Wilson. (1967). *The Theory of Island Biogeography*. Princeton University Press: Princeton, New Jersey.

Mock, D. (1984). Infanticide, siblicide and avian nestling mortality. In: *Infanticide: Comparative and Evolutionary Perspectives* (ed. by G. Haufstater and S.G. Hrdy). Aldine: New York.

Montevecchi, W.A., V.L. Birt, and D.K. Cairns. (1988). Dietary changes of seabirds associated with local fisheries failures. *Biological Oceanography*, *5*, 153-161.

Morris, R.D. (1986). Seasonal differences in courtship feeding rates on male common terns. *Canadian Journal of Zoology*, *64*, 501-507.

Moynihan, M. (1955a). Remarks on the original sources of displays. *Auk*, *72*, 240-246.

Moynihan, M. (1955b). Some aspects of reproductive behavior in the Black-headed Gull (*Larus* *ridibundus* L.) and related species. *Behaviour Supplement*, *4*, 201 pp..

Moynihan, M. (1958). Notes on the behavior of some North American gulls. III: pairing behavior. *Behaviour*, *13*, 112-130.

Nelson, J.B. (1977). Some relationships between food and breeding in the marine Pelecaniformes. In: *Evolutionary* *Ecology* (ed. by B. Stonehouse and C. Perrins), pp. 77- 87. University Park Press: Baltimore, Maryland.

Nelson, J.B. (1983). Contrasts in breeding strategies between some tropical and temperate marine pelecaniformes. Studies in Avian Biology, 8, 95-114.

Nisbet, I.C.T. (1973). Courtship feeding, egg-size and breeding success in Common Terns. Nature, 241, 141-142.

Nisbet, I.C.T. (1977). Courtship feeding and clutch size in Common Terns, *Sterna hirundo*. In: Evolutionary Ecology (ed. by B. Stonehouse and C. Perrins), pp. 101-109. University Park Press: Baltimore, Maryland.

Pianka, E.R. (1970). On r- and k-selection. American Naturalist, 104, 592-597.

Ricklefs, R.E., D.C. Duffy, and M. Coulter. (1984). Weight gain of Blue-footed Booby chicks: an indicator of marine resources. Ornis Scandinavica, 15, 162-166.

Royama, T. (1966). A re-interpretation of courtship feeding. Bird Study, 13, 116-129.

Tasker, C.R. and J.A. Mills. (1981). A functional analysis of courtship feeding in the Red-billed Gull, *Larus novaehollandiae scopulinus*. Behaviour, 77, 221-241.

Tinbergen, N. (1952). "Derived activities," their causation, biological significance, origin and emancipation during evolution. Quarterly Review of Biology, 27, 1-32.

Chapter 2

BREEDING BIOLOGY OF BLACK-LEGGED KITTIWAKES AT CAPE ST. MARY'S AND GULL ISLAND IN 1990 AND 1991

2.1 ABSTRACT

The breeding biology of Black-legged Kittiwakes was examined at two colonies in Newfoundland (Cape St. Mary's and Gull Island) in 1990 and 1991. There were inter-year and inter-colony differences in breeding success; the role of food supply as it influenced these differences was the focus of this investigation. Comparisons were made with previous Newfoundland studies.

To evaluate the relationship between food availability and breeding success, data were collected on timing of breeding, clutch size, egg size, hatching success, chick growth rates and fledging success (Gull Island - N = 107 nests in 1990, N = 254 nests in 1991; Cape St. Mary's - N = 51 nests in 1990, N = 45 nests in 1991). Adult attendance patterns during incubation and chick rearing, and chick begging and feeding were also noted in order to assess their effectiveness as indicators of food shortages (Gull Island - 2372.6 nest-hours in 1990, 1014.3 nest-hours in 1991).

In general, breeding success on Gull Island was significantly lower in 1991 than in 1969/1970. At Cape St. Mary's a significant decrease in breeding success from 1990 to 1991 was also apparent. There were few significant differences in breeding success between Cape St. Mary's and Gull Island in 1991, however in 1990 food shortages were localized as reproductive success was high at Cape St. Mary's.

Part of the reason for the lower breeding success in recent years on Gull Island may be an expanding population of Herring Gulls. However,

evidence is presented that is consistent with food shortage occurring in 1990 and 1991. At both colonies, timing of breeding was later, there was a greater amount of non-breeding, clutch sizes were smaller, eggs were smaller and hatching and fledging success were lower than in previous years.

The behavioural evidence for food shortages was more ambiguous. Contrary to expectation, eggs and chicks were left unattended longer in 1990, the year with better productivity. This may be explained by the effect of food shortages on Herring Gulls in 1991 and the subsequent greater predation pressure on kittiwakes. Parental attendance is a balance between the need to forage and the need to protect chicks from bad weather and predation. Also unexpected were the higher chick feeding rates in 1991, the year with poor productivity, however no estimate of bolus size was made. As expected, chicks begged more intensely and had fewer successful begging bouts in 1991.

The weight of biological and behavioural evidence suggests that poor foraging success was responsible for the serious reduction in breeding success in 1991 and these food shortages were confirmed by other researchers involved in the direct measurement of fish stocks.

2.2 INTRODUCTION

Black-legged Kittiwakes are small- to medium-sized, essentially pelagic gulls with circumpolar distribution (Lack 1968). They breed in large, dense colonies on the narrow ledges of sheer, high cliffs with a range that extends through subarctic, boreal, and temperate zones. Kittiwakes form monogamous pair bonds renewed each breeding season. They breed for the first time at 3-8 years of age (Coulson 1966, Wooller and Coulson 1977). The modal clutch size is 2 eggs (Coulson and White 1958) and both parents incubate and tend young to fledging. The food of kittiwakes is mainly marine fish and invertebrates (Cramp 1983). Chicks are fed on regurgitated food taken from the parent's throat, rather than from the ground as in ground-nesting Laridae (Cullen 1957).

Extensive studies of the breeding biology and behaviour of the Black-legged Kittiwake have been done in Norway (Barrett and Runde 1980, Runde and Barrett 1981), Alaska (Braun and Hunt 1983, Nysewander 1983, Hatch 1986), France (Danchin 1986, 1988), the U.S.S.R. (Belopol'skii 1961), and in the United Kingdom in Scotland (Galbraith 1983), Devon (Daniels, Heath and Rawson 1984) and northeast England at North Shields (Coulson 1966, Coulson and Wooller 1976, Thomas 1983, Coulson and Porter 1985, Coulson and Thomas

1985a, Chardine 1987) and in the Farne Islands (Pearson 1968). As only one intensive study of kittiwakes has previously been conducted in Newfoundland (Maunder and Threlfall 1972), the present research was planned to address this deficiency and to examine the relationship between variability in reproductive success and ecological conditions.

The breeding ecology of kittiwakes has been partitioned into five sections: timing of breeding, clutch size, egg size and survivorship, incubation period, and the nestling period. However it is important to stress that while such divisions may be useful, they tend to mask the fact that these aspects are closely linked and may impose similar demands on parent birds.

As this research was conducted over two consecutive seasons and at two locations in Newfoundland, it afforded the opportunity to perform inter-year and inter-colony comparisons. In addition, comparisons were made with the data obtained from one of these Newfoundland colonies in 1969 and 1970 (Maunder and Threlfall 1972) and in 1988 (Chatman 1989, J.M. Porter, pers. comm.[1]).

Coulson and colleagues (Coulson and White 1958, 1961, Coulson 1963,1966, 1972, Coulson et al. 1969, Coulson and

---

[1] Names and addresses of all personal communications listed in Appendix B.

Horobin 1976, Thomas 1983, Chardine 1987) have firmly established the role of intrinsic factors, such as the age and breeding experience of each member of the pair and the character of the pair bond (same or change mate), in determining breeding success in kittiwakes. Consequently, the role of an extrinsic factor, food supply, was the focus of this investigation.

2.2.1 TIMING OF BREEDING (BREEDING SEASONS)

Lack (1954) suggested that the ultimate factor affecting timing of breeding is food supply, and that egg laying is timed in such a way that the period of peak food abundance will coincide with the chick rearing period. This idea has been supported by a number of studies (Newton 1979, Perrins 1979), but for some species, Lack's idea is an oversimplification. For these species an important constraint on the timing of breeding is food availability for the female when forming eggs. Some authors have found that clutch initiation was earlier in years or places of greater food abundance (Safina et al. 1988, Monaghan et al. 1989, Wanless and Harris 1992); presumably these females were better able to accumulate sufficient nutritional reserves to begin laying earlier.

Safina et al. (1988) also found greater synchrony of laying in a year of greater food supply and explained this by suggesting that when food is plentiful, birds of differing fishing ability can all find sufficient food and so come into laying condition quite synchronously, but when food is scarce, skill differences between birds will be accentuated and some birds will take longer to build up the reserves necessary for laying.

Birds may be able to overcome the problem of food shortages early in the season by amassing food reserves in the wintering grounds (Lesser Snow Goose - Ankney and McInnes 1978) or by males providing additional food for their partners through courtship feeding. Nisbet (1977), comparing two Common Tern colonies, found the mean laying date to be earlier at the colony which he inferred, from rate of courtship feeding, to have better food resources. Courtship feeding will be discussed in more detail in Chapter 3.

Within a species at a particular colony, birds that breed earlier in the nesting season or at the peak of laying usually have higher reproductive success (e.g. larger clutch sizes and larger eggs) than do birds that lay later (Parsons 1972, 1975, 1976, Mills 1973, Davis 1975, Ryder 1980). The number of chicks fledged per pair decreases over the breeding season, however this decrease arises from reductions in clutch size and hatching success and not seasonal variation in fledging success (Parsons 1975, Coulson and Thomas 1985b).

2.2.2 CLUTCH SIZE

Lack (1954) hypothesized that the clutch size of birds has evolved to favour individuals with clutch sizes that produce the largest number of fledged young in a season. He considered the amount of food that parents could bring to the nest to feed young to be the most important selection factor on clutch size. Although Lack's theory agrees with the data for a number of species, Klomp (1970) found exceptions where the most common clutch size was smaller than the most productive one. Lack had not taken adult survival into account; by laying a slightly smaller clutch, adult survival may be enhanced (Charnov and Krebs 1974). This is not the case in kittiwakes, where those females which lay larger than normal clutches fledge more young per season and have higher survivorship (Coulson and Porter 1985). Coulson and Porter (1985) felt that these results could be attributed to high quality individuals confounding the trend associating higher adult survivorship with the modal clutch size. Apart from the effect of the first year of breeding, there is little change in breeding success with increased breeding experience in kittiwakes (Coulson and Thomas 1985a,b).

The importance of food in determining clutch size is clearly demonstrated by a comparison of inshore and offshore feeding seabirds. Nearly all offshore feeding seabirds lay single-egg clutches, whereas most inshore feeders have two to three eggs per clutch (Lack 1967, 1968). Inshore species such as gulls, terns and cormorants are able to make several feeding visits to their young each day, whereas offshore feeders, such as the procellariiformes, are able to feed their young only once every few days (Lack 1968). The modal clutch size of kittiwakes is two eggs rather than the three normally laid by most other gulls and this has been attributed to the kittiwake's more offshore feeding habits (Lack 1968) and to their cliff-nesting habit which results in chicks being confined to the nest until they fledge (Cullen 1957).

The time of laying is the single most important factor affecting clutch size in the kittiwake (Coulson and White 1961). The progressive decrease in clutch size as the season proceeds is not solely the result of older, more experienced birds breeding earlier: individual females tend to lay a smaller clutch if they breed later (Coulson and White 1961). Ecological factors, such as variable weather and food supplies, also can affect clutch size, assuming primary importance when conditions are severe. Work done by some researchers (Belopol'skii 1961, Wanless and Harris 1992) has indicated that clutch size is smaller in years or areas of food scarcity, but others have found no significant differences in clutch size (Monaghan et al. 1989, Roberts and Hatch 1993). Safina et al. (1988) found a significant increase in clutch size in a better food year for Common Terns, but not for Roseate Terns, suggesting some species are more limited by fluctuating food supplies than others.

2.2.3 EGG SIZE AND SURVIVORSHIP

There is a very extensive literature on the relationship between egg size and time of laying. A decrease in egg size as the laying period progresses has been shown in several seabird species (Coulson 1963, Nelson 1966, Coulson et al. 1969, Parsons 1972, Mills 1979), and for the Red-billed Gull at least, timing of breeding has a greater influence on egg size than female age (Mills 1979).

Increased egg size results in greater hatching success (Thomas 1983) and improved chick survivorship, at least during the first few days after hatching (Parsons 1970, 1975, Nisbet 1973, 1978, Davis 1975, Lundberg and Vaisanen 1979, Thomas 1983). In a complex series of manipulative experiments, Parsons (1970) demonstrated that Herring Gull chick survivorship, regardless of order of hatching, was correlated with egg size. In species with more than one chick, size may be critical in providing the chicks with sufficient vigour to establish a competitive advantage within the brood and to chick survival during the time it takes the adults to switch from incubation behaviour to chick care.

In Black-legged Kittiwakes, the volume of the second-laid, B-egg is usually less than that of the first laid, A-egg (Coulson 1963, Maunder and Threlfall 1972, Runde and Barrett 1981), although both Coulson (1963) and Runde and Barrett (1981) found the B-eggs larger than the A-eggs almost 20% of the time. Egg production is apparently a demanding process in the kittiwake, with the weight of a 2-egg clutch being equal to approximately 24% of the female's body mass (Maunder and Threlfall 1972 - mean egg mass = 51.7 g and mean adult mass = 437.0 g).

Differences in egg volumes between colonies or years could reflect differences in food availability or quality. In some studies of seabirds, egg size has been reported to be responsive to food fluctuations (Nisbet 1973, 1977, 1978, Gaston and Nettleship 1982, Pierotti and Bellrose 1986, Verbeek 1986), but others have found no food-related differences in egg size (Morris 1986, Safina et al. 1988, Monaghan et al. 1989).

Fluctuations in environmental conditions may obscure the contribution of egg size to reproductive success. Barrett and Runde (1980), in a study of kittiwakes in

Norway, found that chick survival was independent of egg volume. They reported high levels of predation in their study colonies and felt that this factor masked any effects of egg size.

2.2.4 INCUBATION PERIOD

The mean incubation period in the Black-legged Kittiwake is 27 days (Coulson and White 1958, Maunder and Threlfall 1972) and, as in other gulls, both members of the pair share the incubation duties (Coulson and Wooller 1984).

At the highly successful North Shields colony in northeast England, fledging success is generally high in kittiwakes (87%, Coulson and Thomas 1985a), so that breeding success is primarily determined by the relatively low hatching success (67%, Coulson and Thomas 1985a). Coulson and Wooller (1984) attributed the failure of about a third of the eggs to hatch to inadequacies in incubation, caused by differences in attentiveness to eggs by parent birds. In a seven-year study done in Alaska (Hatch and Hatch 1990), where kittiwakes have much lower breeding success than in the north Atlantic (Maunder and Threlfall 1972, Coulson and Thomas 1985a), incubation was also the stage of breeding at which annual productivity was most strongly regulated.

2.2.5 THE NESTLING PERIOD

In numerous studies of seabirds, abundant food supplies resulted in increased fledging success (Barrett and Runde 1980, Anderson et al. 1982, Schaffner 1986, Safina et al. 1988, Monaghan et al. 1989,Harris and Wanless 1990, Wanless and Harris 1992).

Variations in food supply have been linked to changes in chick growth rates in kittiwakes (Barrett and Runde 1980, Coulson and Porter 1985, Harris and Wanless 1990) and other seabirds (Harris 1969, Ricklefs et al. 1984, Safina et al. 1988). Growth may vary little in young chicks whose food needs are small, but food shortages should be most apparent in the growth rates of older chicks whose food needs are greater (Barrett and Runde 1980). The behavioural correlates of chick growth rates are rates of chick feeding and food begging, assuming that variation in the intensity of food begging by chicks is an indication of hunger levels.

Adult kittiwake attendance patterns at the nest may provide additional information about food supplies. The need to brood chicks until they become homeothermic at 6-7 days (Maunder and Threlfall 1972), and to protect them from predators, must be balanced against the parents' need to spend time foraging. If food supplies are plentiful, kittiwake pairs can forage alternately, leaving one parent always present with the brood until close to fledging

(Pearson 1968, Coulson and Wooller 1984). However, if feeding conditions are poor, parent birds may forage simultaneously, leaving large numbers of broods unattended for longer periods. This situation has been associated with low breeding success (Barrett and Runde 1980, Galbraith 1983, Harris and Wanless 1990, Wanless and Harris 1992, Roberts and Hatch 1993). Low food supplies can lead to increases in predation pressure if these low food supplies also cause predators to be hungry, encouraging greater parental attendance than might occur when food shortages are less severe.

The present study examined the reproductive parameters of Black-legged Kittiwakes from egg laying to fledging at two colonies in Newfoundland in 1990 and 1991. An effort was made to establish whether a decrease in food supplies was the reason for a decrease in breeding success in 1991. It is predicted that the traditional measures of productivity (mean date of egg laying, clutch size, egg volumes, chick growth rates and chick fledging success) will vary positively with food availability. Changes in adult and chick behaviour are expected to have good potential as indicators of food supply. In poor-food years or locations, adults will leave their eggs and chicks unattended a greater percentage of the time, chicks will beg for food more, and chick feeding rates will be lower.

Food abundance, availability and quality were not sampled directly in this study, but to the extent possible, data from government-sponsored stock monitoring in the vicinity of the colonies will be used to verify any conclusions arising from the breeding success data and behavioural measures.

2.3 METHODS

2.3.1 STUDY SITES

Data on the breeding biology of Black-legged Kittiwakes were obtained from two colonies in Newfoundland, Canada: Cape St. Mary's (46°50'N, 54°12'W) and Gull Island (47°15'N, 54°46'W) near Witless Bay (Figure 2-1).

Cape St. Mary's, located at the entrance to Placentia Bay, has several species of seabirds nesting along 4 km of high (130 m) mainland cliffs and on a rock stack, inaccessible to humans. The main seabird species found there are: Northern Gannets (~5,500 pairs), Black-legged Kittiwakes (~10,000 pairs), Common Murres (~10,000 pairs) and Thick-billed Murres (~1,000 pairs). Small numbers of Herring and Great Black-backed gulls, Razorbills, and Common Ravens also breed there (Cairns et al. 1989).

Gull Island is the northernmost of three islands comprising the Witless Bay Ecological Reserve. It is located on the eastern shore of the Avalon Peninsula. It is about 3.3 km from the nearest point of land and is about 1.5 km long and 0.75 km wide. The interior is heavily wooded (black spruce and balsam fir) with a grassy perimeter, and relatively low (<35 m) cliffs falling to the sea. The major seabird species found nesting there are Leach's Storm-Petrels (~530,000 pairs), Atlantic Puffins (~30,000 pairs), Black-legged Kittiwakes (~10,000 pairs) and Herring Gulls (~4,000 pairs; Cairns et al. 1989). There are also small numbers of nesting Great Black-backed Gulls, Common Murres and Razorbills.

Gull Island is strongly influenced by the Labrador Current, which brings cold (< 0° C) water of relatively low salinity (28-30 ppt) southward to the Grand Banks. The main branch of the Labrador Current flows around the east side of the Grand Banks, while a secondary branch flows through the Avalon Channel, a relatively deep (> 150 m) nearshore trough between the Grand Banks of Newfoundland and the Avalon Peninsula (Petrie and Anderson 1983). Gull Island is on the western side of the Avalon Channel. Capelin spawn along the southeast coast of the Avalon Peninsula from late June into mid-July (Templeman 1948) and during this period they are the most abundant schooling fish nearshore. Capelin are a major food of breeding seabirds in the area (Brown and Nettleship 1984, Piatt and Methven 1986), and the timing of their arrival inshore to spawn coincides with sea surface temperatures of 4 - 5° C. Piatt (1987) found that over the long term, nearshore water temperatures in Witless Bay are influenced by the Labrador Current, pack ice and icebergs, whereas daily variations in water temperatures are coupled with changes in wind speed and direction.

Cape St. Mary's is less affected by the inshore arctic waters that influence Gull Island. The Labrador Current is mixed with warmer coastal waters and water masses from the south, resulting in generally warmer water in the spring and summer with mean sea surface temperatures in August of 13 - 14° C at Cape St. Mary's, as compared to 12 - 13° C at Gull Island (Steele, Green and Carter 1979). Cape St. Mary's is also less affected by pack ice or icebergs; for example, in March the average ice conditions are 5/10 to 8/10 coverage in Witless Bay and 1/10 to 5/10 coverage at Cape St. Mary's (Steele et al. 1979). The average surface salinity at Cape St. Mary's is 31 ppt in the summer. Although capelin is undoubtedly an important food for breeding seabirds at Cape St. Mary's, herring are also available in spring and mackerel in July (Steele et al. 1979).

At Cape St. Mary's, two study plots were established one above the other 75 - 100 m above the sea on a cliff face in a narrow chasm in the rock. They were viewed from a point approximately 25 m away on the other side of the chasm. All observations were made with 8.5 x 44 binoculars, and as the birds seemed unaware of the presence of observers, no blind was used and no control plot was considered necessary. This location was chosen as it permitted a good view of the birds and was the closest approach to nesting kittiwakes at Cape St. Mary's. Sample sizes of nests and scheduling of visits for 1990 and 1991 are shown in Table 2-1.

On Gull Island in 1990, study nests in 3 plots ranging in size from 19 to 31 nests (sites C, E, F - Figure 2-1 and site F - Plate 2-1) were chosen so as to be accessible to the researchers for egg and chick measuring, weighing and marking. Behavioural observations were made, using 8.5 X 44 binoculars, from a blind (dimensions 1 m^3) located 10 to 15 m from the nests (N = 20). Larger sample sizes were desired in 1991, so six additional study plots (range = 4 to 42 nests) were added (sites A-H, J - Figure 2-1).

Control plots were chosen on Gull Island to act as controls for observer effects. In 1990, there was one control plot of 28 nests (I - Figure 2-1 and Plate 2-1). These nests were located on a cliff face approximately 30 m above the sea and were viewed from a distance of 150 m using 10X binoculars. An additional control plot (N = 44) was added in 1991 (K - Figure 2-1); it was similarly inaccessible to humans and observations were made using binoculars from a distance of 300 m. In 1991, 7 nests at "I" were used for behavioural observations. Additional data on parental attendance during incubation were obtained at J (Figure 2-1) using a blind located 8 m from the nests. A schedule of visits and total sample sizes are shown in Table 2-1.

Study plots A, C and possibly B were plots also studied by J.M. Porter (pers. comm.) and Chatman (1989) in 1988. There were three study plots (C, E, and F) which were the same in 1990 and 1991 and one control plot (I). Consequently, study plot C was the only plot which was common to 1988, 1990 and 1991. Differences in study plot quality were not assessed as the plots used in 1988 were very close to and very similar in topography and sub-colony size to the study plots used in 1990 and 1991. There were differences in site characteristics between study and control plots in 1990 and 1991 and comparisons were made in the different parameters of breeding success between these two types of plots.

2.3.2 COLLECTION OF BREEDING BIOLOGY DATA

Nests in both study and control plots were checked daily for the presence or loss of eggs and chicks when extended visits to the particular colonies were taking place. The only exception to this was during the incubation period in 1991 on Gull Island; once the peak of egg laying had passed, nests in the study plots were checked every other day to reduce disturbance to the birds.

Whenever possible, the following measures of breeding biology were recorded: laying dates, clutch sizes, hatching dates, hatching and fledging success, egg volume and chick mass. When dates of egg laying or hatching were unknown, they were determined by calculating backwards or forwards using mean values for kittiwakes in Newfoundland obtained from Maunder and Threlfall (1972). The Cape St. Mary's study sites were inaccessible to humans, so all the data on egg volume and chick mass were obtained on Gull Island.

Eggs were measured with Vernier calipers to the nearest 0.05 mm and the volume (in cc) was calculated using the formula given by Coulson (1963):

$$\text{Volume} = 0.4866 \times \text{breadth}^2 \cdot \text{length}.$$

In 1990, the largest egg in each nest was marked with a waterproof marking pen and was called the A-egg if it subsequently hatched first. In 1991, the first-laid egg in each nest was labelled the A-egg.

Eggs were measured in 1988, 1990 and 1991 by 4 different people. Paired groups t-tests were done on samples of 10 - 15 eggs to assess bias between measurers. T-tests were chosen as each pair of observers measured a different set of eggs. No differences were found between 3 of these people, but the fourth person consistently measured larger than the others. An appropriate correction factor was applied to her egg volumes before analyses of egg size data were done. It was not possible to assess the potential for bias in the egg measurements made in 1969 and 1970.

The following definitions for the different parameters of breeding success were taken, where possible, from Maunder and Threlfall (1972) to facilitate comparison between years. **Laying date** refers to the date of laying of the first egg in individual clutches. **Hatching success** is the number of eggs hatched per number of eggs laid and is a measure of egg survivorship. In 1990, **fledging** was defined as first flight, but in 1991, chicks 35 days of age or older when last seen were considered to have fledged. **Fledging success** is the number of chicks fledged per number of chicks hatched and is a measure of chick survivorship. Number of chicks fledging per nest is a measure of basic **productivity. Incubation period** is the time from the laying of the last egg of a clutch to hatching of that egg. During the incubation period in 1990, scans of adults in **attendance** at the nest were done every 10 minutes, while in 1991 adult attendance patterns were timed precisely, although for statistical comparison they were formatted as in 1990 (see Table 2-2 for total sampling efforts and Figure 2-2 for the diurnal distributions of observer efforts in 1990 and 1991). **Nest** was defined as an occupied nest, meaning there was new nesting material and a flag of excrement developed below, regardless of the presence or absence of eggs or chicks.

Weather data (sea state, wind speed, precipitation, and high and low temperatures) were collected daily during the extended visits to the colonies and weather for each day was categorized as adverse or not adverse. Adverse weather was defined as a day where any one of the following occurred: wind and sea state at Beaufort Force 5 (wind 31 - 40 km/h, large waves, numerous whitecaps) or above, heavy rain, or a daily high temperature of less than 10° C.

2.3.3 COLLECTION OF BEHAVIOURAL DATA

Adult and chick behaviour was monitored using all occurrences sampling (Altmann 1974). Activities assessed for each nest included the percentage of time chicks were left unattended, food begging by the chick(s), the percentage of begging bouts that were successful (i.e. ended in chick feeding) and the number of food boluses per hour fed to the chicks. These attributes were calculated for groups of chicks of 3 different ages: 0 - 5 days (before linear part of growth curve, Barrett and Runde 1980, Coulson and Porter 1985), 6 - 20 days (period of linear growth) and 21+ days (after linear growth), and for the chick-rearing period as a whole. Parental attendance patterns during the nestling period were recorded in both years in the same way as attendance patterns during incubation.

A **begging bout** was defined as any series of pecks by the chick with pauses of less than 2 min between pecks. **Begging** was considered **successful** if the chick received food within 2 min of begging. **Feeding rates** were the number of feeds/h and number of food items or boluses/h (as feeds often consisted of more that 1 bolus). A feed was over when 2 or more min passed with no begging or feeding. A **bolus** was any discrete packet of food, no matter what the size, swallowed by a chick.

In 1990, watches were concentrated in the morning and late afternoon or early evening as it was predicted (based on diurnal variation in courtship feeding reported by J.W. Chardine, pers. comm.) there would be more feeding activity then. Circumstances permitting, two 4-h watches were done at each of two sites (C and E, Figure 2-1).

In 1991, changes in the research objectives meant less effort was devoted to behavioural observations, but on many days two 4-h watches were done, with watches spread fairly evenly throughout the day, and on two days all-day watches from 06:00 to 21:00 hours took place.

2.3.4 DATA ANALYSES

In the field, data were recorded by hand in notebooks (breeding biology data) or on check sheets (behavioural data) and then entered into the mainframe computer (VAX/VMS system) at Memorial University of Newfoundland. SPSS-X (SPSS Inc. 1988) was used for statistical analyses and Sigmaplot, Version 4.01, (Jandel Corporation 1990) was used for graphing.

Tests of significance chosen depended on the measurement scale of the data, the Chi-squared statistic for nominal data and the t-test and ANOVA for interval and ratio data. Where possible data were examined to confirm conformity to the assumptions implicit in parametric tests, however parametric tests were the only alternative when comparison was made with data from 1969 and 1970 as only means, standard deviations and sample sizes were available. To assess the extent to which two measures varied together, the Spearman rank order statistic was used regardless of the measurement scale, as it is better suited to working with small sample sizes (Martin and Bateson 1986). Small sample sizes are more likely to violate the assumptions of normality and homogeneity of variance required by parametric tests of significance, such as the Pearson correlation coefficient. The null hypothesis was rejected if $p < 0.05$.

For the chick behavioural data, means were calculated per nest per hour for data pooled over three chick ages, 0 - 5 days, 6 - 20 days and 20+ days, based on age of chick in relation to the period of linear growth. Sample sizes were insufficient to consider 1- and 2-chick broods separately.

There appeared to be pronounced differences in the breeding success parameters between study and control plots in 1991 and values appear, where appropriate, for both groups of nests in the following tables. If no significant difference between these plots was established for a particular dependent measure, subsequent analyses were done on the combined sample.

To evaluate the effect of timing of breeding on clutch size and egg volume, the laying period was divided into 3 periods of equal length, "early", "middle" and "late" denoting relative position during the laying period. On Gull Island in 1990, early = 18 May - 29 May, middle = 30 May - 11 June and late = 12 June - 23 June and in 1991, early = 27 May - 6 June, middle = 7 June - 18 June and late = 19 June - 29 June. At Cape St. Mary's in 1990, early = 9 May - 15 May, middle = 16 May - 23 May and late = 24 May - 30 May.

2.4 RESULTS

2.4.1 TIMING OF BREEDING

On Gull Island, the mean laying date in 1991 (10 June) was four days later than in 1990 (6 June) and this difference was significant ($t = 3.21$, $df = 192$, $p < 0.01$, Table 2-3). Comparing the mean laying date in 1990 with the later year from the Maunder and Threlfall (1972) study, 3 June in 1969, the difference was significant ($t = 2.10$, $df = 159$, $p < 0.05$).

At Cape St. Mary's in 1990, the mean laying date was 19 May and this was substantially earlier than any of the other years or locations available for comparison (Table 2-3). Not enough time was spent at Cape St. Mary's in 1991 to determine the mean laying date, but circumstantial evidence indicates that the timing of breeding was delayed that year. No chicks seen during the first visit to "the Cape" on 21 June, and based on estimates of chick size on the second visit on 17 July, egg laying must have begun around 28 May.

The spread of laying for Gull Island in 1990 was bimodal (Figure 2-3) and this may be the consequence of a number of instances of relaying as the second peak was roughly two weeks after the first, the usual relaying interval for kittiwakes (Maunder and Threlfall 1972). Researchers did not arrive on Gull Island until after laying had begun in 1990 (Table 2-1), consequently some laying dates were obtained through working backwards from hatching dates (Section 2.3.2). In 1991 laying, although delayed, was normally distributed (Figure 2-3). The Cape St. Mary's laying distribution in 1990 (Figure 2-4) was highly synchronous.

There were no sample sizes with the reports of mean hatching dates for 1969 and 1970 (Maunder and Threlfall 1972), so it was not possible to compare these two years statistically with 1990 and 1991 (Table 2-3). The mean hatching date for Cape St. Mary's in 1990 (14 June) was obtained by adding 27 days (mean incubation period as reported by Maunder and Threlfall, 1972) to the mean laying date that year. As a consequence, only statistical comparisons between 1990 and 1991 for Gull Island were made. In 1991, eggs hatched significantly earlier ($t = 4.27$, $df = 20$, $p < 0.001$) in the study plots ($N = 4$) than in the control plots ($N = 18$). There were no significant differences between the mean hatching date in 1990 and 1991 in either the control plots ($t = 1.47$, $df = 78$, $p = 0.15$) or the study plots ($t = 0.52$, $df = 64$, $p = 0.60$).

Weather apparently had the greatest direct effect on timing of breeding. Spring seemed colder in 1991 than in 1990, but air temperatures were only slightly below normal in May (0.9° C) and June (1.9° C) (St. John's weather office). Water temperatures in 1991 (mean = 5.9° C), from 19 June to 15 July, were 1.4° C to 3.3° C colder than any of the three preceding years at a beach 45 km north of Witless Bay (Methven and Piatt 1991).

In 1990, 41% of the days between 15 June and 19 July had adverse weather, usually rain. In 1991, only 20% of the days between 15 June and 19 July had adverse weather. There was less rain in 1991 than during this time in 1990 and the cold temperatures (daily high less than 10° C) in 1991 occurred in the month preceding 15 June. In 1990, Spearman rank order correlations between the weather (adverse = 1, not adverse = 2) and egg loss ($r_s = 0.082$, $n = 28$, $p = 0.34$) and chick loss ($r_s = 0.157$, $n = 22$, $p = 0.24$) were not significant. In 1991, Spearman rank order correlations between the weather and date of egg laying ($r_s = 0.013$, $n = 31$, $p = 0.94$) and egg loss ($r_s = 0.151$, $n = 39$, $p = 0.36$) were also not significant. Too few chicks hatched to correlate weather with chick loss in 1991.

2.4.2 CLUTCH SIZE

On Gull Island, there was a decrease in the proportion of 2-egg clutches from 86% in 1969/1970 to 28% in 1991 (Table 2-4). The decrease from 1969/1970 to 1988 was significant (Chi-squared = 21.01, df = 2, p < 0.001), as was the decrease from 1990 to 1991 (Chi-squared = 13.02, df = 2, p < 0.001). In 1988 and 1990, clutch sizes were determined in a single visit to the colony as hatching was beginning, while in the other years daily visits occurred. To examine whether clutch composition in 1991 would vary under a different visit schedule, it was calculated as though only 1 visit was made as hatching was beginning. There was no significant difference in clutch composition between the different visit schedules (Chi-squared = 1.43, df = 1, p = 0.23), so the values obtained on daily visits were used.

At Cape St. Mary's there was also a significant decrease in clutch size from 1990 to 1991 (Chi-squared = 32.28, df = 2, p < 0.001, Table 2-4). Between colonies, kittiwakes at Cape St. Mary's laid a larger proportion of 2-egg clutches in 1990 (Chi-squared = 28.40, df = 2, p < 0.001) than they did on Gull Island. This also occurred in 1991, but the difference was not significant (Chi-squared = 0.68, df = 1, p = 0.41).

In neither year were there significant seasonal (early-, middle- or late-laid eggs) differences in clutch size on Gull Island, although the data showed a trend toward lower clutch sizes in late-laying birds (Table 2-5). At Cape St. Mary's in 1990, there was a significant seasonal decrease in clutch size (Chi-squared = 13.31, df = 4, p =

0.01), with late-laid clutches being smallest.

Another breeding parameter which differed between colonies and years was the proportion of occupied nests with eggs (Table 2-6). On Gull Island, this decreased from 92% in 1969/1970 to 57% in 1991. The decrease from 1969/1970 to 1988 was significant (Chi-squared = 10.58, df = 1, $p < 0.001$) as was the further decrease from 1990 to 1991 (Chi-squared = 22.47, df = 1, $p < 0.001$). There was no significant difference between study and control plots in 1991 (Chi-squared = 0.75, df = 1, $p = 0.39$), so they were combined.

At Cape St. Mary's, the proportion of occupied nests with eggs decreased from 96% in 1990 to 69% in 1991 (Chi-squared = 12.72, df = 1, $p < 0.001$). Inter-colony differences were also significant in 1990 (Chi-squared = 5.20, df = 1, $p < 0.02$), but not in 1991 (Chi-squared = 2.20, df = 1, $p = 0.14$).

2.4.3 EGG SIZE AND SURVIVORSHIP

For clutches where the order of laying was known (1991), the mean volume of A-eggs was significantly greater than that of B-eggs (paired groups t-test: $t = 4.82$, df = 46, $p < 0.001$). A-eggs were larger than B-eggs in all but one clutch, where the A-egg equalled the B-egg in size.

There was a general decrease in egg volumes since 1988

(Figure 2-5). An analysis of variance was done on A- and B-eggs for the years 1988, 1990 and 1991 and in both cases there was a significant difference in egg size, for A-eggs, $F = 6.75$, $df = 2,84$, $p < 0.01$ and for B-eggs, $F = 14.33$, $df = 2,89$, $p < 0.001$. Multiple comparisons tests showed a decrease in each year for both eggs, the sole exception being no decrease in the size of A-eggs from 1990 to 1991. Single eggs were not measured in 1990, but the difference in volume of these eggs between 1988 and 1991 was significant ($t = 3.37$, $df = 101$, $p < 0.001$).

When seasonal differences in egg volumes were evaluated in 1990 and 1991 for single eggs, A- and B-eggs (Table 2-7) and 2-egg clutches as a whole (Figure 2-6), significant decreases occurred only in 1990 for middle- to late-laid B-eggs ($F = 3.70$, $df = 2,16$, $p = 0.05$) and 2-egg clutches ($F = 3.94$, $df = 2,33$, $p = 0.03$) as a whole.

Sample sizes of hatched chicks were too low in 1991 for within-year comparisons (Table 2-8). However in 1990, in 2-egg clutches, B-eggs that hatched were significantly larger than those which did not ($t = 2.88$, $df = 26$, $p < 0.01$) and the same was true for the clutch as a whole ($t = 3.20$, $df = 54$, $p < 0.01$). There was no significant difference in size between A-eggs that hatched and those that did not ($t = 1.82$, $df = 26$, $p = 0.08$). When data for 1990 and 1991 were combined, eggs that hatched were larger than those which did not ($t = 3.50$, $df = 183$, $p < 0.001$).

In a summary of egg fates for the two years (Table 2-9), the difference between 1990 and 1991 in the percentage of eggs hatched and missing is striking. In 1990, 53% of the eggs laid hatched and in 1991, only 14% hatched (Chi-squared = 56.18, df = 1, $p < 0.001$). In 1991, 83% of eggs went missing, while only 33% of eggs fell into that category in 1990 (Chi-squared = 79.78, df = 1, $p < 0.001$). Most of the egg loss in 1991 occurred in the study plots (Figure 2-7). In both years, it was usually the case that the entire clutch in multi-egg clutches was taken. In 1990, the "miscellaneous" category included damaged eggs, embryos which died pipping and eggs knocked from the nest and in 1991, only eggs found to be cold. Nests were checked daily in 1990 and every other day in 1991, consequently there is likely to be some overlap between the "missing" and "miscellaneous" categories, particularly in 1991. Even taking this into account, the proportion of eggs missing in 1991 is substantially greater than in 1990.

Table 2-10 shows inter-colony and inter-year comparisons of hatching success. On Gull Island, there was a significant decrease in hatching success between 1969 and 1990 (Chi-squared = 13.52, df = 1, $p < 0.001$) and between 1990 and 1991 for study and control plots combined (Chi-squared = 42.14, df = 1, $p < 0.001$). There was no significant decrease in hatching success when 1990 was compared to the control plots alone in 1991 (Chi-squared = 0.95, df = 1, p = 0.33), indicating substantial differences in egg survivorship between study and control plots in 1991 (Figure 2-7, Table 2-10). At Cape St. Mary's, there was also a significant decrease in hatching success between 1990 and 1991 (Chi-squared = 9.97, df = 1, p < 0.01).

Considering inter-colony comparisons, in each of 1990 and 1991, hatching success was significantly lower at Gull Island than at Cape St. Mary's (p < 0.001). On the other hand, in 1991 this difference disappeared if Cape St. Mary's was compared to the control plots alone on Gull Island (Chi-squared = 1.95, df = 1, p = 0.16), suggesting again substantial differences between study and control plots.

2.4.4 INCUBATION PERIOD

The mean incubation period on Gull Island was 27.0 days (SD = ± 0.82, N = 4) in 1990 and 29.3 days (SD = ± 1.83, N = 8) in 1991. In 1970, Maunder and Threlfall (1972) determined the mean incubation period to be 27.2 days (SD = ± 1.05, N = 66) and an independent groups t-test comparing 1970 and 1991 was significant (t = 4.88, df = 72, p < 0.001).

Parental attendance during incubation was monitored to attempt to establish the reasons for egg loss. In 1990, eggs were left unattended 11.1% of the time (sampling effort =

436.5 h from 31 nests), while in 1991, eggs were left unattended only 3.9% of the time (sampling effort = 773.8 h from 23 nests). It may seem contradictory that eggs took longer to hatch in 1991, yet they were attended more. A possible explanation for this can be made with the subjective observation that although adult birds were frequently seen in attendance at their nests in 1991, it also seemed they stood over their eggs more frequently than in 1990. In both years there was a significant negative correlation (Spearman rank order) between the length of time eggs were left alone and hatching success for 2-egg clutches (1990: $r_s = -0.75$, $n = 10$, $p < 0.01$; 1991: $r_s = -0.61$, $n = 10$, $p < 0.05$), but not for 1-egg clutches in 1991 ($r_s = -0.40$, $n = 13$, $p = 0.09$). In 1990, the four 1-egg clutches were never left unattended.

In 1991, Herring Gulls were twice seen forcing adults off their nests and taking the eggs. One of these Herring Gulls had a distinctive stain on its neck making it individually identifiable and for a few days it was frequently seen standing above study plot J (Figure 2-1), perhaps defending it as territory. In 1990, Herring Gulls were never directly seen taking attended or unattended eggs.

2.4.5 NESTLING PERIOD

In 1990, chicks in the control plot (I - Figure 2-1) initially had higher survivorship than those in the study plots, but in the end both groups survived equally poorly (Figure 2-8). Growth rates were measured for chicks between 6 and 20 days of age (Figure 2-9) in 1990. Although 41% (N = 17) had low growth rates (growth rates < 13.9 g/day, the mean growth rate for C-eggs in clutches of three in Coulson and Porter 1985), the rest grew at a rate similar to that reported in the literature (Barrett and Runde 1980, Coulson and Porter 1985, Galbraith 1983), suggesting adequate food supplies at that time. However, growth was not monitored after 21 days of age, so food shortage cannot be ruled out as the cause of the decrease in survivorship in Figure 2-8.

In 1991, only 4 chicks (from 179 nests) hatched in the study plots and they were all gone by 8 days of age (Figure 2-8). None of these chicks lived long enough for the computation of daily growth increments, but 3 out of 4 chicks either lost mass or failed to gain. Masses of chicks 1 to 10 days of age from both years were plotted in Figure 2-10, and although there were only a few points for 1991, it is obvious that chicks were not gaining mass at the rate observed in 1990. In the control plots (I and K - Figure 2-1) in 1991, 19 chicks hatched (from 75 nests), and of these 13 subsequently fledged (Figure 2-8).

On Gull Island, fledging success was significantly lower in 1990 than in 1970 (Chi-squared = 9.55, df = 1, $p < 0.01$), but increased slightly and non-significantly in 1991 (Chi-squared = 0.001, df = 1, $p = 0.97$, Table 2-11). Fledging success as a proportion was not available for Gull Island in 1988, but a similar alternative measure was low: 0.63 chicks fledged/nest. At Cape St. Mary's there was a significant decrease in fledging success between 1990 and 1991 (Chi-squared = 6.23, df = 1, $p = 0.01$).

Inter-colony comparisons indicated significantly lower fledging success in 1990 at Gull Island than at Cape St. Mary's (Chi-squared = 29.95, df = 1, $p < 0.001$), but the difference in fledging success between the two colonies was not significant in 1991 (Chi-squared = 2.13, df = 1, $p = 0.14$, Table 2-11).

A basic measure of productivity, chicks fledged/nest, mirrored these comparisons of fledging success (Table 2-11). In the years available for comparison, Cape St. Mary's in 1990 had the highest productivity with 1.4 chicks fledged/nest. Productivity on Gull Island was constant and low from 1990 to 1991, approximately 0.3 chicks fledged/nest. Productivity at Cape St. Mary's in 1991 was only slightly higher, 0.4 chicks fledged/nest.

Tests of significance for differences in fledging success between eggs of different sizes were not done as the number of chicks fledging was too low (Table 2-8). No chicks in the study sites fledged in 1991 (4 chicks hatched) and 4 fledged in 1990.

Parental attendance patterns were also monitored during the chick rearing period (Table 2-12). The percentage of time that chicks were left alone varied with chick age in 1990, but was always low. Chicks were never seen unattended in 1991. In 1990, there was no correlation between length of parental absences during chick rearing and fledging success for 1-egg clutches ($r_s = 0.26$, $n = 11$, $p = 0.22$) or 2-egg clutches ($r_s = 0.24$, $n = 18$, $p = 0.17$).

Herring and Great Black-backed gulls were seen twice in 1991 and several times in 1990 taking chicks from attended nests, but the circumstances were slightly different in each year. In 1990, they preyed upon chicks that were almost fully grown but not yet fledged, and in 1991, loss to gulls occurred when the chicks were less than 10 days old.

For chicks from 0-5 days of age, begging was almost four times as frequent in 1991 as in 1990 ($t = 4.04$, $df = 20$, $p < 0.001$), and overall, twice as frequent in 1991 as in 1990 ($t = 2.63$, $df = 25$, $p = 0.01$, Table 2-13). For chicks from 6 - 20 days, there was no significant difference between 1990 and 1991 in the frequency of begging ($t = 1.52$, $df = 20$, $p = 0.14$). The percentage of begging bouts that were successful, was significantly lower for chicks of all ages in 1991 (0 - 5 days, Chi-squared = 33.93, df = 1, $p < 0.001$; 6 - 20 days, Chi-squared = 8.33, df = 1, $p < 0.01$; overall, Chi-squared = 34.96, df = 1, $p < 0.001$).

Begging rate (bouts/h) and percentage of successful begging bouts in successful and unsuccessful pairs were compared for 2-egg clutches in 1990 (sample sizes of 1-egg clutches in both years and 2-egg clutches in 1991 were insufficient for statistical comparison). Successful pairs were defined as those that kept both chicks alive for more than one week, while unsuccessful pairs had one or both chicks die within the first week. No significant difference was found between successful and unsuccessful pairs in the begging intensity of their chicks ($t = 0.45$, df = 10, $p = 0.95$; 1990: mean = 0.63 bouts/h, SD = ± 0.21; 1991: mean = 0.62 bouts/h, SD = ± 0.33). The number of chicks surviving more than one week was positively and significantly correlated (Spearman rank order correlation) with percentage of successful begging bouts ($r_s = 0.59$, $n = 12$, $p < 0.05$).

There were no significant differences in chick feeding rates (bolus/h) between the two years for chicks of any age (overall, $t = 0.54$, df = 25, $p = 0.59$), though the trend was for chicks in 1991 to be fed more often (Table 2-14). Note that neither the size or composition of the food bolus was known.

Feeding rate in successful and unsuccessful pairs was compared for 2-egg clutches in 1990. Successful pairs (mean = 0.90 bolus/h, SD = ± 0.21, N = 5) fed their chicks significantly more often ($t = 3.38$, df = 10, $p < 0.01$) than unsuccessful pairs (mean = 0.46, SD = ± 0.23, N = 7).

2.5 DISCUSSION

Laying dates, clutch sizes, growth and fledging success of seabirds have been linked to food supplies by a number of workers (Hunt 1972, Nisbet 1977, 1978, Anderson et al. 1982, Gaston and Nettleship 1982, Braun and Hunt 1983). Body size (Pearson 1968), dietary specialization (Anderson et al. 1982), the depth at which food is obtained (Pearson 1968), and flexibility of the time budget (Burger and Piatt 1990) are species characteristics which will influence productivity when food fluctuations occur. Black-legged Kittiwakes are expected to be sensitive indicators of food shortages as they are small in size compared to many seabirds, their summer diet is relatively specialized (Threlfall 1968, Maunder and Threlfall 1972), and they are capable of feeding only at the surface of the sea.

A second way of linking reproductive success with food supply is through the direct measurement of food, and a few studies that have done so (Anderson et al. 1982, Schaffner 1986, Safina et al. 1988) have found a positive relationship. Assessment of fish stocks was not carried out in this study, but direct evidence of food shortages in the vicinity of Gull Island in 1991 was obtained by others.

Capelin is a major food of breeding seabirds in Witless Bay (Brown and Nettleship 1984, Piatt and Methven 1986) and at a capelin spawning beach 45 km north of there, the initiation of spawning was delayed by 20-29 days and the nearshore abundance of capelin was low in 1991 (Methven and Piatt 1991). The capelin were late to come in because of the cold water temperatures (1.4° C to 3.3° C colder than any of the three preceding years), as capelin need temperatures of 5° C to 6° C before they will come up to the surface and inshore to spawn (Methven and Piatt 1991). In 1991, the late arrival of capelin coincided with low catches of cod in the inshore commercial trap fishery (Methven and Piatt 1991), relatively low numbers of baleen whales (J. Lien, pers. comm.) and few fledged young for other surface feeding seabirds (Herring and Black-backed gulls, personal observation) in the Witless Bay Area.

The poor productivity of Herring Gulls in 1991 points to an alternate explanation for the breeding failure suffered by Black-legged Kittiwakes. Because Herring Gulls were also feeling the effects of food shortages, they may have preyed more heavily on kittiwake eggs and young than in previous years.

Finally, reduced breeding success in 1991 could have been the direct effects of weather. No significant relationships were discovered between days of adverse weather (any of high wind, rough sea surface, heavy rain or a daily high temperature of less than 10° C) and egg laying, egg loss or chick loss. In seabirds, weather may have its greatest effect indirectly through changes in food supplies. Aebischer et al. (1990) found parallel long-term trends between the weather and abundances of phytoplankton, zooplankton, herring and kittiwake breeding performance, but concluded that weather did not affect any trophic level directly, rather there was a complex feedback system between weather, current systems and the different trophic levels. Anderson et al. (1982) obtained similar results; in relating northern anchovy abundance in different sized areas to Brown Pelican reproduction, they suggested that events which influence large geographic areas (such as weather-patterns) affect reproduction through food webs.

Although this study was carried out for only 2 seasons, the following results suggest food shortages at all stages of the breeding season may limit reproductive success in

Black-legged Kittiwakes.

2.5.1 TIMING OF BREEDING

Researchers disagree on the importance of food in affecting the timing of clutch initiation (Powell 1983, Murphy et al. 1984), but many believe that the level of food availability prior to egg laying may be the most important factor in the timing of birds' breeding seasons (Perrins 1970, Ashmole 1971), due to the female's need to accumulate nutritional reserves for egg formation.

The mean laying date on Gull Island was significantly later in 1991 than in 1990, which was in turn significantly later than in 1970. The mean laying date at Cape St. Mary's was substantially earlier in 1990 than any other years or colonies available for comparison, while circumstantial evidence indicated breeding was much later there in 1991. From these results, it can be inferred that food was most abundant at Cape St. Mary's in 1990 and that food shortages were widespread in 1991.

There was greater synchrony of kittiwake clutch initiation at Cape St. Mary's in 1990 than on Gull Island in 1990 or 1991, which may be an additional indication that food supplies were abundant at Cape St. Mary's in 1990. If nutrient reserves must reach a threshold before females can produce eggs, then birds that are less proficient foragers should take longer to begin breeding when food is scarce, with the result that variance about the mean clutch initiation date should increase. If food is very plentiful, most birds will reach breeding condition at approximately the same time and commence egg laying synchronously. Clutch initiation was less synchronous on Gull Island, perhaps providing evidence of food shortages at this colony.

2.5.2 CLUTCH SIZE

At Gull Island, there was a significant decrease in clutch size from 1969/1970 to 1988 and from 1990 to 1991, as there also was at Cape St. Mary's from 1990 to 1991. In inter-colony comparisons in 1990, clutch sizes were significantly larger at Cape St. Mary's, while in 1991 there were no significant differences. These results set the pattern for inter-year and inter-colony differences in subsequent measures of productivity and are consistent with the hypothesis of this study, that clutch size will vary positively with food availability.

From this evidence, it appears that food supplies were low at both Cape St. Mary's and Gull Island in 1991 and perhaps also in 1988 and 1990 at Gull Island, if a modal clutch size of 2 eggs is taken as standard for kittiwakes. This was the clutch size obtained at Cape St. Mary's in 1990, Gull Island in 1969/1970 and at North Shields

(Coulson and White 1961), a colony known to have fairly abundant food supplies (Coulson and Thomas 1985a). There is evidence that in colonies with variable and often low food supplies, a greater proportion of 1-egg clutches are laid (Russia - Belopol'skii 1961, Norway - Barrett and Runde 1980, Alaska - Hatch and Hatch 1990).

An alternate explanation for the overall reduction in clutch sizes may be the timing of breeding, as clutch size decreases over the season (Coulson and White 1961). Breeding was late in 1990 and 1991 on Gull Island and that may have been enough to cause the reduced clutch sizes. There was no significant seasonal decrease in clutch size on Gull Island in 1990 or 1991, apparent food shortages overriding the usual effect of timing of breeding. Seasonal decreases in clutch size were significant at Cape St. Mary's in 1990, when breeding began early and food supplies were seemingly abundant.

If food is in very short supply during the breeding season, adult birds will abandon breeding altogether (Drent and Daan 1980) or in kittiwakes specifically, if arrival at the colony is too late, many birds will not breed (Porter 1988, 1990). Both factors may have come into play in 1990 and 1991, as illustrated by changes in the proportion of occupied nests with eggs. This variable showed the same inter-colony and inter-year pattern of decreases as clutch size. The effect of food shortages was particularly evident in 1991, with only 60% of the occupied nests containing eggs on Gull Island.

The relationship between food and clutch size has not yet been firmly established for kittiwakes, but this study provides positive evidence for the link. Recent food supplementation studies in other species are inconsistent regarding the influence of food on clutch size. In several studies, supplemented birds laid larger clutches (Hogstedt 1981, Dijkstra et al. 1982, Powell 1983), but in others they did not (von Bromssen and Jansson 1980, Ewald and Rohwer 1982, Poole 1985). Perhaps, as Safina et al. (1988) suggest, some species are simply more sensitive to fluctuations in food supplies than others. In the long-term study of kittiwakes in northeast England, clutch size was the first component of breeding biology to be significantly affected by food shortages occurring in the pre-laying period (Coulson and Thomas 1985a).

2.5.3 EGG SIZE AND SURVIVORSHIP

Again the results of this study are consistent with the hypothesis that decreases in productivity reflect food shortage. On Gull Island, eggs decreased significantly in size from 1988 to 1990 and from 1990 to 1991. These decreases suggest that food levels were low in 1991 and also for at least part of the 1990 season, something that was not obvious from the chick growth rates or chick begging and feeding rates that year. In contrast, kittiwake egg volumes at North Shields decreased only slightly and nonsignificantly during a 10-year period of decreased herring stocks in the North Sea (Coulson and Thomas 1985a). The reason for the difference in these results is not clear.

It is possible to tease out the relative importance of food shortages and timing of breeding in reducing egg size, through a comparison of egg volumes in early-, middle- and late-laid eggs. In 1991, timing of breeding had no significant effect on egg size, but in 1990 there was a significant decrease in egg volume from middle- to late-laid eggs. This suggests food shortages may have been more severe in 1991 as eggs were significantly smaller throughout the season.

The biological effects of increased egg size in kittiwakes are increased hatching and fledging success (Thomas 1983). In neither 1990 nor 1991 were there a sufficient number of fledged chicks to evaluate fledging success in relation to egg size. However, where sample sizes permitted comparisons, eggs that hatched were significantly larger than those that did not.

Hatching success showed the same pattern of inter-year and inter-colony decreases as clutch size and egg volumes.

Coulson and Thomas (1985a) found a progressive decline in hatching success (excluding eggs lost to predation) which coincided with suspected food shortages in the spring before egg laying. They explained this by suggesting that food shortages at this time affected the condition of the adults and consequently the viability of the eggs. In this study, it is likely that reduced hatching success in kittiwakes was caused by higher levels of predation by Herring Gulls, which were also affected by food shortages.

The effects of predation can be seen in a comparison of hatching success in the study and control plots in 1991. Eggs from study plots had poorer survivorship than eggs from control plots for a number of reasons. Study plots were often completely surrounded by nesting Herring Gulls and the nests were also easily accessible; in many cases, gulls could walk right up to them. Secondly, the study plot nests were subject to observer disturbance and despite attempts to minimize this by checking the nests less often, observer disturbance may have contributed to egg loss in the study plots.

The difference in topography between study and control nests is illustrated in Plate 1. Study plots were chosen for their ease of access to researchers, while control plots were chosen for their ease of observation without disturbance to the birds. In retrospect, an effort should have been made to chose a control plot that was similar in topography to the study plots.

The widespread food shortages in 1991 may have caused Herring Gulls to exploit alternative sources of food, such as kittiwake eggs, more vigorously than in previous years. In 1991, Herring Gulls were twice seen forcing incubating kittiwakes off their nests to take their eggs and it is likely that this also occurred at other times. In 1990, Herring Gulls were not seen taking eggs. Although predation had its most obvious effect on study plots in 1991, the reason for the overall reduction in hatching success on Gull Island may be the increase in the number of nesting Herring Gulls from an estimated 2000 pairs in 1968 (Haycock and Threlfall 1975) to roughly 4000 pairs in 1989 (Cairns et al. 1989).

2.5.4 INCUBATION PERIOD

The mean incubation period on Gull Island was significantly longer in 1991 than in 1970, however the difference was less than the documented 15% variation in incubation lengths within a species (Boersma 1982). Boersma (1982) attributed variation in length of incubation period to temperature differences due to weather or the thermal properties of the nest. For example, increases in average air temperature shorten the incubation time of the eggs of

House Wrens and Chipping Sparrows (Kendeigh 1952, Walkinshaw 1952). In 1991, air temperatures on Gull Island during incubation were approximately 2° C cooler than normal. The longer incubation period in 1991 may also be explained by the subjective observation that birds were apparently standing over their eggs, rather than incubating, more frequently than in 1990.

It was hypothesized that adults would leave their eggs unattended a greater percentage of time when food supplies were low, however eggs were left unattended a greater proportion of the time in 1990 than in 1991. In 1991, kittiwake adults may have been responding to probable increased predation pressure by Herring Gulls. However, in both years eggs were left unattended longer (4 - 11% of the time) than in a study carried out at North Shields (0.3% of the time, Coulson and Wooller 1984), perhaps an indication of food shortages.

2.5.5 THE NESTLING PERIOD

The chick survivorship curves for Gull Island provide evidence of differences in the patterns of food shortages between the two years of this study. Chick survivorship curves in 1990 showed extensive mortality of older chicks and observations from a blind indicated that the deaths of these chicks were likely caused by predation by Herring Gulls. Masses of chicks older than 20 days were not obtained, but this increased predation may indicate inadequate food supplies at this time. There may also have been a shortage of food earlier in the breeding season as a substantial proportion of chicks younger than 20 days were found to be growing slowly. In 1991, most predation occurred earlier in the season and relatively few eggs survived to hatch. For those very few chicks which did hatch, the survivorship curve had the customary shape (Paynter 1966), with most chick mortality occurring in the first two weeks. Three quarters of the chicks from the study plots either lost mass or failed to gain in 1991.

The chick survivorship curves demonstrate the effects of observer disturbance in 1991, with the marked difference in the slopes of the curves for study and control plots. Nests were checked every other day in an attempt to minimize this disturbance. The difference in chick survivorship between study and control plots was not nearly so great in 1990, even though nests were checked daily that year.

In general, inter-colony and inter-year comparisons of fledging success (proportion of chicks hatched that fledged) and chicks fledged/nest showed the same pattern of decreases as the previous measures and added weight to the hypothesis that decreases in productivity indicate food shortages.

Fledging success was not available for Gull Island in 1988, but mean number of chicks fledged/nest seemed to indicate reduced breeding success that year when comparison was made with the highly productive Cape St. Mary's colony in 1990.

The findings of the analysis of parental attendance patterns during chick rearing were not as hypothesized. Adults were expected to leave their chicks unattended longer and at a younger age when food supplies were poorest. Chicks were not seen left alone at all in 1991, although sample sizes were small. The decreased egg volumes, low percentage of 2-egg clutches, relatively large percentage of slowly growing chicks and the predation by Herring Gulls on older kittiwake chicks seem to indicate a food shortage in 1990 as well, and in that year chicks were occasionally left unattended (overall, less than 3% of the time). In 1990, the most serious food shortage may have occurred during the chick rearing period, while in 1991, conditions were altogether more severe and began earlier as evidenced by the greater amount of non-breeding.

The pattern of attendance at colonies in Newfoundland and at the highly successful colony in North Shields seems to be different from that seen at colonies that routinely experience food shortages. At North Shields (Hodges 1969), chicks were constantly attended until the age of 25-34 days and on Gull Island in 1990, they were left alone less than

2% of the time up to 20 days of age and only 7% of the time after that. In Alaska, Roberts and Hatch (1993) reported that chicks from 21-30 days old were left alone roughly 20% of the time, while older chicks were left unattended 40% of the time. Barrett and Runde (1980) made similar observations on Runde, Norway. Productivity in Alaska was 0.2 chicks/nest (Roberts and Hatch 1993), compared with 0.4 chicks/nest on Gull Island.

The conclusions drawn from the analysis of attendance patterns relies on the assumptions that most of the time an adult is away from the nest is spent in pursuit of food and that adults spend as much time as possible at the nest. Potential benefits of nest site attendance include protection of the young, defense and retention of the site, and communication and coordination of activities between mates. As central place foragers (Orians and Pearson 1979), breeding kittiwakes should show flexibility in the length of their feeding trips with changing food resources.

Contrary to expectation, there was no significant difference in feeding rates between the two years in this study, however there may have been differences in bolus size. Some species, such as the Common Murre, have time budgets that are sufficiently flexible to permit them to respond to fluctuations in prey levels by spending more time foraging and also by taking more of other species of fish

(Burger and Piatt 1990). In support of this interpretation, there was an apparent lack of change in reproductive success of murres and puffins, both diving feeders, in Witless Bay in 1991 (Chardine, pers. comm.). Such flexibility may not be possible for kittiwakes who are smaller and capable of feeding only at the surface.

It is often difficult to make comparisons with feeding rates in other studies as the definition of a feed may not be directly comparable. In Alaska (Roberts and Hatch 1993), kittiwakes were fed at the rate of 0.4 boluses pair^{-1} h^{-1} in the year they experienced almost complete breeding failure. This is roughly comparable to the value obtained in this study, 0.5 boluses pair^{-1} h^{-1} for 16 daylight h. Two studies done in the United Kingdom (Pearson 1968, Galbraith 1983) documented higher feeding rates than were obtained on Gull Island. On the Farne Islands, Pearson (1968) recorded a feeding rate of 5 to 8 feeds brood^{-1} day^{-1} for 1 and 2 chick broods respectively, in an 18 h day. Pearson (1968) did not state the average bolus number per feed, however if each of his feeds consisted of a single bolus, 8 feeds/day would approximate that obtained in this study. Feeds rarely consisted of a single bolus in this study and it is likely that they were also larger on the Farne Islands, leading to a higher feeding rate in the Pearson (1968) study. On the

Isle of May, kittiwake chicks received 3.7 feeds brood^{-1} day^{-1} in a 10 h period (Galbraith 1983). It must be noted that in none of these studies was bolus size evaluated.

The frequency and success of chick begging was obtained as an additional measure of chick hunger and provided clear evidence for severe food shortages in 1991. Chick begging in 1991 was twice as frequent as in 1990 and averaged 1.1 bouts pair^{-1} h^{-1}. Only 19% of begging bouts were successful (ended in chick feeding) in 1991, compared with 38% in 1990. In a year of low productivity, Roberts and Hatch (1993) recorded 22% of begging bouts as being successful, while the previous year, a good year for kittiwake productivity in the Pacific, 35% of begging bouts were successful. At best however, Pacific kittiwakes have low productivity compared with populations in regions of the northeastern Atlantic (Hatch et al. 1991).

In summary, variation in kittiwake behaviour and breeding biology indicated differences in food supply between years and perhaps between locations. The mean laying date was later, clutch sizes were smaller, eggs were smaller, hatching and fledging success had decreased and chicks failed to gain mass in 1991, strongly suggesting food shortage that year. The behavioural evidence for food shortage was mixed. Chicks begged more intensely and had fewer successful begging bouts in 1991, but there were no significant differences between years in chick feeding rate or parental attendance patterns during incubation or chick rearing. Reports of low catches of cod, cold water temperatures and delayed spawning and decreased biomass of capelin gave independent evidence that food shortages occurred in 1991.

The breeding success of Black-legged Kittiwakes was significantly lower on Gull Island in 1990 and 1991 compared to that experienced in 1969 and 1970. This decrease had begun at least by 1988, as evidenced by the lower percentage of 2-egg clutches and low number of chicks fledged/nest. Part of the reason for the overall decrease may be the increase in the number of nesting Herring Gulls, however behavioural and biological evidence clearly point to food shortage as being the reason for the low breeding success of kittiwakes in 1991 at both Cape St. Mary's and Gull Island. The poor productivity of Herring Gulls in 1991 suggests that they were also affected by food shortage and consequently may have been preying more heavily on kittiwake eggs and young than in previous years. Food shortage may also have been an important cause of the low productivity of kittiwakes on Gull Island in 1990, as shown in the low egg volumes and the low percentage of 2-egg clutches compared with 1969/1970. In 1990, food shortage seemed to be localized as reproductive success was high at Cape St. Mary's.

The different components of breeding success differed in their sensitivity to reduced food supplies. Mean laying date, chick growth rates and proportion of successful begging bouts may be the best indicators of variation in feeding conditions; they showed clear significant differences between years, and decreases in these values have few alternate explanations. Decreases in clutch size, egg volume, percentage of occupied nests with eggs, and fledging success function less well as indicators of food shortages as they may also be variously explained by timing of breeding, changes in the age structure of the population or predation. When assessing chick feeding rates it is important to take into account food type and bolus size to get an indication of amount fed. Components of breeding success showing no significant differences between colonies or years were incubation period and parental attendance during incubation and chick rearing, suggesting low sensitivity to reduced food supply. Alaskan studies have shown reduced parental attendance during extreme food shortages, but these colonies may not have had the kind of accessibility for predation that occurred on Gull Island, where the heavy predation of Herring Gulls may have kept parental attendance high. Hatching success did show significant differences between colonies and years, however it is likely that reductions were caused by high levels of predation, driven by food shortage, rather than food shortage directly.

The evidence that food shortage was responsible for the low breeding success of Black-legged Kittiwakes is mostly circumstantial but, taken as a whole, convincing. This study also suggests the importance of capelin for surface-feeding seabirds in the Witless Bay Ecological Reserve. Should an increased commercial fishery for capelin develop, it is essential for the integrity of the marine ecosystem in this area to allocate an adequate portion of the biomass to seabirds.

Table 2-1

Schedule of visits to study colonies in 1990 and 1991 and sample sizes of nests studied.

	1990	1991
A. Gull Island		
Extended visits	11 June - 1 August	10 May - 19 July
Short visits	19-22 August	31 July, 14 August
N (study nests)	79	179
N (control nests)	28	75
B. Cape St. Mary's		
Extended visits	2 May - 31 May	none
Short visits	10 June, 18 July, 5 August	21 June, 17, 28 July, 11 August
N (study nests)	51	45
N (control nests)	none	none

Table 2-2

Sampling effort for behavioural data at Gull Island in 1990 and 1991.

	Nest-hours (N = nests)	
	1990	1991
Nests with eggs	436.5 (31)	773.8 (23)
Nests with 1 chick		
0-5 days	79.0 (5)	95.5 (5)
6-20 days	744.8 (13)	64.0 (4)
> 20 days	119.8 (5)	-
Nests with 2 chicks		
0-5 days	311.5 (10)	45.0 (3)
6-20 days	590.5 (4)	36.0 (2)
> 20 days	90.5 (2)	-
Total	2372.6	1014.3
Mean length of watch	3.1	6.0
Range	0.5 - 4.0	3.0 - 15.0

<u>Note.</u> Nest-hours = number of nests X number of hours observed.

Table 2-3

The timing of breeding of Black-legged Kittiwakes at Cape St. Mary's (CSM) and Gull Island (GI), Newfoundland in five years between 1969 and 1991.

Location and year[1]	Mean laying date SD (N)	Mean hatching date SD (N)
CSM '90	19 May 5.2 (49)	14 June[5]
GI '69[2]	3 June 6.8 (103)	28 June 4.1
GI '70[3]	29 May 7.0 (122)	25 June 4.8
GI '90	6 June 11.3[4] (58)	4 July 11.4 (62)
GI '91 study	10 June 6.0 (96)	1 July 4.4 (4)
GI '91 control	10 June 6.0 (40)	8 July 2.6 (18)
GI '91 all	10 June 6.0 (136)	7 July 3.9 (22)

[1] data not available for CSM '91 and GI '88
[2] Maunder and Threlfall 1972
[3] Maunder and Threlfall 1972
[4] back-calculated from the mean hatching date
[5] forward-calculated from the mean laying date

<u>T-TESTS</u>

<u>Mean Laying Date</u>
GI 1969 vs. GI 1990 t = 2.10, df = 159, p < 0.05
GI 1990 vs. GI 1991 t = 3.21, df = 192, p < 0.01

<u>Mean Hatching Date</u>
GI 1990 vs. GI 1991 (study) t = 0.52, df = 64, n.s.
GI 1990 vs. GI 1991 (control) t = 1.47, df = 78, n.s.
GI 1991 (study) vs. (control) t = 4.27, df = 20, p < 0.001
Sample sizes not available for GI 1969, 1970 and CSM 1990.

Table 2-4

Black-legged Kittiwake clutch size composition at Cape St. Mary's (CSM) and Gull Island (GI) in 1969, 1970, 1988, 1990 and 1991.

	Eggs laid/clutch						
	1		2		3		
	%	N	%	N	%	N	Mean
Location and year							
CSM '90	6	(3)	86	(42)	8	(4)	2.02
CSM '91	65	(20)	35	(11)		(0)	1.35
GI '69, '70[1]	16	(36)	82	(185)	2	(4)	1.85
GI '88[2]	38	(43)	60	(67)	2	(2)	1.63
GI '90	49	(44)	49	(44)	2	(1)	1.49
GI '91	72	(105)	28	(41)		(0)	1.28

[1] Maunder and Threlfall 1972
[2] Chatman 1989 and J.M. Porter, pers. comm.

<u>COMPARISON</u>	<u>CHI-SQUARED</u>	<u>DF</u>	<u>P-VALUE</u>
GI '69, '70 vs. GI '88	21.01	2	* 0.00
GI '88 vs. GI '90	2.51	2	0.29
GI '90 vs. GI '91	13.02	2	* 0.00
CSM '90 vs. CSM '91	32.28	2	* 0.00
CSM '90 vs. GI '90	28.40	2	* 0.00
CSM '91 vs. GI '91	0.68	1	0.41

Table 2-5

Seasonal trends in Black-legged Kittiwake clutch size in 1990 and 1991 in early, middle and late laid eggs.

	Gull Island - 1990[1]			Gull Island - 1991[2]			Cape St. Mary's - 1990[3]		
	Early % (N)	Middle % (N)	Late % (N)	Early % (N)	Middle % (N)	Late % (N)	Early % (N)	Middle % (N)	Late % (N)
Clutch size									
1	25 (3)	40 (4)	60 (21)	72 (23)	72 (66)	90 (9)	(0)	7 (2)	50 (3)
2	75 (9)	50 (5)	35 (12)	28 (9)	28 (26)	10 (1)	100 (12)	86 (27)	50 (3)
3	(0)	10 (1)	5 (1)	(0)	(0)	(0)	(0)	7 (2)	(0)
Mean SD N	1.75 0.45 12	1.70 0.67 10	1.41 0.56 34	1.28 0.46 32	1.28 0.45 92	1.10 0.32 10	2.00 - 12	2.00 0.37 31	1.50 0.55 6
Chi-squared	7.31, df = 4 p = 0.12			1.56, df = 2 p = 0.46			13.31, df = 4 p = 0.01 *		

Note. Statistical tests done on tabulated data, means shown for ease of comparison.

[1] 1990: early = 18 May - 29 May, middle = 30 May - 11 June, late = 12 June - 23 June
[2] 1991: early = 27 May - 6 June, middle = 7 June - 18 June, late = 19 June - 29 June
[3] 1990: early = 9 May - 15 May, middle = 16 May - 23 May, late = 24 May - 30 May

Table 2-6

Changes in the proportions of occupied nests with eggs for Black-legged Kittiwakes at Cape St. Mary's (CSM) and Gull Island (GI) in 1969/1970, 1988, 1990 and 1991.

	Cape St. Mary's		Gull Island	
	%	(N)	%	(N)
1969/1970[1]		-	92	(246)
1988[2]		-	80	(140)
1990	96	(51)	83	(107)
1991 study		-	59	(179)
1991 control		-	53	(75)
1991 all	69	(45)	57	(254)

[1] Maunder and Threlfall 1972

[2] Chatman 1989 and J.M. Porter, pers. comm.

Comparison	Chi-squared	P-value
GI 1969/1970 vs. GI 1988	10.58	* 0.001
GI 1988 vs. GI 1990	0.40	n.s.
GI 1990 vs. GI 1991 all	22.47	* 0.001
GI 1991 study vs. 1991 control	0.75	n.s.
CSM 1990 vs. CSM 1991	12.72	* 0.001
CSM 1990 vs. GI 1990	5.20	* 0.02
CSM 1991 vs. GI 1991 all	2.20	n.s.

Table 2-7

Seasonal trends in Black-legged Kittiwake egg volumes on Gull Island in 1990 and 1991 in early, middle and late laid eggs.

	1990[1]			1991[2]		
	Early	Middle	Late	Early	Middle	Late
1-egg clutch						
Mean vol (cc)	-	-	-	41.5	42.0	40.9
SD				5.69	2.82	5.66
N				17	49	7
				F = 0.03, df = 2,72 p = 0.97		
2-egg clutch						
A-egg Mean vol (cc)	46.2	47.2	43.3	41.7	42.5	39.5
SD	5.31	2.75	3.65	3.08	3.08	
N	4	3	10	5	15	1
	F = 1.51, df = 2,16 p = 0.26			t = 0.51, df = 18 p = 0.62		
B-egg Mean vol (cc)	42.1	45.6	40.3	38.0	38.3	35.2
SD	3.96	1.55	2.87	4.04	3.02	
N	4	3	10	6	15	1
	F = 3.70, df = 2,16 p = 0.05 * middle & late different[3]			t = 0.16, df = 19 p = 0.87		

[1] 1990: early = 18 May - 29 May, middle = 30 May - 11 June,
late = 12 June - 23 June

[2] 1991: early = 27 May - 6 June, middle = 7 June - 18 June
late = 19 June - 29 June

[3] Student-Newman-Keuls multiple comparison test

Table 2-8

Comparisons of Black-legged Kittiwake egg volumes (cc) from Gull Island, and their relationship to hatching and fledging success.

	Hatched		Not hatch		Fledged		Not fledge	
	1990	1991	1990	1991	1990	1991	1990	1991
1-egg clutch								
mean volume	-	42.8	-	41.5	-	0	-	42.8
SD		1.4		2.9				1.4
N		4		76				4
2-egg clutches A-egg	|----p = 0.08----|[1]							
mean volume	44.6	0	42.1	42.0	46.7	-	44.1	-
SD	4.0		3.2	2.9	5.4		4.2	
N	15		13	24	2		10	
B-egg	|----p < 0.01----|							
mean volume	42.3	0	39.1	37.9	45.6	-	41.4	-
SD	3.7		2.0	3.1	0.1		3.9	
N	13		15	25	2		10	
All eggs	|----p < 0.01----|							
mean volume	43.5	42.8	40.5	40.9	46.1	0	42.8	42.8
SD	4.0	1.4	3.0	3.3	3.2		4.1	1.4
N	28	4	28	125	4		20	4
1990 + 1991	|---p < 0.001---|							
mean volume	43.4		40.5		46.1		42.8	
SD	3.7		4.4		3.2		3.8	
N	32		153		4		24	

[1] p represents significance level in two-sample t-tests

Table 2-9

Black-legged Kittiwake egg fates from Gull Island in 1990 and 1991.

Egg fate	1990		1991	
	%	(N)	%	(N)
Hatched	53	(62)	14	(25)
Missing	33	(38)	83	(156)
Miscellaneous	14	(16)	3	(6)

Table 2-10

An inter-colony and inter-year comparison of hatching success at Cape St. Mary's (CSM) and Gull Island (GI) in 1969, 1970, 1990 and 1991.

	Cape St. Mary's		Gull Island	
	%	(N)	%	(N)
1969[1]		-	71.6	(81)
1970[1]		-	72.9	(181)
1990	78.8	(99)	45.9	(135)
1991 study		-	3.0	(132)
1991 control		-	38.2	(55)
1991 all	52.0	(42)	13.4	(187)

[1] Maunder and Threlfall 1972

Comparison	Chi-squared	P-value
GI 1969 vs. GI 1990	13.52	* 0.001
GI 1990 vs. GI 1991 control	0.95	0.33
GI 1991 study vs. control	41.42	* 0.001
GI 1990 vs. GI 1991 all	42.14	* 0.001
CSM 1990 vs. CSM 1991	9.97	* 0.01
CSM 1990 vs. GI 1990	25.66	* 0.001
CSM 1991 vs. GI 1991 control	1.95	0.16
CSM 1991 vs. GI 1991 all	32.00	* 0.001

Table 2-11

An inter-colony and inter-year comparison of fledging success in Black-legged Kittiwakes at Cape St. Mary's (CSM) and Gull Island (GI) in 1969, 1970, 1990 and 1991.

Year	Cape St. Mary's			Gull Island		
	%	(N)	Chicks fl./nest	%	(N)	Chicks fl./nest
1969[1]		-		81.0	(58)	-
1970[1]		-		73.7	(141)	-
1988[2]		-			-	0.63
1990	92.3	(78)	1.41	50.8	(62)	0.35
1991 study		-		0.0	(0)	0.00
1991 control		-		62.0	(21)	0.33
1991 all	73.0	(22)	0.40	52.0	(25)	0.09

[1] Maunder and Threlfall 1972
[2] Chatman 1989 and J.M. Porter, pers. comm.

Comparison	Chi-squared	P-value
GI 1970 vs. GI 1990	9.55	* 0.002
GI 1990 vs. GI 1991 control	0.67	0.41
GI 1990 vs. GI 1991 all	0.001	0.97
CSM 1990 vs. CSM 1991	6.23	* 0.01
CSM 1990 vs. GI 1990	29.95	* 0.001
CSM 1991 vs. GI 1991 control	0.57	0.45
CSM 1991 vs. GI 1991 all	2.13	0.14

Table 2-12

Black-legged Kittiwake parental attendance patterns during chick rearing, Gull Island, 1990 and 1991.

Chick Age (days)	1990			1991		
	% time unattended	nest-hours	N pairs	% time unattended	nest-hours	N pairs
0 - 5	0.3	304.0	18	0	140.5	7
6 - 20	1.6	1117.5	18	0	100.0	5
21+	7.1	492.5	12	-	0.0	0
Overall	2.8	1914.0	30	0	240.5	7

Table 2-13

The rate of Black-legged Kittiwake chick begging bouts and the percentage that resulted in a feed on Gull Island in 1990 and 1991.

Chick age (days)		1990	1991
0 - 5	begging bouts nest^{-1} h^{-1} (SD)	0.35 (0.27)	1.29 (0.83) [1]
	nest-hours (nests)	390.8 (15)	140.5 (7)
	% success (n bouts)	47.8 (186)	18.3 (164) [2]
6 - 20	begging bouts nest^{-1} h^{-1} (SD)	0.50 (0.39)	0.78 (0.21) [3]
	nest-hours (nests)	1335.3 (17)	100.0 (5)
	% success (n bouts)	37.6 (834)	21.7 (83) [4]
21+	begging bouts nest^{-1} h^{-1} (SD)	0.80 (0.68)	-
	nest-hours (nests)	210.3 (7)	0 (0)
	% success (n bouts)	28.8 (170)	-
Overall	begging bouts nest^{-1} h^{-1} (SD)	0.52 (0.43)	1.08 (0.68) [5]
	nest-hours (nests)	1936.3 (20)	240.5 (7)
	% success (n bouts)	38.0 (1190)	19.4 (247) [6]

<u>Tests of Significance</u>

[1] $t = 4.04$, df = 20, $p < 0.001$*

[3] $t = 1.52$, df = 20, $p = 0.14$

[5] $t = 2.63$, df = 25, $p = 0.01$ *

[2] Chi-squared = 33.93, $p < 0.001$*

[4] Chi-squared = 8.33, $p < 0.01$

[6] Chi-squared = 34.96, $p < 0.001$*

Table 2-14

The feeding rate (number of boluses/h) of Black-legged Kittiwake chicks according to age on Gull Island in 1990 and 1991.

Chick age (days)		1990	1991
0 - 5	bolus nest^{-1} h^{-1} (SD)	0.43 (0.34)	0.58 (0.68)
	nest-hours (nests)	390.8 (15)	140.5 (7)
6 - 20	bolus nest^{-1} h^{-1} (SD)	0.44 (0.41)	0.49 (0.30)
	nest-hours (nests)	1335.3 (17)	100.0 (5)
21+	bolus nest^{-1} h^{-1} (SD)	0.47 (0.43)	-
	nest-hours (nests)	210.3 (7)	0 (0)
overall	bolus nest^{-1} h^{-1} (SD)	0.44 (0.38)	0.54 (0.53)
	nest-hours (nests)	1936.3 (20)	240.5 (7)

<u>Tests of Significance</u>

0 - 5 days	$t = 0.70$, $df = 20$, $p = 0.49$
6 - 20 days	$t = 0.25$, $df = 20$, $p = 0.80$
Overall	$t = 0.54$, $df = 25$, $p = 0.59$

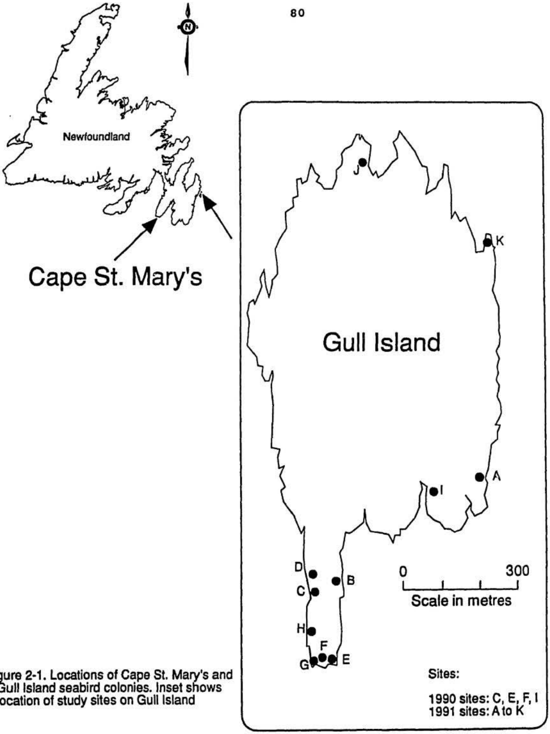


Figure 2-1. Locations of Cape St. Mary's and Gull Island seabird colonies. Inset shows location of study sites on Gull Island

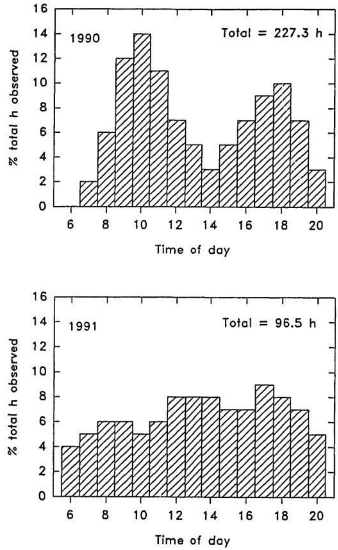


Figure 2-2 - Number of hours of behavioural observation in relation to time of day on Gull Island in 1990 (18/6 - 23/6, 9/7 - 1/8) and 1991 (24/6 - 30/6, 3/7 - 17/7).

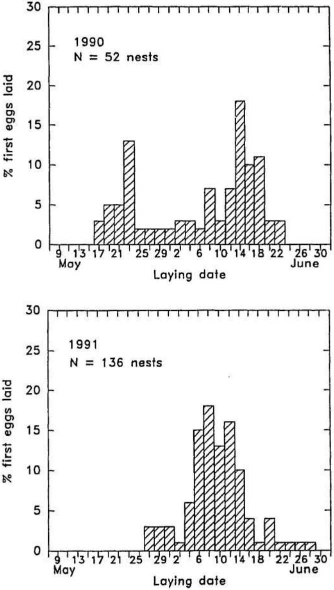


Figure 2–3 – Laying date (date first eggs laid) distribution for Black–legged Kittiwakes on Gull Island in 1990 and 1991.

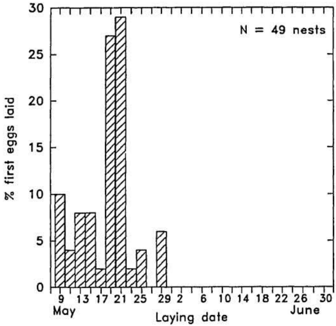
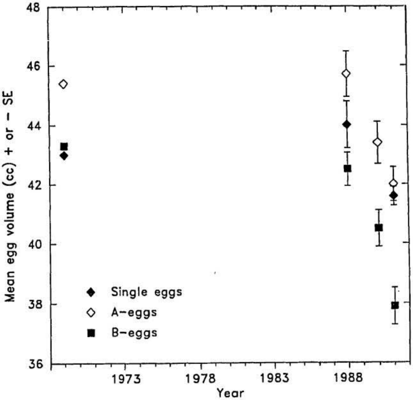


Figure 2–4 – Laying date (date first eggs laid) distribution for Black–legged Kittiwakes at Cape St. Mary's in 1990.



A−eggs F = 6.75 (2,84) $p < 0.01$

B−eggs F = 14.33 (2,89) $p < 0.001$

Single eggs T = 3.37 (101) $p < 0.001$

Figure 2−5 − Black−legged Kittiwake egg volumes from Gull Island (1969, Maunder and Threlfall 1972; 1988, J.M. Porter, pers. comm.; 1990−1991, this study).

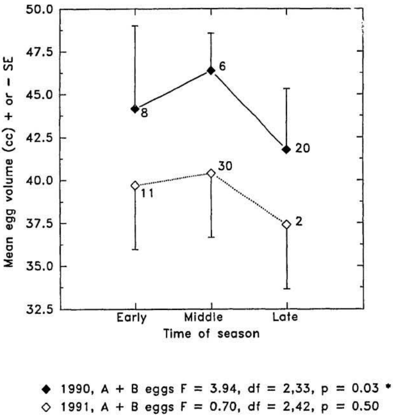


Figure 2–6 – Seasonal trends in Black–legged Kittiwake egg volumes on Gull Island in 1990 and 1991 in early–, middle– or late–laid eggs. Sample sizes indicated.

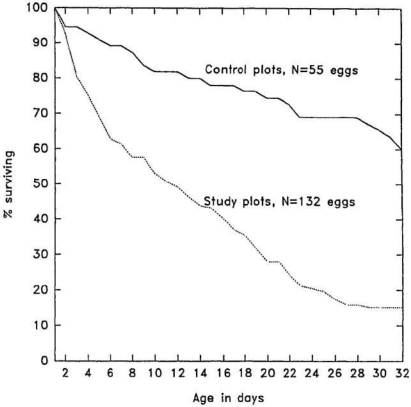


Figure 2–7 – Black–legged Kittiwake egg survivorship curves on Gull Island in 1991.

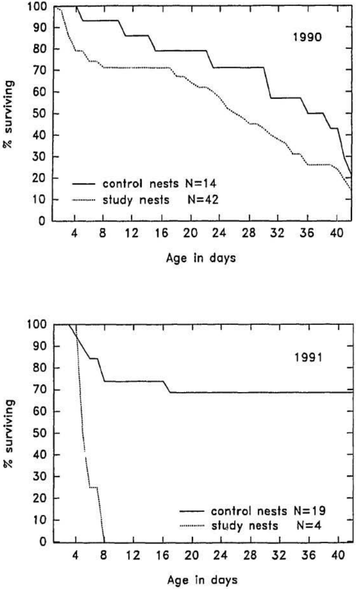


Figure 2-8 – Chick survivorship curves for Black-legged Kittiwakes on Gull Island in 1990 and 1991.

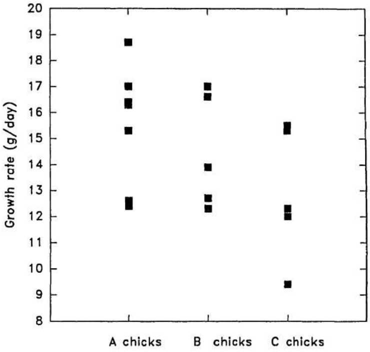


Figure 2-9 – Growth rates of Black-legged Kittiwake chicks during the period of linear growth (6 – 20 days) on Gull Island in 1990.

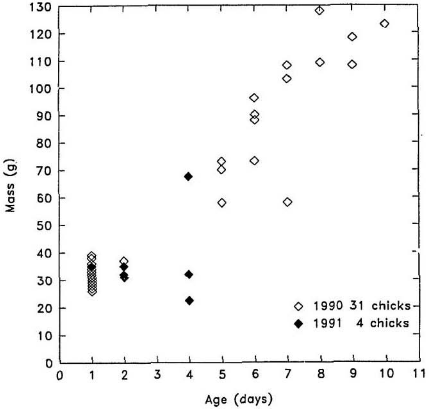


Figure 2–10 – Black–legged Kittiwake chick masses from Gull Island in 1990 and 1991.

Plate 2-1 Representative study and control plots on Gull Island:

Upper - study plot F
Lower - control plot I.

2.6 REFERENCES

Aebischer, N.J., J.C. Coulson, and J.M. Colebrook. (1990). Parallel long-term trends across four marine trophic levels and weather. Nature, 347, 753-755.

Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour, 49, 227-265.

Anderson, D.W., F. Gress, and K.F. Mais. (1982). Brown Pelicans: influence of food supply on reproduction. Oikos, 39, 23-31.

Ankney, C.D. and C.D. McInnes. (1978). Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk, 95, 459-471.

Ashmole, N.P. (1971). Seabird ecology and the marine environment. In: Avian Biology Vol.1. (ed. by D.S. Farner and J.R. King), pp. 223-286. Academic Press: New York.

Barrett, J.T. and O.J. Runde. (1980). Growth and survival of nestling kittiwakes Rissa tridactyla in Norway. Ornis Scandinavica, 11, 228-235.

Belopol'skii, L.O. (1961). Ecology of Sea Colony Birds of the Barents Sea. Jerusalem, Israel Program for Scientific Translations.

Boersma, P.D. (1982). Why some birds take so long to hatch. American Naturalist, 120, 733-750.

Braun, B.M. and G.L. Hunt. (1983). Brood reduction in Black-legged Kittiwakes. Auk, 100, 469-476.

Brown, R.G.B. and D.N. Nettleship. (1984). Capelin and seabirds in the northwest Atlantic. In: Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships (ed. by D.N. Nettleship, G.A. Sanger and P.F. Springer), pp. 184-194. Canadian Wildlife Service Special Publication, Ottawa.

Burger, A. and J. Piatt. (1990). Flexible time budgets in breeding Common Murres: buffers against variable prey abundance. *Studies in Avian Biology*, *14*, 71-83.

Cairns, D.K., W.A. Montevecchi, and W. Threlfall. (1989). *Researcher's Guide to Newfoundland Seabird Colonies*. 2nd ed. Memorial University of Newfoundland, Occasional Papers in Biology, No. 14.

Chardine, J.W. (1987). The influence of pair-status on the breeding behaviour of the kittiwake *Rissa tridactyla* before egg-laying. *Ibis*, *129*, 515-526.

Charnov, E.L. and J.R. Krebs. (1974). On clutch-size and fitness. *Ibis*, *116*, 217-219.

Chatman, E. (1989). The influence of nesting density on the reproductive success of the Atlantic Puffin *Fratercula arctica* (L.) and the Black-legged Kittiwake *Rissa tridactyla* (L.) on Gull Island, Witless Bay, Newfoundland in 1988. Unpublished B.Sc. Honours thesis, Memorial University of Newfoundland, St. John's, Canada.

Coulson, J.C. (1963). Egg size and shape in the kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. *Proceedings of the Zoological Society of London*, *140*, 211-227.

Coulson, J.C. (1966). The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. *Journal of Animal Ecology*, *35*, 269-279.

Coulson, J.C. (1972). The significance of the pair-bond in the kittiwake. *Proceedings of the International Ornithological Congress*, *15*, 424-433.

Coulson, J.C. and J. Horobin. (1976). The influence of age on the breeding biology and survival of the Arctic Tern *Sterna paradisaea*. *Journal of Zoology*, *178*, 247.

Coulson, J.C. and J.M. Porter. (1985). Reproductive success of the kittiwake _Rissa tridactyla_: the roles of clutch size, chick growth rates and parental quality. _Ibis_, _127_, 450-466.

Coulson, J.C., G.R. Potts and J. Horobin. (1969). Variation in the eggs of the Shag (_Phalacrocorax aristotelis_). _Auk_, _86_, 232.

Coulson, J.C. and C.S. Thomas. (1985a). Changes in the biology of the kittiwake _Rissa tridactyla_: a 31 year study of a breeding colony. _Journal of Animal Ecology_, _54_, 9-26.

Coulson, J.C. and C.S. Thomas. (1985b). Differences in the breeding performance of individual kittiwake gulls, _Rissa tridactyla_ (L.). In: _Behavioural Ecology_ (ed. by R.M. Sibly and R.H. Smith), pp. 489-503. Blackwell: Oxford.

Coulson, J.C. and E. White. (1958). The effect of age on the breeding biology of the kittiwake _Rissa tridactyla_. _Ibis_, _100_, 40-51.

Coulson, J.C. and E. White. (1961). An analysis of the factors influencing the clutch size of the Kittiwake. _Proceedings of the Zoological Society of London_, _136_, 207-217.

Coulson, J.C. and R.D. Wooller. (1976). Differential survival rates among breeding Kittiwake Gulls _Rissa tridactyla_ (L.). _Journal of Animal Ecology_, _45_, 205-213.

Coulson, J.C. and R.D. Wooller. (1984). Incubation under natural conditions in the Kittiwake Gull _Rissa tridactyla_. _Animal Behaviour_, _32_, 1204-1215.

Cramp, S. (ed.) (1983). _Handbook of the Birds of Europe, the Middle East and North Africa, Volume 3_, (pp. 863-875). Oxford University Press: Oxford.

Cullen, E. (1957). Adaptations in the kittiwake to cliff-nesting. _Ibis_, _99_, 275-302.

Danchin, E. (1986). The behaviour associated with the occupation of breeding site in the kittiwake gull Rissa tridactyla: the social status of landing birds. Animal Behaviour, 35, 81-93.

Danchin, E. (1988). Social interactions in kittiwake colonies: social facilitation and/or favourable social environment. Animal Behaviour, 36, 443-451.

Daniels, D., Heath, J. and Rawson, W. (1984). A declaration of intent in the kittiwake gull (Rissa tridactyla). Animal Behaviour, 32, 1151-1156.

Davis, J.W.F. (1975). Age, egg-size and breeding success in the Herring Gull. Ibis, 117, 460-473.

Dijkstra, C., L. Vuursteen, S. Daan, and D. Masman. (1982). Clutch size and laying date in the Kestrel Falco tinnunculus: effect of supplementary food. Ibis, 124, 210-213.

Drent, R.H. and S. Daan. (1980). The prudent parent: energetic adjustments in avian breeding. Ardea, 68, 225-252.

Ewald, P.W. and S. Rohwer. (1982). Effects of supplemental feeding on timing of breeding, clutch size and polygyny in Red-Winged Blackbirds Agelaius phoeniceus. Journal of Animal Ecology, 51, 429-450.

Galbraith, H. (1983). The diet and feeding ecology of breeding kittiwakes Rissa tridactyla. Bird Study, 30, 109-120.

Gaston, A.J. and D.N. Nettleship. (1982). Factors determining seasonal changes in attendance at colonies of the Thick-billed Murre Uria lomvia. Auk, 99, 468-473.

Harris, M.P. (1969). Food as a factor controlling the breeding of Puffinus iherminieri. Ibis, 111, 139-156.

Harris, M.P. and S. Wanless. (1990). Breeding success of British Kittiwakes Rissa tridactyla in 1986-88: Evidence for changing conditions in the northern North Sea. Journal of Applied Ecology, 27, 172-187.

Hatch, S.A. (1986). Adult survival of Black-legged Kittiwakes on Middleton Island, Alaska. Unpubl. Admin. Rept., U.S. Fish and Wildl. Serv., Anchorage, Alaska.

Hatch, S.A., G.V. Byrd, D.B. Irons and G.L. Hunt. (1991). Status and ecology of kittiwakes in the North Pacific. In: Status and Conservation of Temperate North Pacific Seabirds (ed. by K. Vermeer, K.T. Briggs, and D. Siegel-Causey). Canadian Wildlife Service Special Publication: Ottawa.

Hatch, S.A. and M.A. Hatch. (1990). Components of breeding productivity in a marine bird community: key factors and concordance. Canadian Journal of Zoology, 68, 1680-1690.

Haycock, K.A. and W. Threlfall. (1975). The breeding biology of the Herring Gull in Newfoundland. Auk, 92, 678-697.

Hodges, A.F. (1969). A time-lapse study of kittiwake incubation rhythms. Ibis, 111, 442-443.

Hogstedt, G. (1981). The effect of additional food on reproductive success in the Magpie. Journal of Animal Ecology, 50, 219-230.

Hunt, G.L. (1972). Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology, 53, 1051-1061.

Jandel Corp. (1990). Sigmaplot, Version 4.01. Jandel Scientific: Corte Madera, California.

Kendeigh, S.C. (1952). Parental care and its evolution in birds. III Biological Monograph, 22, 1-358.

Klomp, H. (1970). The determination of clutch size in birds, a review. Ardea, 58, 1-124.

Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Oxford University Press: Oxford.

Lack, D. (1967). Interrelationships in breeding adaptations as shown by marine birds. *Proceedings XIV International Ornithological Congress, Oxford*, 3-31.

Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. Methuen: London.

Lundberg, C. and R. Vaisanen. (1979). Selective correlation of egg size with chick mortality in the Black-headed Gull (*Larus ridibundus*). *Condor*, *81*, 146-156.

Martin, P. and P. Bateson. (1986). *Measuring Behaviour: An Introductory Guide*. Cambridge University Press: Cambridge.

Maunder, J.E. and W. Threlfall. (1972). The breeding biology of the Black-legged Kittiwake in Newfoundland. *Auk*, *89*, 789-816.

Methven, D.A. and J.F. Piatt. (1991). Seasonal abundance and vertical distribution of capelin (*Mallotus villosus*) in relation to water temperature at a coastal site off eastern Newfoundland. *International Council for the Exploration of the Sea Journal of Marine Science*, *48*, 187-193.

Mills, J.A. (1973). The influence of age and pair bond on the breeding biology of the Red-billed Gull, *Larus novaehollandiae scopulinus*. *Journal of Animal Ecology*, *42*, 147-162.

Mills, J.A. (1979). Factors affecting the egg size of Red-billed Gulls *Larus novaehollandiae scopulinus*. *Ibis*, *121*, 53-67.

Monaghan, P., J.D. Uttley, M.D. Burns, C. Thaine, and J. Blackwood. (1989). The relationship between food supply, reproductive effort and breeding success in Arctic Terns, *Sterna paradisaea*. *Journal of Animal Ecology*, *58*, 261-274.

Morris, R.D. (1986). Seasonal differences in courtship feeding rates of male Common Terns. Canadian Journal of Zoology, 64, 501-507.

Murphy, E.C., R.H. Day, K.L. Oakley, and A.A. Hoover. (1984). Dietary changes and poor reproductive performance in Glaucous-winged Gulls. Auk, 101, 532-541.

Nelson, J.B. (1966). The breeding biology of the Gannet Sula bassana on the Bass Rock Scotland. Ibis, 108, 584.

Newton, I. (1979). Population Ecology of Raptors. Poyser: Berkhampstead.

Nisbet, I.C.T. (1973). Courtship-feeding, egg-size and breeding success in Common Terns. Nature, 241, 141-142.

Nisbet, I.C.T. (1977). Courtship feeding and clutch size in Common Terns, Sterna hirundo. In: Evolutionary Ecology (ed. by B. Stonehouse and C. Perrins), pp.101-109. University Park Press: Baltimore, Maryland.

Nisbet, I.C.T. (1978). Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate Terns, Sterna hirundo and S. Dougallii. Ibis, 120, 207-215.

Nysewander, D.R. (1983). Black-legged Kittiwake (Rissa tridactyla). In: The Breeding Biology and Feeding Ecology of Marine Birds in the Gulf of Alaska (ed. by P.A. Baird and P.J. Gould), pp. 152-203. Final report submitted to the Outer Continental Shelf Environmental Assessment Program, Juneau, Alaska. U.S. Fish and Wildlife Service, National Fisheries Research Center, Anchorage, Alaska.

Orians, G.H. and N.E. Pearson. (1979). On the theory of central place foraging. In: Analysis of Ecological Systems (ed. by D.J. Horn, R.D. Mitchell, and G.R. Stairs), pp. 155-177. Ohio State University Press: Columbus, Ohio.

Parsons, J. (1970). Relationship between egg-size and post-hatching chick mortality in the Herring Gull. Nature, 228, 1221-1222.

Parsons, J. (1972). Egg size, laying date and incubation period in the Herring Gull. Ibis, 114, 536-541.

Parsons, J. (1975). Seasonal variation in the breeding success of the Herring Gull: an experimental approach to pre-fledging success. Journal of Animal Ecology, 44, 553-573.

Parsons, J. (1976). Factors determining the number and size of eggs laid by the Herring Gull. Condor, 78, 481-492.

Paynter, R.A. (1966). A new attempt to construct lifetables for Kent Island Herring Gulls. Bulletin of the Museum of Comparative Zoology Harvard University, 133, 489-528.

Pearson, T.H. (1968). The feeding ecology of seabird species breeding on the Farne Islands, Northumberland. Journal of Animal Ecology, 37, 521-552.

Perrins, C.M. (1970). The timing of birds' breeding seasons. Ibis, 112, 242-255.

Perrins, C.M. (1979). British Tits. Collins: London.

Petrie, B. and A. Anderson. (1983). Circulation on the Newfoundland Continental Shelf. Atmosphere-Ocean, 21, 207-226.

Piatt, J.F. (1987). Behavioural ecology of Common Murre and Atlantic Puffin predation on capelin: implications for population biology. Unpublished Ph.D thesis, Memorial University of Newfoundland, St. John's, Canada.

Piatt, J.F. and D.A. Methven. (1986). Seabird capelin interactions at Witless Bay, Newfoundland. Newfoundland Institute for Cold Ocean Science, St. John's, Canada.

Pierotti, R. and C.A. Bellrose. (1986). Proximate and ultimate causation of egg size and the "third chick disadvantage" in the Western Gull. Auk, 103, 401-407.

Poole, A. (1985). Courtship feeding and Osprey reproduction. Auk, 102, 479-492.

Porter, J.M. (1988). Prerequisites for recruitment of Kittiwakes Rissa tridactyla. Ibis, 130, 204-215.

Porter, J.M. (1990). Patterns of recruitment to the breeding group in the kittiwake Rissa tridactyla. Animal Behaviour, 40, 350-360.

Powell, G.V.N. (1983). Food availability and reproduction by Great White Herons, Ardea herodias: a food addition study. Colonial Waterbirds, 6, 139-147.

Ricklefs, R.E., D.C. Duffy, and M. Coulter. (1984). Weight gain of blue-footed booby chicks: an indicator of marine resources. Ornis Scandinavica, 15, 162-166.

Roberts, B.D. and S.A. Hatch. (1993). Behavioral ecology of Black-legged Kittiwakes during chick rearing in a failing colony. Condor, 95, 330-342.

Runde, O.J. and R.T. Barrett. (1981). Variations in egg size and incubation period of the kittiwake Rissa tridactyla in Norway. Ornis Scandinavica, 12, 80-86.

Ryder, J.P. (1980). The influence of age on the breeding biology of colonial nesting seabirds. In: Behavior of Marine Animals, V.4, Marine Birds (ed. by J. Burger, B. Olla, and H. Winn), pp. 153-168. Plenum Press: New York.

Safina, C., J. Burger, M. Gochfeld, and R.H. Wagner. (1988). Evidence for prey limitation of Common and Roseate Tern reproduction. Condor, 90, 852-859.

Schaffner, F.C. (1986). Trends in Elegant Tern and Northern Anchovy populations in California. Condor, 88, 347-354.

SPSS Inc. (1988). SPSS-X User's Guide, 3rd Edition. Chicago.

Steele, D.H., J.M. Green, and J. Carter. (1979). A Biological and Oceanographic Study of the Atlantic Southwest Coast Marine Region. Report submitted to Parks Canada, Dept. of Indian and Northern Affairs.

Templeman, W. (1948). The life history of the caplin (Mallotus villosus O.F. Muller) in Newfoundland waters. Newfoundland Government Laboratory Research Service Bulletin, 17, 1-151.

Thomas, C.S. (1983). The relationships between breeding experience, egg volume and reproductive success of the kittiwake Rissa tridactyla. Ibis, 125, 567-574.

Threlfall, W. (1968). The food of three species of gulls in Newfoundland. Canadian Field Naturalist, 82, 176-180.

Verbeek, N.A.M. (1986). Aspects of the breeding biology of an expanded population of Glaucous-winged Gulls in British Columbia. Journal of Field Ornithology, 57, 22-33.

von Bromssen, A. and C. Jansson. (1980). Effects of food addition to Willow Tit, Parus montanus, and Crested Tit, Parus cristatus, at time of breeding. Ornis Scandinavica, 11, 173-178.

Walkinshaw, L.H. (1952). Chipping sparrow notes. Bird-banding, 23, 101-108.

Wanless, S. and M.P. Harris. (1992). Activity budgets, diet and breeding success of Kittiwakes Rissa tridactyla on the Isle of May. Bird Study, 39, 145-154.

Wooller, R.D. and J.C. Coulson. (1977). Factors affecting the age of first breeding of the Kittiwake Rissa tridactyla. Ibis, 119, 339-349.

Chapter 3

INTER-OBSERVER RELIABILITY

3.1. ABSTRACT

Data in a study of the functions of courtship feeding in Black-legged Kittiwakes were obtained through continuous sampling of 28 nests by two observers. To assess inter-observer reliability, correlations were calculated on counts of the different measures obtained by summing the frequencies of these different behaviour patterns over each hour (N = 16 h) for each of the two observers working concurrently. If correlations in the relatively small reliability samples were low, separate plots were made for each observer, using the entire data set (N = 190.5 h), to see if poor observer agreement was confirmed.

Variables which scored reliably (consistent agreement between observers when measuring the same behaviour on the same occasion) were adult returns to the nest and copulations, although agreement for copulation attempts was weak. Seasonal changes in the mean number of cloacal contacts per mount showed evidence of random error, while the three variables associated with courtship feeding (feeding bouts/h, food boluses/h and food boluses/courtship feeding bout) all showed evidence of systematic error. Food solicitation bouts/h showed evidence of both random and systematic errors. The implications of these results for the courtship feeding study varied depending upon the type of error shown in the coding of a particular variable and the questions to be answered.

Extensive training for inexperienced observers, fewer nests, a larger reliability sample and wiser choice of variables to record would improve inter-observer reliability. The results of this study underline the importance of assessing inter-observer reliability in the collection of behavioural data and argue for greater attention to this issue.

3.2 INTRODUCTION

This study of inter-observer reliability was made in the context of an examination of courtship feeding in Black-legged Kittiwakes, carried out at Cape St. Mary's, Newfoundland in May, 1990 (Chapter 4), in order to assess the influence of observer bias on the results of the courtship feeding study. This was done as the principle investigator was new to the study of seabird behaviour, and as prior research experience gained observing and recording the behaviour of human infants had emphasized the importance of inter-observer reliability in the collection of behavioural data.

Most researchers who have reviewed observational measurement issues have dealt with the concept of reliability (Johnson and Bolstad 1973, Hollenbeck 1978, Caro et al. 1979, Martin and Bateson 1986). The issues surrounding reliability in observational research comprise a series of interrelated problems, and research on these problems is sketchy and scattered throughout the literature of several disciplines.

Firstly, definition is a problem because meanings given to terms such as "agreement," "accuracy," "precision," and even "reliability" vary in practical usage from author to author (Reber 1985, Martin and Bateson 1986). This confusion in terminology reflects a failure to integrate traditional psychometric theories of reliability with a theory of observation. The term "psychometric" refers to the mental testing of human beings, for example assessment of personality, the evaluation of intelligence or the determination of aptitudes. Reliability in a psychometric sense is the relative absence of random errors in a measuring instrument (in observational research, the observer is the primary instrument). An instrument that can be used with precision on a repeated basis is consistent and reliable.

In this chapter, the theory underlying observational research is assumed to be congruent with traditional psychometric theory, however it should be pointed out that there is a fundamental difference between these two theories. When behaviour is sampled psychometrically, it is usually assumed that each person's response to any particular item on a test is independent of their responses to other items. In observational samples, the behaviour sampled is usually interrelated. One of the reasons for doing observational research may be to look for these relations among behaviour patterns. The difference between these two measurement theories needs to be fully explored before it is possible to apply the concept of reliability equally to both. Nevertheless, the traditional psychometric concept of reliability can provide a standard for measuring the performance of observational theory and measurement.

A concept often confused with reliability is validity - does the instrument of measurement measure what it purports to measure, or more generally, the property of being true, correct and in conformity with reality. Valid measures are accurate and specific, while reliable measures are precise. Accuracy and precision are not synonymous; accuracy indicates freedom from systematic errors (bias), while precision means random error is small.

Inter-observer reliability measures the extent to which two or more observers obtain similar results when measuring the same behaviour on the same occasion. If the two observers consistently show relatively high agreement, it is assumed that the observations reflect the subject's performance relatively accurately. Although accuracy of observations is frequently inferred from inter-observer agreement, it is not actually tested. Accuracy usually refers to the extent to which observations scored by an observer match those of a predetermined standard for the same data. Confusion arises because many researchers discussing reliability in the context of behavioural observations generally feel that it encompasses both accuracy and consistency (Johnson and Bolstad 1973, Hartmann 1977, Hollenbeck 1978, Caro et al. 1979).

The optimal reliability statistic varies with the sampling technique. In this study, continuous sampling (Altmann 1974) was used; the subject was watched continuously and all behaviour was recorded against a time base. A decision that needs to be made with continuous sampling is whether to assess reliability on a per subject basis (in this case, nest), or whether to use total frequencies of a behaviour in a particular time period. An example will clarify this problem. It could be the case that each observer records 20 instances of "adult returns to the nest" in 1 h, but there was no nest for which they agreed that an adult had returned. Looking at total frequencies, the agreement would be perfect, but for individual occurrences, it would be zero. Although such an extreme example is unlikely to occur, it is clear that these two methods can give widely differing results. Inter-observer reliability should be calculated at the level and for the time period in which the data will ultimately be analyzed (Hartmann 1977, Caro et al. 1979). For this study, behaviour was analyzed in terms of total frequencies/h or rates/h (see Chapter 4), so reliability was calculated on these totals over the same time period.

A correlation coefficient is the most appropriate method for the estimation of inter-observer reliability for continuous sampling. The most commonly used reliability statistic, percent agreement between two observers, is not suitable for continuous sampling because a decision must be made about how far apart in time the events can occur in the two records to be considered an agreement. Even though the variables used in this study have the properties of a ratio scale, the nonparametric Spearman rank correlation (r_s) was chosen as it is better suited to working with small sample sizes (Martin and Bateson 1986), and while slightly less powerful than the Pearson correlation coefficient, it is more robust to violations of assumptions of normality and homogeneity of variance.

A correlation indicates the degree of linear association between two measures (or variables). When assessing the correlations to follow, statistical significance is important, but the strength of association, as shown in the r_s value, must also be evaluated. For parametric correlations (for example the Pearson *r*) a method exists for calculating the minimum strength of correlation which is acceptable in indicating the reliability of two observer's observations. This method utilises the r^2, or coefficient of determination. With a minimum correlation of 0.7, approximately 50% of the variance in one set of scores is accounted for statistically by the other set of scores, since $r^2 = 0.7^2 = 0.49$. These are rough guidelines only, as no magic figure exists below which nothing is reliable and above which all measures are acceptable. Acceptability depends on several factors, including the importance of the category and the ease with which it can be measured. As the Spearman rank correlation yields similar values to the Pearson correlation when calculated for the same data (Sokal and Rohlf 1981), $r_s = 0.7$ will be taken as the minimum acceptable level for reliability in this study. To summarize, if a given correlation is significant, but $r_s < 0.7$, then the measure is not considered to have adequate inter-observer reliability. R_s values greater than 0.7, but not statistically significant, also indicate inadequate reliability.

There are a few additional points to consider when using correlation coefficients. The test samples used to assess reliability should be representative samples of the behaviour that is actually measured in the study, and reliability should be measured under the normal conditions of the study (Caro et al. 1979). This means that if behavioural samples are normally recorded from live animals, rather than videotapes, samples scored for reliability must be obtained in the same way. Finally, note that the level of statistical significance of the correlations says little about the degree of reliability, because the level of significance depends on the sample size as well as the strength of association. Provided it is significant, the size of the correlation coefficient, not its level of significance, is what matters. For example a correlation of 0.5 would represent a poor degree of reliability, yet this correlation is highly statistically significant ($p < 0.001$) with a sample size > 26 pairs, or in a more extreme case, with a sample size of 100, a correlation of 0.20 is statistically significant ($p < 0.05$) but represents a weak association ($r_s^2 = 0.04$; i.e., only 4% of the variation in one measure is accounted for by variation in the other).

Correlation coefficients have an important limitation pointed out by Johnson and Bolstad (1973) and Mash and McElwee, (1974): as only random components contribute to error to reduce r values, if one observer consistently overestimates behavioural rates relative to the other observer it is still possible to obtain high correlation coefficients even though agreement is poor. This difference can be large, but if it is consistently in one direction, the correlation will be high. This observer bias can be assessed using the t-test of the difference between the correlated scores.

A further factor affecting reliability that will be examined here is the frequency of occurrence of a particular behaviour pattern. It might be expected that events occurring at a low frequency will be less likely to be detected, while rapidly occurring behaviour patterns will also lead to biased reports because it may be physically impossible to record all events if they are occurring at a high rate. For each observer there will be an optimal range of frequencies at which behaviour patterns can be scored most accurately. These values may vary with the experience of the observers and the amount of training they receive.

3.3 METHODS

3.3.1 STUDY SITE

This work was carried out at Cape St. Mary's, Newfoundland (46°50'N and 54°12'W), using a group of 28 nests located on a cliff face 75 - 100 m above the sea. The birds were viewed with 8.5 X 44 binoculars from a location approximately 25 m away from, and slightly above, the nests. No blind was used as the presence of observers did not appear to affect the birds. For more information on this site and a map showing the location see section 2.3.1 and Figure 2-1.

3.3.2 COLLECTION OF DATA

3.3.2.1 Schedule of Observations and Sampling Effort

To assess inter-observer reliability, two observers scored behaviour patterns defined for use in the study of the function of courtship feeding in Black-legged Kittiwakes (Chapter 4). The observers simultaneously scored events taking place in the same nests (N = 28) in 6 sessions ranging in length from 1.3 h to 3 h. The sessions were scheduled over 4 days between 8 May and 31 May, 1990 to cover the beginning, middle and end of the data collection period. These dates were selected to evaluate observer drift, the tendency of observers to change the manner in which they apply the definitions of the behaviour patterns over time (Kazdin 1977). The sessions scored by two observers represented 8% (16.0 h/190.5 h) of the total hours of observation.

For the remainder of the observations (174.5 h), the observers worked in rotating shifts (mean length = 2.9 h) throughout the day, alternating from day to day in taking the first shift. This was to ensure that each observer contributed equally to data collected at all times of the day.

Prior to 8 May, efforts were made to standardize observations between observers. Their training included watching a short film of adult kittiwakes engaging in courtship behaviours after reading descriptions of these behaviour patterns in Paludan (1955) and Cramp (1983). Six h were then spent at the study site in discussion and practice with the specific coding scheme and data sheets to be used. After this time, there was no further comparison or communication between observers. If observers consistently work together and communicate, they may develop similar variations of the original behavioural definitions. Thus, observer drift may occur even though inter-observer agreement has been maintained.

3.3.2.2 Behavioural Observations

Kittiwake courtship behaviour patterns were monitored using continuous (all occurrences) sampling (Altmann 1974): the subjects were watched continuously and the frequency and duration of all behaviours were recorded. At the beginning of their shifts, observers began by scanning the nests to look for courtship feeding or copulation. If neither activity was seen, the observer waited for the next returning adult to begin recording. Courtship feeding and copulation occurred sufficiently infrequently that it was possible to record all occurrences of each behaviour, although if these events occurred simultaneously at different nests, details such as food boluses and cloacal contacts could only be recorded for the first nest noticed. A complete list of the behaviour patterns scored for each nest was as follows:

- male and female returns to the nest (with or without nesting material)
- greeting ceremony (spontaneous or following a return)
- food solicitation (head-tossing plus female food begging) *
- feeding bouts/h *
- food boluses/feeding bout *

- copulation attempts *
- copulation successes *
- cloacal contacts/mount *

The asterisked items were those which eventually proved useful in evaluating hypotheses about the function of courtship feeding, and with the addition of adult returns, were the variables subjected to reliability analyses.

Behaviours were considered to be within the same sequence if they followed within 2 min of the previous behaviour, and a food bolus was defined as any discrete packet of food swallowed by the female, no matter what the size. A successful copulation was a mount with cloacal contact, while an attempted copulation was a mount without cloacal contact. Names and descriptions of these behaviour patterns follow those given by Paludan (1955) and selected quotations from his paper can be found in Appendix A.

3.3.3 ANALYSES OF DATA

In the field, data were recorded by hand on check sheets and then entered into the mainframe computer (VAX/VMS system) at Memorial University of Newfoundland. SPSS-X (Statistical Package for the Social Sciences, SPSS Inc. 1988) was used for the statistical analyses and Sigmaplot, Version 4.01, (Jandel Corporation 1990) was used for graphing.

With the data collected during the reliability sampling, counts of different dependent measures (e.g. courtship feeds, copulation attempts) were obtained by summing the frequencies of these different behaviour patterns over each h ($N = 16$ h). Each pair of scores (i.e. values for observer 1 and observer 2) was plotted, so that any systematic biases in the data could be seen. If agreement was good, the points should cluster around the line $y=x$. The two observers' scores were then correlated using the Spearman rank order statistic and if the correlation was statistically significant and $r_s > 0.7$, agreement between observers was considered to be satisfactory. In the following discussion of the results, this "y=x" plot was drawn for each variable and will be the first figure presented for each of the variables.

If r_s values (calculated from the reliability sample alone) were low for any variables, plots were done for each observer, using the entire data set, to see whether poor agreement in the relatively small amount of data sampled for inter-observer reliability was reflected in the data set as a whole. This second graph, shown for only some of the dependent variables, has a different form from that of the first graph and shows seasonal trends in the rate of occurrence of the different courtship behaviour patterns for each observer plotted separately. This was done to assess differences between the observers when data were summarized in the form desired for the functional analysis of courtship feeding in Chapter 4.

To create these graphs, data were pooled over two-day intervals from 14 days before egg laying to 10 days after laying. Rates/h were calculated for each two-day interval for each kittiwake pair and a mean of the rates for all individual pairs in each two-day period was then obtained. This same process was used to generate the graphs in Chapter 4, but there the two observers' data were combined, while in this chapter they were separated. Observers' values for each day relative to egg laying were correlated and t-tests for paired samples (two-tailed) were done to evaluate the significance of any observer bias. A parametric statistic was deemed appropriate here, as with only a few exceptions the dependent variables were normally distributed and displayed homogeneity of variances (food solicitation - variances not homogeneous, food boluses/bout - not normally distributed). A paired test was chosen because both observers were observing the same population, although not at the same time.

To assess the effect of frequency of occurrence on the reliability of recording of particular behaviours, plots were made of the average frequency of the two observers against the ratio of the smaller value/larger value for each variable, as outlined by Caro et al. (1979).

3.4 RESULTS

In this section, each of the dependent variables will be discussed in the sequence in which the behaviour patterns normally occur. The first figure for each variable uses data collected during the reliability sampling ($N = 16$ h), while the second figure, if it exists, consists of seasonal plots *using the entire data set* ($N = 190.5$ h).

1. Adult returns to the nest:

Inter-observer agreement was high and significant ($r_s = 0.80$, $n = 16$, $p < 0.001$) and points clustered closely around the y=x line (Figure 3-1). Therefore, it appears that this variable was scored reliably and no further analysis was done.

2. Adult returns followed by food solicitation:

Food solicitation bouts included instances of head-tossing and/or female food begging following adult returns to the nest. Virtually all food solicitation bouts occurred following adult returns; they were seen to occur spontaneously on only a few occasions. Inter-observer agreement was low and not significant ($r_s = 0.37$, $n = 16$, $p = 0.08$) and there was a tendency for observer 2 to score more of these than observer 1 (Figure 3-2). When seasonal plots were made using the entire data set, not just the 16 h reliability sample, a consistent difference between the two observers was obvious (Figure 3-3). The r_s value was moderate and not significant ($r_s = 0.48$, $n = 13$, $p = 0.10$) and a paired groups t-test showed a highly significant difference between observers ($t = 3.29$, $df = 12$, $p = 0.007$). Though the absolute rates differed, similar seasonal trends were obtained by both observers.

3. Courtship feeding bouts/h:

As shown by the Spearman correlation, inter-observer agreement was low, negative and not significant ($r_s = -0.14$, $n = 16$, $p = 0.32$) and there seemed to be evidence of a tendency for observer 2 to see more feeds in each hour than observer 1 (Figure 3-4). The bias was seen clearly when the data set as a whole was plotted (Figure 3-5). Because this difference was so consistent, the correlation coefficient was very high and significant ($r_s = 0.94$, $n = 13$, $p < 0.01$) and on its own indicated good reliability, but a paired groups t-test indicated the 2 observers scored significantly differently ($t = 3.51$, $df = 12$, $p = 0.004$). Again it must be noted that both observers obtained similar seasonal patterns, though the absolute rates differed,

4. Food boluses/h:

From the reliability sample, inter-observer agreement for food boluses/h was also low ($r_s = 0.05$, $n = 16$, $p = 0.43$) and there was the same consistent bias between observers (Figure 3-6). In the seasonal plots using the entire data set (Figure 3-7), the two observers were moderately but significantly correlated ($r_s = 0.59$, $n = 13$, $p < 0.05$), however, the difference in scoring was again significant in a paired groups t-test ($t = 2.16$, $df = 12$, $p = 0.05$).

5. Mean boluses/feeding bout:

Inter-observer agreement was low, negative and not significant for this variable ($r_s = -0.23$, $n = 16$, $p = 0.30$; Figure 3-8), but confidence in this conclusion is hampered by the low sample size of events (feeds). In 1/4 of the sample (4 h), neither observer recorded any feeding and in the remaining 12 h, observer 1 recorded 13 feeds and observer 2, 16 feeds. For this variable there was a tendency for observer 1 to record more boluses/feeding bout than observer 2 (Figure 3-8). An examination of the data set as a whole (Figure 3-9) resulted in a moderate, but non-significant correlation ($r_s = 0.65$, $n = 9$, $p = 0.08$) and a significant difference ($t = 2.53$, df = 8, $p = 0.04$) between observers. These analyses were done using data from day -12 to day +4 as sample sizes of events from day -14 and days +6 to +10 were small (≤ 3 feeding bouts per two day period).

6. Copulations per hour - successes, attempts and total:

From the reliability sample, inter-observer agreement was high for successful copulations (Figure 3-10; $r_s = 0.92$, $n = 16$, $p < 0.001$) and total (successes + attempts) copulations (Figure 3-11; $r_s = 0.86$, $n = 16$, $p < 0.001$), but not for attempts to copulate (Figure 3-12; $r_s = 0.34$, $n = 16$, $p = 0.10$). This pattern of results seems to indicate that observers have no trouble recognizing copulations, but classifying them as successes or attempts is more difficult. These results must be treated cautiously, however, as the sample sizes of events were low, with 5 - 8 h out of 16 h having no copulatory activity. Because reliability seemed to be satisfactory for successful and total copulations, no further analysis was done on those variables. In Figure 3-12, no clear observer bias or systematic error was seen for the variable "attempts to copulate" and that was also the case for the data set as a whole (Figure 3-13; $t = 0.35$, $df = 12$, $p = 0.73$). With the larger data set, the Spearman correlation between the rates scored by both observers indicated satisfactory agreement ($r_s = 0.71$, $n = 13$, $p < 0.02$).

7. Mean cloacal contacts/mount:

This variable showed good inter-observer reliability ($r_s = 0.81$, $n = 16$, $p = 0.03$) and only a slight tendency for observer 2 to score higher than observer 1 (Figure 3-14). Because the sample size of events (mounts) was low in the reliability sample, seasonal plots were drawn of the entire data set to see if good observer agreement was confirmed (Figure 3-15). There was no evidence of a difference between observers ($t = 0.24$, $df = 7$, $p = 0.82$), but the correlation coefficient was low and not significant ($r_s = -0.25$, $n = 8$, $p > 0.10$). These analyses were done using data from day -12 to day +2 as sample sizes of events were low on day -14 and days +4 to +10 (≤ 3 mounts per two day period).

The results of these analyses for all dependent variables are summarized in Table 3-1.

To evaluate the effect of frequency of occurrence on the reliability of recording of different behaviour patterns, frequency plots were made of each of the variables previously discussed (Figure 3-16). For several of these variables (Figure 3-16 C,E,F,G), the difference between observers decreased as the absolute rate increased. "Adult returns to the nest," (Figure 3-16 A) occurred much more frequently than the other variables and showed a different pattern, with the best agreement between the observers (smaller/larger value equal to or closest to 1) occurring at intermediate levels of activity, 8 - 12 returns pair^{-1} h^{-1}. For very high levels of activity, it may be physically impossible to record all events.

3.5. DISCUSSION

In this study of courtship feeding in kittiwakes, of seven variables examined, two were reliably scored. These were adult returns to the nest and copulations (successful, attempts and total). There were two stable characteristics which distinguished these variables from those not scored reliably. Adults returned to the nest frequently and this facilitated strong observer agreement; when a behaviour occurs infrequently, a few disagreements constitute a larger proportion of the whole than when a behaviour pattern occurs frequently. Copulations were conspicuous events, noticeable even out of the corner of the eye and consequently were seldom missed.

Five variables were not reliably scored: adult returns followed by food solicitation, courtship feeding bouts/h, food boluses/h, mean number of food boluses/feeding bout and mean number of cloacal contacts/mount. In the first three, there was evidence of systematic error: when the data were plotted separately for each observer a consistent observer bias was evident (observer 2 > observer 1, t-tests significant), while r_s was high and significant. The fourth variable, mean number of food boluses/feeding bout, also showed a consistent observer bias, but in this case observer 1 > observer 2.

These examples clearly illustrate the value of plotting the data and a limitation of the correlation coefficient. Correlations are sensitive only to random errors and if there is a source of systematic error, such as consistent over or under estimation by one observer, correlations may be high but give misleading confidence in the strength of agreement between observers. The effects of this observer bias were reduced in the overall analyses of the courtship feeding data (Chapter 4) when the data from both observers were combined. In addition, while systematic error will affect the absolute values obtained, it will not alter conclusions based on relative seasonal patterns of the different courtship displays of kittiwake. The specific effect of these reliability analyses on the conclusions of the courtship feeding study is discussed in more detail in Chapter 4.

For the fifth variable, mean number of cloacal contacts per mount, there was no systematic error, but observer correlations were low, indicating sources of random error. Adult returns followed by food solicitation also showed evidence of random error with a low and non-significant correlation. It is not always necessary to throw out data affected by random error, since any significant positive results that emerge do so despite a large amount of "noise", and thus must represent a strong effect. Low reliability has serious implications for the meaning of negative results however, as one cannot be certain whether the lack of significance simply represents no effect or is due to Type II error.

There are many possible reasons for the poor inter-observer agreement, the chief among which may be the lack of experience and training of both observers. Neither observer had done detailed behavioural observations before, and only 6 h were spent on training. Research by others has shown that reliability estimates will be affected by the amount of training the second observer receives. Work done by Caro et al. (1979) showed the importance of experience with the task at hand in obtaining observer agreement: three out of the four observers had watched kittens for many months and yet they were not significantly correlated on all measures. As the sessions subjected to reliability check were spread throughout the data collection period, they could have provided an opportunity for additional training. However due to the low rate of occurrence of many of the behaviour patterns and the insufficient time devoted to reliability check, it was not clear in the field that any correction was needed.

Poor reliability may also be a result of the low frequency at which some behaviour patterns occur. On average, feeding occurred slightly less than once in every 5 h on a per nest basis (from Figure 3-5, at day -2, observer 2 = 0.21 feeds/h and observer 1 = 0.14 feeds/h, mean = 0.18 feeds/h). Successful copulations occurred even less often, reaching a maximum at day -6 of 0.13 copulations/h (Figure

4-6 in Chapter 4), but as they are much more obvious and dramatic events than feeds, they were not as likely to be affected by the reduced vigilance that comes with periods of low activity. It may be possible to improve reliability for feeds by using only the morning hours, which typically are the peak daily feeding times (J.W. Chardine, pers. comm.), for observer comparison.

Better choice of variables to score may also have helped to improve reliability. Some behaviours occurred very frequently at times (adult returns, the greeting ceremony and whether a returning bird was carrying nest material) and in an effort to record all of these, observers may have missed recording feeds as accurately as might have been possible.

Definitions of the behaviour patterns were also a problem in some cases. This was particularly true for food solicitation. Begging and head-tossing were originally scored separately, but then combined for the final analyses into the single category of food solicitation, because it was often difficult to tell when head-tossing had stopped and begging had begun, or sometimes to identify which behaviour was occurring. If the decision had been made to make head-tossing and female food begging one category before scoring began, reliability might have been improved. Another difficulty was in determining whether a particular behaviour, such as begging, was part of one bout (the same sequence) or the next bout (a different sequence). In theory, behaviours were considered to be within the same sequence if they followed within two minutes of the previous behaviour, but in the field this proved difficult to track.

Ten behaviour categories were observed (adult returns, sex of returning bird, nest material, greeting ceremony, begging, head-tossing, feeding, number of boluses, copulation attempts and successes), but in the end copulation and the different measures of feeding proved to be most useful as a means of differentiating between hypothesized functions of courtship feeding. In addition, 28 nests were too many to watch for scoring as detailed as was originally planned. Different scanning rates may have produced much of the variation in whether a behaviour was observed or not, and the initial assumption, that courtship feeding and copulation occurred sufficiently infrequently to permit recording of all occurrences, may have been incorrect. This demonstrates the value of a trial study to determine what to observe and the sample sizes needed.

An assessment of observer drift (the tendency of observers to change the manner in which they apply the definitions of the behaviour patterns over time; Kazdin 1977) was planned when sessions at the beginning, middle and end of the data collection period were coded by two observers. This proved impossible to do as too small a proportion of the data was sampled for reliability, resulting in sample sizes too small to examine for seasonal differences. As a rule of thumb, 20% of the data should be subjected to reliability check (S. Goldberg, pers. comm.), and in this case only 8% or 16 h were. Sixteen h also represents insufficient time for the assessment of reliability in behaviour patterns which occur relatively infrequently. For example copulation attempts had a low Spearman correlation in the reliability sample but the correlation between observers was high and significant when the data set as a whole was used.

Reliability could be improved by spending more time on the training of observers. The use of videotaped sessions would be useful for training purposes, and reliability sessions themselves should be videotaped, with scoring done from the tapes used as the standard against which to evaluate the accuracy of the observers. That was a shortfall of this study; reliability was often unsatisfactory, but because there was no pre-established standard against which to compare the results, it was impossible to say which observer was having difficulties.

It is also important to estimate the influence of assessment circumstances on observer reliability. Observers who know they are being assessed maintain high levels of agreement during assessment, but not during covertly monitored sessions (Reid 1970, Taplin and Reid 1973).

Inter-observer agreement is a subject seldom addressed when observations of seabird behaviour have been made. However, if the difficulties discovered in this study are at all representative of field observations of animal behaviour in general and avian behaviour in specific, more effort should be spent by researchers in this field on the assessment of inter-observer reliability.

Table 3-1

A summary of the results of the analyses of inter-observer reliability in the study of courtship feeding in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.

Variable	Reliability (16 h)		All data (190.5 h)				
	r_s value	p	r_s value	p	Paired t-test	df	Type of error
Adult returns	high	$p < 0.001$	-		-		reliable
Returns followed by food solicitation	low	n.s.	low	n.s.	$p < 0.001$	12	random, systematic
Feeding bouts/h	low	$p < 0.01$	high	$p < 0.01$	$p < 0.01$	12	systematic
Food boluses/h	low	n.s.	moderate	$p < 0.05$	$p = 0.05$	12	systematic
Boluses/feeding bout	low	n.s.	moderate	$p = 0.08$	$p < 0.05$	8	systematic
Copulations/h							
Successes	high	$p < 0.001$	-		-		reliable
Attempts	low	n.s.	high	$p < 0.02$	n.s.	12	reliable
Total	high	$p < 0.001$	-		-		reliable
Cloacal contacts/mount	high	$p < 0.05$	low	n.s.	n.s.	7	random

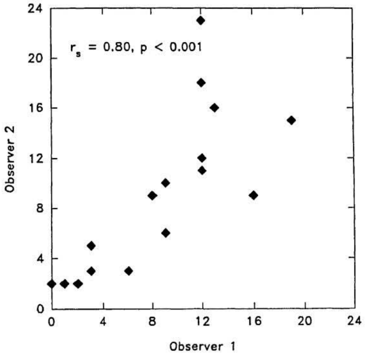


Figure 3–1 – Correlation between observer 1 and observer 2 in returns to the nest (mean/pair/h) in adult Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. From the reliability sample (16.0 h). Each point represents 1 score by each observer.

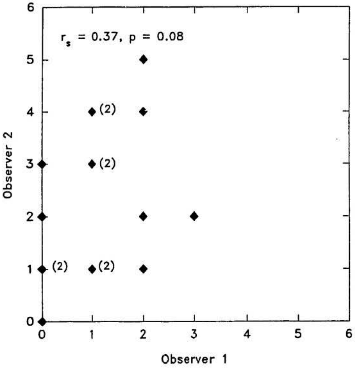
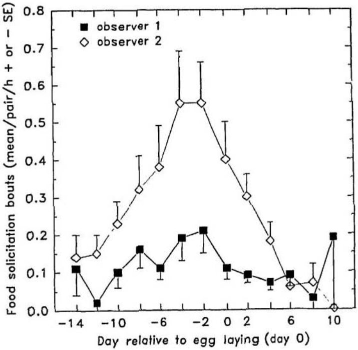


Figure 3–2 – Correlation between observer 1 and observer 2 in food solicitation bouts (mean/pair/h) in adult Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. From the reliability sample (16.0 h). Unless otherwise indicated, each point represents 1 score by each observer.



$r_s = 0.48$, $p = 0.10$
paired t-test: $t = 3.29$, $df = 12$, $p < 0.01$

Figure 3-3 – Seasonal changes in food solicitation bouts (mean/pair/h) in adult Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. For each observer shown separately.

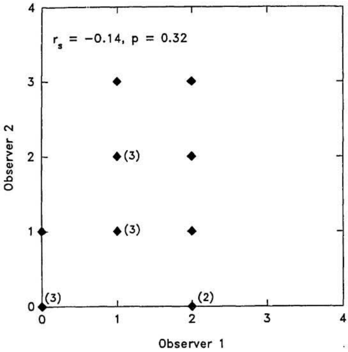
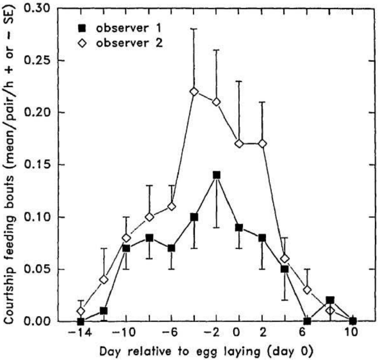


Figure 3–4 – Correlation between observer 1 and observer 2 in courtship feeding bouts (mean/pair/h) in Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. From the reliability sample (16.0 h). Unless otherwise indicated, each point represents 1 score by each observer.



$r_s = 0.94$, $p < 0.01$
paired t-test: $t = 3.51$, $df = 12$, $p < 0.01$

Figure 3–5 – Seasonal changes in courtship feeding bouts (mean/pair/h) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. For each observer shown separately.

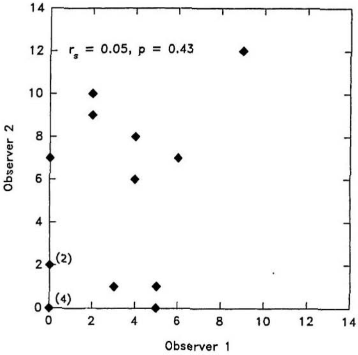
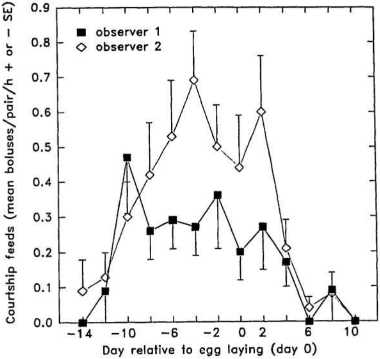


Figure 3–6 – Correlation between observer 1 and observer 2 in courtship feeds (mean boluses /pair/h) in Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. From the reliability sample (16.0 h). Unless otherwise indicated, each point represents 1 score by each observer.



$r_s = 0.59$, $p < 0.05$
paired t−test: $t = 2.16$, $df = 12$, $p = 0.05$

Figure 3−7 − Seasonal changes in courtship feeds (mean boluses/pair/h) in Black−legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. For each observer shown separately.

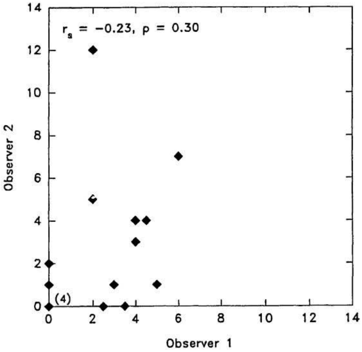
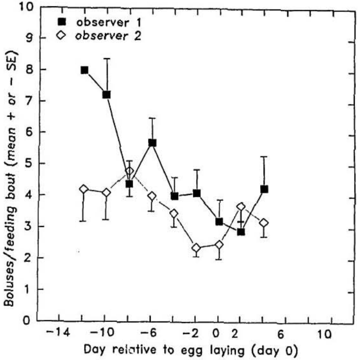


Figure 3–8 – Correlation between observer 1 and observer 2 in boluses/courtship feeding bout (mean number) in Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. From the reliability sample (16.0 h). Unless otherwise indicated, each point represents 1 score by each observer.



$r_s = 0.65$, $p = 0.08$
paired t−test: $t = 2.53$, $df = 8$, $p \approx 0.04$

Figure 3−9 − Seasonal changes in boluses/courtship feeding bout (mean number) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. For each observer shown separately.

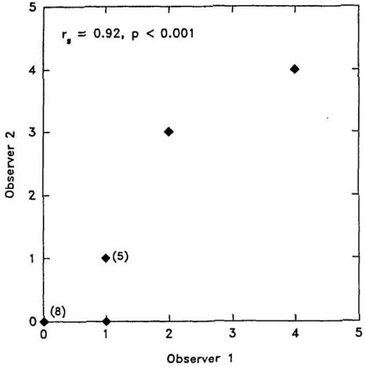


Figure 3–10 – Correlation between observer 1 and observer 2 in successful copulations (mount with cloacal contact – mean/pair/h) in Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. From the reliability sample (16.0 h). Unless otherwise indicated, each point represents 1 score by each observer.

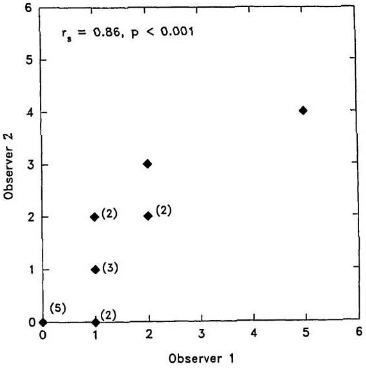


Figure 3–11 – Correlation between observer 1 and observer 2 in total copulations (successes + attempts – mean/pair/h) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. From the reliability sample (16.0 h). Unless otherwise indicated, each point represents 1 score by each observer.

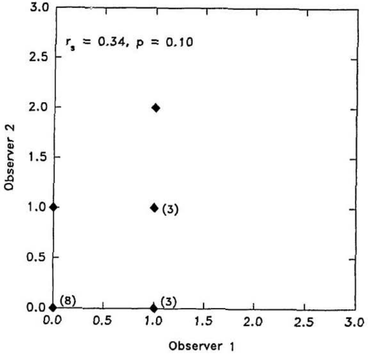
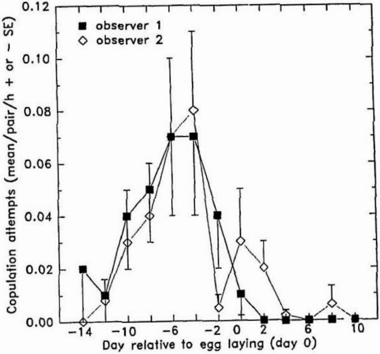


Figure 3-12 – Correlation between observer 1 and observer 2 in copulation attempts (mount, no cloacal contact – mean/pair/h) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. *From the reliability sample* (16.0 h). Unless otherwise indicated, each point represents 1 score by each observer.



$r_s = 0.71$, $p < 0.02$
paired t−test: $t = 0.35$, $df = 12$, $p = 0.75$

Figure 3−13 − Seasonal changes in attempts to copulate (mount, no cloacal contact − mean/pair/h) in Black−legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. For each observer shown separately.

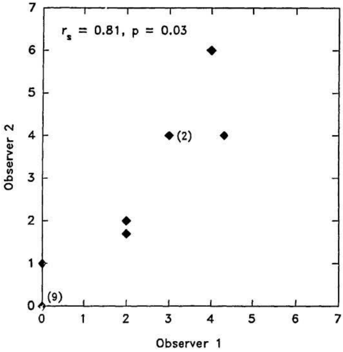
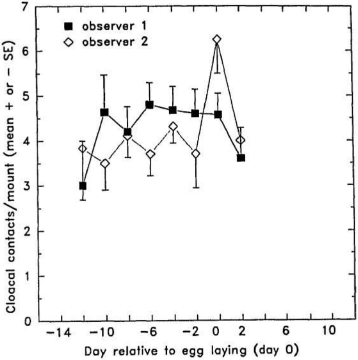
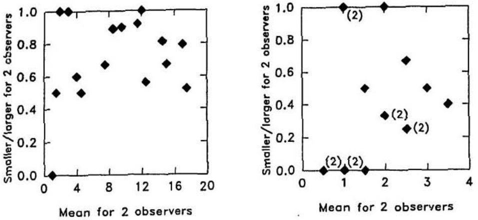


Figure 3–14 – Correlation between observer 1 and observer 2 in cloacal contacts/mount (mean number) in Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. From the reliability sample (16.0 h). Unless otherwise indicated, each point represents 1 score by each observer.



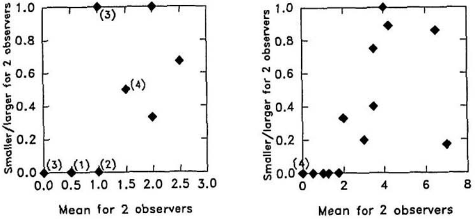
$r_s = -0.25$, $p > 0.10$
paired t-test: $t = 0.24$, df = 7, $p = 0.82$

Figure 3−15 − Seasonal changes in cloacal contacts /mount (mean number) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. For each observer shown separately.



A. adult returns/pair/h

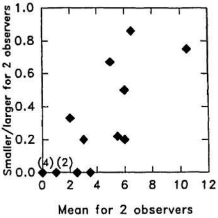
B. food solicitation bouts/
pair/h



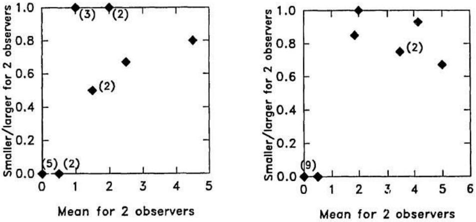
C. courtship feeding bouts/
pair/h

D. mean boluses/courtship
feeding bout

Figure 3-16 – Frequency plots of the different courtship behaviours in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. Unless otherwise indicated, each point represents 1 score by each observer.



E. food boluses/pair/h



F. total copulations/pair/h

G. mean cloacal contacts/mount

Figure 3–16 continued – Frequency plots of the different courtship behaviours in Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. Unless otherwise indicated, each point represents 1 score by each observer.

3.6 REFERENCES

Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour, 48, 1-41.

Caro, T.M., R. Roper, M. Young, and G.R. Dank. (1979). Inter-observer reliability. Behaviour, 69, 303-315.

Cramp, S. (ed.) (1983). Handbook of the Birds of Europe, the Middle East and North America. Volume 3, (pp. 863-875). Oxford University Press: Oxford.

Hartmann, D.P. (1977). Considerations in the choice of interobserver reliability estimates. Journal of Applied Behavior Analysis, 10, 103-116.

Hollenbeck, A.R. (1978). Problems of reliability in observational research. In: Observing Behavior, Vol.II, Data Collection and Analysis Methods (ed. by G.P. Sackett), pp. 79-98. University Park Press: Baltimore.

Jandel Corp. (1990). Sigmaplot, Version 4.01. Jandel Scientific: Corte Madera, California.

Johnson, S.M. and O.D. Bolstad (1973). Methodological issues in naturalistic observation: some problems and solutions for field research. In: Behavior Change (ed. by L.A. Hammerlynck, L.C. Handy and E.J. Mash), pp. 7-67. Research Press: Champaigne, Illinois.

Kazdin, A. E. (1977). Artifact, bias and complexity of assessment: the ABC's of reliability. Journal of Applied Behavior Analysis, 10, 141-150.

Martin, P. and P. Bateson. (1986). Measuring Behaviour: An Introductory Guide. Cambridge University Press: Cambridge.

Mash, E.J. and J.D. McElwee. (1974). The effects of prior information and behavioral predictability on observer accuracy. Child Development, 46, 513-519.

Paludan, K. (1955). Some behaviour patterns of Rissa tridactyla. Vidensk. Medd. fra Dansk. Naturh. Foren., 117, 1-21.

Reber, R.S. (1985). The Penguin Dictionary of Psychology. Penguin Books: London.

Reid, J. B. (1970). Reliability assessment of observation data: a possible methodological problem. Child Development, 41, 1143-1150.

Sokal, R.R. and F.J. Rohlf. (1981). Biometry, 2nd edition. W.H. Freeman: San Francisco.

SPSS Inc. (1988). SPSS-X User's Guide, 3rd edition. Chicago.

Taplin, P.S. and J.B. Reid. (1973). Effects of instructional set and experimenter influence on observer reliability. Child Development, 44, 547-554.

Chapter 4

THE FUNCTIONAL SIGNIFICANCE OF COURTSHIP FEEDING IN BLACK-LEGGED KITTIWAKES

4.1 ABSTRACT

The aim of this study was to investigate two hypothesized functions of courtship feeding: that it has nutritional importance to the female and that it facilitates copulation. Observations were carried out on Black-legged Kittiwakes at Cape St. Mary's, Newfoundland in May, 1990. Kittiwake courtship displays were monitored in two study plots (N = 51 nests) using continuous sampling. Time spent daily in observation by two observers averaged 7.9 h (Total = 190.5 h). Timing of laying, clutch size and hatching and fledging success were also recorded. An examination of inter-observer reliability in the collection of behavioural data was made in the context of the courtship feeding study. Results of these analyses indicated that conclusions based on the absolute rate of courtship displays should be made with caution, while conclusions based on seasonal changes in these displays may be made with confidence.

Despite these qualifications, data confirmed the nutritional importance of courtship feeding to the female. Seasonal increases in the frequency of food solicitation and courtship feeding coincided with the beginning of yolk formation in kittiwakes, and reached a peak of approximately 8 boluses/day at 4 days before egg laying when the energy demands caused by the developing follicles may be the greatest. However courtship feeding rate was not significantly correlated with laying date, clutch size, hatching success or fledging success.

Evidence confirming the role of courtship feeding in facilitating successful copulation was more ambiguous. Although courtship feeding was

not essential for successful copulation, if feeding did occur, subsequent copulations were significantly more likely to be successful (end in cloacal contact). However, the quantity of food given did not appear to increase the likelihood of copulation success. The rate of successful copulations was positively correlated with courtship feeding rate and showed a similar seasonal pattern of increase. There was no seasonal variation in the proportion of total copulations which were successful or in the number of cloacal contacts/mount.

4.2 INTRODUCTION

The courtship behaviour of some seabird species, in particular gulls, terns and skuas, includes feeding of the female by her mate - this is called "courtship feeding". There are a number of hypothesized functions for courtship feeding in seabirds, the most important of which are: 1) pair formation and/or maintenance (Lack 1940), 2) facilitation of copulation (Brown 1967, Tasker and Mills 1981) and, 3) the provision of additional food at the time of egg formation (Royama 1966, Brown 1967, Krebs 1970, Nisbet 1973). Determining the ultimate function of courtship feeding in Black-legged Kittiwakes is beyond the scope of this study, but the current research provides evidence bearing on the last two hypotheses: that courtship feeding in Black-legged Kittiwakes increases the likelihood that copulation attempts will be successful (end in cloacal contact) and that it has nutritional importance to the female.

Courtship feeding was originally believed to be important only in the establishment and maintenance of pair bonds between male and female partners (Lack 1940). In this context, courtship feeding may have an intrinsic, symbolic value, in addition to providing practical information for the females in mate choice (Nisbet 1973). In species among which it occurs, courtship feeding rates have been positively correlated with average egg size and clutch size (Nisbet 1977) and are a predictor of the male's future performance in feeding the chicks (Nisbet 1973, Niebuhr 1981). This information would probably not be of use in the current season, as courtship feeding reaches a peak so close to the time of egg laying that any females looking for a new mate so late in the season would be at a considerable disadvantage (Nisbet 1973, Tasker and Mills 1981). In Common Terns, males seeking a mate carry fish around the colony and display to unmated females, but do not feed them regularly until pairs become established (Nisbet 1973). It is possible that during this early phase of courtship, females can evaluate the quality of a prospective mate by assessing the type and length of prey selected by the male for display (Taylor 1979).

There is now no doubt that in some species courtship feeding must also be important in the nutrition of the female during the period of egg formation (Royama 1966, Brown 1967, Krebs 1970, Nisbet 1973, 1977, Tasker and Mills 1981, Morris 1986). Courtship feeding may be particularly important in gulls and terns, since the females of these species produce a comparatively expensive clutch, the three eggs together comprising some 29% (mean value for Laridae) of their body mass. This is a greater proportion than in most avian families (Hunt 1980). Direct evidence of the nutritional importance of courtship feeding has been provided for the Common Tern; Nisbet (1973) showed that the total fresh mass of the clutch and the fresh mass of the third egg were correlated with the amount of food given to the female. Fledging success from third eggs was positively related to the masses of those eggs. The amount of food brought to the female during courtship feeding was therefore an important factor influencing breeding success. Subsequent research by Nisbet (1977) corroborated this by determining that the amount of food that males can provide is a factor limiting both the number and size of the eggs a female can lay.

Additional circumstantial evidence attesting to the nutritional importance of courtship feeding for egg formation can be found in the phenology of this behaviour in relation to egg laying. Several researchers have shown that courtship feeding in gulls begins to increase in frequency roughly 14-20 days before the first egg is laid, reaching a peak at 6-14 days before egg laying (Brown 1967, Niebuhr 1981, Tasker and Mills 1981, Chardine 1987). The differences in timing depend upon the species, for example Roudybush et al. (1979) determined that yolk formation in Herring Gulls took 11-13 days, and Niebuhr (1981) found a peak in courtship feeding in this species occurring about 14 days before egg laying. In kittiwakes, yolk formation takes 9 days (Roudybush et al. 1979) and in Chardine's (1987) study of that species, courtship feeding began to increase in frequency 14 days before egg laying, reaching a peak at 6-8 days before egg laying. The connection between the peak of courtship feeding and the beginning of yolk formation seems a close one.

In their study of the Red-billed Gull, Tasker and Mills (1981) further attested to the nutritional importance of courtship feeding. Peak courtship feeding rates averaged four feeds/day, with up to 28 g of euphausiids/feed. The rapid increase in the frequency of courtship feeding coincided with the beginning of egg formation and the peak of feeding occurred at the time of most rapid yolk deposition. In addition, Tasker and Mills (1981) demonstrated that females who were fed at a high rate by their partners did not have to spend as much time foraging as "inadequately" fed females.

Tasker and Mills (1981) also considered that courtship feeding contributed to successful copulation by stimulating the male to mount while making the female more receptive. Their data show that the greater the quantity of food given, the greater the probability cloacal contact would occur. Courtship feeding was not essential though, as copulations were seen to occur in its absence. This was also found to be true for Lesser Black-backed Gulls (Brown 1967), Herring Gulls, (Niebuhr 1981), and kittiwakes (Chardine 1987) among other species.

Chardine (1987) analyzed differences in the frequency of courtship feeding between pairs that retained their mates from the previous year (SAME) and those pairs that changed mates (CHANGE). The pattern of courtship feeding was very similar in each group. However, the earliest courtship feeding seen in CHANGE pairs occurred a week before the earliest feeding in SAME pairs, providing some evidence for the importance of feeding in establishing the pair bond.

When the performance of individual males in courtship feeding is positively correlated with the number and/or size of the eggs laid by their mates (Nisbet 1973, 1977), one may conclude that courtship feeding has nutritional importance. This has a potential confound. Clutch size and egg size may be limited by characteristics of the female. "High quality" males are often mated with "high quality" females (high quality as measured by their performance in bringing food to their chicks, Nisbet 1977). One way of measuring the female's contribution to final clutch and/or egg size may be through an analysis of her begging behaviour during courtship - begging rate may be important in determining how actively the male forages for her.

In this study, the nutritional importance of courtship feeding will have been supported if 1) the frequency of feeds increases, reaching a peak approximately 9 days before egg laying, coinciding with the beginning of yolk formation and 2) the feeding rate is positively correlated with such measures of reproductive success as laying date, clutch size, and hatching and fledging success. Evidence that courtship feeding facilitates copulation will have been obtained if 1) the feeding rate is positively correlated with the rate of copulation, 2) successful copulation (i.e., with cloacal contact) is more likely to occur with prior feeding, and 3) the size of prior feedings affects the success of subsequent mounts.

4.3 METHODS

4.3.1 THE STUDY SITE

This study was conducted at Cape St. Mary's, Newfoundland (46°50'N and 54°12'W) from 8 to 31 May, 1990. For more information on this location and a map see Figure 2-1 and section 2.3.1. Two study plots were established one above the other 75 - 100 m above the sea on a shear cliff face in a narrow chasm in the rock and were viewed with 8.5 x 44 binoculars from a rocky promontory approximately 25 m away on the other side of the chasm. No blind was used as the presence of observers did not appear to affect the birds. This location was chosen as it permitted a good view of the birds and nest contents and permitted the closest approach to nesting kittiwakes at Cape St. Mary's, important criteria at a colony known for much spring fog.

Both behavioural and breeding success data were collected from the group of 28 nests found in the highest study plot. The second study plot included 23 nests, and the initial plan was to use these to increase the sample sizes for the parameters of breeding success (laying date, clutch size, chick mortality and fledging success). However, approximately two weeks into the study (21 May), a decision was made to include these nests in behavioural observations as well.

4.3.2 COLLECTION OF DATA

4.3.2.1 Schedule of Observations and Sampling Effort

Observations were made at Cape St. Mary's during the courtship and egg laying period from 8 to 31 May, 1990. Visits to the study site were made daily during that time, weather permitting. No behavioural observations were carried out when it was raining heavily or snowing. One-day visits were made on 10 June, 18 July and 5 August to obtain data on hatching and fledging success.

Prior to 8 May, 6 hours were spent by both observers practising with the specific coding scheme and data sheets to be used. From 8 May, time spent daily in continuous observation ranged from 1 to 15 h and averaged 7.9 h (Total = 190.5 h). Observers worked in rotating shifts (mean length = 2.9 h) throughout the day, alternating from day to day in taking the first shift. This was to ensure that each observer contributed equally to data collected at all times of the day. Study plot 1 (28 nests) yielded 4578 nest-hours of observation, and study plot 2 (23 nests) yielded 621 nest-hours due to the delay in including this plot in the behavioural sample. Table 4-1 shows information on seasonal changes in sampling effort. On four days, all-day watches from 0600 to 2100 were carried out. A somewhat larger percentage of the observations were conducted in the morning (Figure 4-1) than at other times of the day as previous research on kittiwakes (J.W. Chardine, pers. comm.) had shown that courtship feedings occurred at a higher rate at that time of day. However, an effort also was made to obtain a representative sample from the remainder of the daylight hours.

4.3.2.2 Collection of Breeding Success Data

Clutch size, and hatching and fledging success were recorded for the 51 nests in study plots 1 and 2. Initial clutch size was accurately determined on daily visits to the study plots during the egg laying period. Nests were scanned until all incubating birds had either stood up or shifted their position sufficiently to make nest contents visible. Hatching and fledging success were obtained in three visits to the study plots during the chick rearing period. Hatching success was defined as the proportion of eggs laid that hatched. In cases where the number of chicks in a given nest did not equal the clutch size on the previous visit, it was assumed that this was caused by egg loss, leading to a conservative value for hatching success and perhaps inflating fledging success. Chicks 35 days of age or older when last seen were considered to have fledged and fledging success was defined as the proportion of chicks hatched that fledged.

4.3.2.3 Behavioural Observations

Kittiwake courtship behaviour patterns were monitored using continuous (all occurrences) sampling (Altmann 1974); the subjects were watched continuously and the frequency and duration of all behaviours were recorded. At the beginning of their shifts, observers began by scanning the nests to look for courtship feeding or copulation. If neither activity was seen, the observer waited for the next returning adult to begin recording. Courtship feeding and copulation occurred sufficiently infrequently that it was possible to record all occurrences of each behaviour, although if these events occurred simultaneously at different nests, details such as food boluses and cloacal contacts could be recorded only for the first nest noticed. Behaviour patterns scored for each nest were as follows:

- male and female returns of birds to the nest
- head-tossing
- female food begging
- courtship feeding bouts/h
- food boluses/feeding bout
- copulation attempts (mount, no cloacal contact)
- copulation successes (mount with cloacal contact)
- cloacal contacts/mount

Names and descriptions of these behaviour patterns follow those given by Paludan (1955) and can be found in Appendix C. As courtship behaviour in the kittiwake occurs in specific sequences (Chardine 1983, Paludan 1955) and as the performance of at least portions of the sequence appear to be essential if courtship feeding or copulation are to occur (Chardine 1983), all the above behaviours were recorded, not just those directly concerned with courtship feeding behaviour. Begging and head-tossing were scored separately, but combined for the final analyses into the single category of food solicitation, because it was often difficult to tell when head-tossing had stopped and begging had begun, leading to observers applying different criteria to when a particular behaviour started or terminated.

Behaviours were considered to be within the same sequence if they followed within 2 min of the previous behaviour. Thus, a feeding bout was considered to have ended when 2 min had passed with no feeding or begging on the part of the female. A food bolus was defined as any discrete packet of food swallowed by the female, regardless of size. Spot observations of the number of birds (0, 1 or 2) at each nest site were made every 10 min to determine attendance patterns.

4.3.2.4 Inter-observer Reliability

As some of the behavioural dependent measures may have involved subjective judgements on the part of observers, inter-observer reliability was assessed. For example, it was sometimes difficult to see whether a food bolus was transferred, or to determine whether a particular behaviour, such as begging, was part of one bout (the same sequence of behaviours) or the next bout (a different sequence). In the examination of observer agreement, the two observers simultaneously scored events taking place in the same nests (study plot 1, N = 28) in six sessions ranging in length from 1.3 to 3 h. The sessions were scheduled over 4 days to cover the beginning, middle and end of the entire data collection period, in an attempt to prevent observer drift, the tendency of observers to change the manner in which they apply the definitions of the behaviour patterns over time. The sessions scored by two people represented 8% (16.0 h/190.5 h) of the total data set.

As inter-observer reliability is rarely examined in the field collection of behavioural data from wild animals, a discussion of the issues surrounding reliability in observational research, and a detailed presentation of the inter-observer reliability obtained in this study are presented in Chapter 3.

4.3.3 ANALYSES OF DATA

In the field, data were recorded by hand on data sheets and then entered into the mainframe computer (VAX/VMS system) at Memorial University of Newfoundland. SPSS-X (Statistical Package for the Social Sciences, SPSS Inc. 1988) was used for the statistical analyses and Sigmaplot, Version 4.01, (Jandel Corporation 1990) was used for graphing.

In order to evaluate seasonal trends in the rate of occurrence of behaviour patterns associated with courtship, data from both observers was averaged and then pooled over two-day intervals from 14 days before egg laying to 10 days after laying. Days before egg laying were identified with a "-", while those after egg laying were identified with a "+". Rates/h of the different behaviour patterns were calculated for each two-day interval for each pair and summarized, taking a mean of the rates for all individual pairs in each two-day period. The chi-squared test was used over tabulated data to test for seasonal changes in the number of boluses/feeding bout and the number of cloacal contacts/mount. Regression analyses were done to examine seasonal changes in the proportion of bouts of food solicitation followed by courtship feeding, the influence of multiple boluses on the success of subsequent copulations and the effect of season on the proportion of all copulations involving cloacal contact. The null hypothesis was rejected if $p < 0.05$.

In the reliability analyses, the two observers' total counts in each time period ($N = 16$) were correlated using the Spearman rank order statistic. If the correlation was statistically significant and $r_s > 0.7$, the observers were considered to be reliable on that measure. For the parametric Pearson correlation, $r > 0.7$ is often used as the cutoff between agreement/nonagreement as it indicates that 50% of the variance in one set of scores is accounted for statistically by the other set ($r^2 = 0.49$) (Martin and Bateson 1986). As the Pearson correlation and the Spearman rank correlation yield similar values when calculated for the same data (Sokal and Rohlf 1981), $r_s > 0.7$ was taken as the minimum acceptable level for reliability in this study.

4.4 RESULTS

4.4.1 INTER-OBSERVER RELIABILITY

As mentioned previously, detailed results of the analyses of inter-observer reliability are presented in Chapter 3 (for a summary see Table 3-1), however in this chapter they will be summarized again briefly to clarify the implications they have for any conclusions regarding the functions of courtship feeding.

Variables scored reliably were: rate of adult returns to the nest and rate of copulations (successful, attempts and total). The remaining five variables examined showed less satisfactory agreement:

(1) rate of adult returns followed by food solicitation
(2) courtship feeding bouts/h
(3) food boluses/h
(4) mean number of food boluses/bout
(5) mean number of cloacal contacts/mount

For variables (1) to (3), plots of each observer's data showed evidence of a consistent observer bias with observer 2 > observer 1 (t-tests for paired samples, two-tailed, significant for each variable). Variable (4) also showed evidence of systematic error, however in this case observer 1 > observer 2 (t-test for paired samples, two-tailed, $p < 0.05$). For variable (1) correlations were low, indicating random error in addition to the systematic error. For the last variable, mean number of cloacal contacts/mount, there was no observer bias, but correlations were low, indicating random error.

4.4.2 SEASONALITY OF COURTSHIP DISPLAYS

There was clear seasonal variation in the rates of adult returns to the nest, food solicitation, courtship feeding and copulation in kittiwakes (Figures 4-2, 4-3); all showed an increase roughly 12 days before egg laying and reached their peaks from 6 to 2 days before egg laying. Both courtship feeding (mean = 0.20 bouts/h, SE = ± 0.05) and total copulations (mean = 0.18 mounts/h, SE = ± 0.03) were relatively rare events, occurring at most once every 5 h/pair, while adult returns (mean = 1.13 returns/h, SE = ± 0.23) occurred on average once pair^{-1} h^{-1}. Copulation reached a peak before courtship feeding and then dropped off sharply once egg laying began, while feeds remained high for an additional 2 days.

Rates of bouts of food solicitation followed the same pattern of seasonal change (Figure 4-3) as feeding bouts/h. As females begged more frequently, they were fed more frequently. Seasonal differences in the proportion of begging bouts resulting in feeding showed an increase in the proportion of begging bouts followed by courtship feeding as the date of egg laying approached, $r = 0.84$, $p < 0.01$, N =

10 (Figure 4-4).

Courtship feeding bouts (Figure 4-5) started to increase at day -12 and reached their peak at day -2; levels remained high until day +2 and then dropped off sharply. On the other hand, there was a significant seasonal difference in feed size, as measured by food boluses/feeding bout (on tabulated data, 1 & 2, 3-5, 6+ boluses/bout, using days -14 to 0, Chi-squared = 35.51, df = 14, p = 0.001), and Figure 4-6 indicates that feeds were larger earlier in the season. However, the variable that most clearly represents changes in quantity of food fed may be food boluses/h (Figure 4-7), which integrates variation in feeding rates and boluses/feed. The mean (pair^{-1} h^{-1}) of boluses fed started to increase at day -12, reached a peak at day -4, and then levels remained high until day +2.

Figure 4-8 shows the changes in the frequency of total copulations, successful copulations and attempts to copulate relative to the date of egg laying. At day -12, copulations started to increase at a steady rate until a peak was reached at day -6 and then started to decrease, falling to almost zero when the clutch was complete at day +2. Copulations early in the season were as likely to be successful (achieve cloacal contact) as those later in the season, r = 0.41, p = 0.22 (Figure 4-9). However, successful copulations can vary in the number of cloacal contacts/ mount and thus, perhaps, in the amount of sperm transferred. When graphed the data showed a clear upward trend with increased numbers of cloacal contacts/mount as the date of laying approached (Figure 4-10), however this trend was not significant (on tabulated data, 1 & 2, 3-5, 6+ cloacal contacts/mount, Chi-squared = 17.82, df = 14, p = 0.22).

4.4.3 COURTSHIP FEEDING RATE AS A PREDICTOR OF REPRODUCTIVE SUCCESS

Feeding rate (boluses/h) was not significantly correlated with such general measures of reproductive success as laying date, clutch size and number of chicks hatched/nest and number fledged/nest (Table 4-2). Overall breeding success was high: mean clutch size = 2.02, hatching success = 79%, fledging success = 92% and mean number chicks/nest fledged = 1.41. (See Chapter 2 for more information on breeding success at Cape St. Mary's in 1990.) Feeding rate was significantly correlated with mean rate of food solicitation bouts, r = 0.57, p < 0.01 (Table 4-2).

4.4.4 COURTSHIP FEEDING AS A PREDICTOR OF COPULATION SUCCESS

Although 60% of successful copulations occurred without prior feeding, if feeding occurred, subsequent copulation was significantly more likely to be successful than if feeding had not occurred (Table 4-3, Chi-squared = 6.08, df = 1, $p < 0.05$). Prior feeding thus increased the proportion of subsequent copulations which were successful, but was obviously not essential for successful copulation to occur.

The correlation between feeding rate (boluses/h) and rate of successful, but not total, copulations was statistically significant, $r = 0.41$, $p < 0.05$ (Table 4-[illegible]). In Figure 4-11, feed size (number of boluses/bout) had no significant effect on the success of subsequent copulations.

4.5 DISCUSSION

4.5.1 INTER-OBSERVER RELIABILITY

The two variables scored reliably were rate of adult returns to the nest and rate of copulations (successes, attempts and total). There were two characteristics which distinguished these variables from those not scored reliably. Adults returned to the nest frequently and this facilitated strong observer agreement; when a behaviour occurs infrequently, a few disagreements constitute a larger proportion of the whole than when a behaviour pattern occurs frequently. Copulations are conspicuous events, noticeable even out of the corner of the eye, and consequently are seldom missed.

In the final evaluation of seasonal trends in the different courtship behaviour patterns, data from both observers were averaged as observation time was shared equally by both observers. This may lessen the impact of observer bias in those variables exhibiting systematic error (food solicitation, feeding bouts and food boluses/h and boluses/feeding bout). Thus, conclusions based on the absolute rate at which a behaviour pattern occurs (for example, feeds/h) should be interpreted somewhat cautiously. However, conclusions based on the seasonality of courtship displays (for example, courtship feeding was found to increase and reach a peak on the same day by both observers) are probably valid.

Random errors are potentially not so serious as systematic errors, as any significant results that emerge do so despite "noise" in the data and must represent a strong effect. However, random error does affect interpretation of any negative results obtained by increasing Type II error.

Possible reasons for the poor agreement and suggestions for improvement are outlined in Chapter 3. However, despite the above qualifications and reservations, there is evidence that courtship feeding plays a dual role, being nutritionally important to the female and acting as an inducement for successful copulation. This evidence will be examined in the following sections.

4.5.2 The NUTRITIONAL IMPORTANCE OF COURTSHIP FEEDING

The frequency of courtship feeding was seen to increase rapidly from 10 to 8 days before egg laying, coinciding with the beginning of yolk formation, which takes 9 days in kittiwakes (Roudybush et al. 1979). Chardine (1987) found that courtship feeding in kittiwakes began to increase in frequency at -14 days and reached a peak at -6 to -8 days. In this study the peak of courtship feeding (boluses/h) occurred at 4 days before egg laying, somewhat later than expected, but perhaps that was the time of the most rapid yolk deposition as laying of the first egg would occur in 4 days and the development of the yolk of the second laid egg must be well advanced.

At the peak of courtship feeding the male fed the female 0.50 (± 0.09) boluses/h (Figure 4-7). With 16 h of daylight the female would then receive approximately 8 boluses in a day. While no estimation of bolus size was made in this study, subjective observations indicated that many boluses could be substantial chunks of fish or whole capelin. Thus, they could represent a large proportion of her daily intake of food.

The value of 8 boluses/day may slightly overestimate daily feeding rate as a somewhat larger percentage of the observations were conducted in the morning than at other times of the day. However, daily observation periods averaged approximately 8 h and an effort was made to obtain a representative sample from the rest of the day. It is not likely that feeding occurred away from the nest as spot observations, made every 10 min of the number of birds at each nest site, determined that both adults were away from the nest together only 5% of the time in the 2 weeks prior to egg laying.

In contrast, there were some results that seemed to provide evidence contrary to the nutritional importance of courtship feeding; feeding rate (boluses/h) was not significantly correlated with any of the general measures of reproductive success, laying date, clutch size, chicks hatched/nest and fledged/nest. As mentioned, breeding success was very high at Cape St. Mary's in 1990 and because of this there may have been too little variability in breeding success for any relationship with feeding rate to appear. Although there was variability in feeding rates, as shown by error bars in the previous figures, food supplies may have been more than the necessary minimum for all bird pairs. The variability in feeding rates may have been a result of differences in female behaviour, as feeding rate was significantly correlated (Table 4-2) with the rate of food solicitation.

Support for the nutritional importance of courtship feeding is valid, despite the systematic error in the recording of feeding rates. The above conclusions depend either on the phenology of events and thus are unaffected by the reliability results, or are based on averages of the two observer's scores, reducing the effects of systematic error.

4.5.3 COURTSHIP FEEDING FACILITATES COPULATION

As copulations were generally recorded reliably, most of the following statements can be made with confidence, except where noted.

Courtship feeding was not essential for successful copulation as 60% of successful copulations occurred without prior feeding. However if feeding had occurred, subsequent copulations were significantly more likely to be successful. Further, the quantity of food given did not appear to increase the probability of success in subsequent mounts, but the systematic error in the recording of number of boluses/bout make it difficult to state this with certainty. Courtship feeding rate was positively correlated with rate of successful copulation.

In this study, copulations reached a peak at 5-6 days before egg laying, which is approximately 2 days later than was found for kittiwakes at a colony in England (Chardine

1987), however both peaks seem earlier than necessary if fertilisation was the only goal. In the domestic chicken the minimum time from copulation with cloacal contact to the release of the fertilized egg is 3 days; the sperm take 48 h to travel up the oviduct and the fertilized egg then takes another 24 h to pass down the oviduct, acquiring albumen, membranes and shell (Gilbert 1971). If the time period is similar for kittiwakes, then copulations which fertilize eggs will be those on day -3 or later. It is not known whether kittiwakes can store sperm and if so for how long it remains viable. Sperm-storage glands are known to occur in four taxonomically distant orders of birds (Hatch 1983) and may occur more widely or even universally in birds (Birkhead and Moller 1992). If kittiwakes cannot store sperm then additional copulations would be necessary to fertilize the second and third eggs.

Although it has been determined that a single pair copulation is sufficient to fertilize an entire clutch, male birds apparently use multiple copulations with their partners as a paternity guard (Birkhead and Moller 1992). Males can reduce the probability of extra-pair paternity by increasing the copulation rate with their partner. Studies show relatively high levels of copulation with multiple partners in monogamous, colonially breeding species (Birkhead and Moller 1992) such as the kittiwake. When females mate with several males, the paternity of the resulting offspring is determined by mating order and the interval between copulations (Birkhead and Moller 1992). Where the risks of extra-pair copulation are high, males will copulate frequently with their partners to displace or dilute the sperm of possible competitors.

Copulations early in the season were as likely to be successful (achieve cloacal contact) as those occurring later in the season and there was no apparent seasonal variation in the number of cloacal contacts/mount, which was often quite high. This conclusion is weakened though by the random error in the recording of cloacal contacts/mount. Sturkie (1965) pointed out that in the chicken the volume of sperm can be very low after 3-4 successive ejaculations. Fertilization is likely not the only function of copulation in kittiwakes. Brown (1967) hypothesized that one of the functions of copulation in Lesser Black-backed Gulls was to stimulate the final growth phase of the ovary. This may also explain why rates of copulation peaked relatively early. It may be that frequent copulation may act to maintain a relatively high concentration of fresh sperm in the female's reproductive tract, thus reducing the chances of sperm from another male having the opportunity to fertilize an ovum (Birkhead 1979). Frequent copulation may also serve to advertise to neighbouring males and to the male's mate, the quality of the male and his ability to defend his fertile female.

Table 4-1

The number of nests and number of hours of observation in relation to the date of egg laying. Data are pooled over 2-day intervals. Nest-hours = (number of nests) x (hours watched).

Relative date (0 = day first egg is laid)	Nest-hours (N)	Nests (N)
-14	88.25	7
-12	163.50	17
-10	309.25	18
-8	382.25	20
-6	451.50	24
-4	427.50	26
-2	306.00	36
0	222.25	39
2	491.25	43
4	510.25	40
6	354.50	42
8	303.75	41
10	215.50	41

Table 4-2

Food boluses ($pair^{-1}$ h^{-1}) correlated with food solicitation, copulation and measures of reproductive success in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.

	Food boluses $pair^{-1}$ h^{-1}		
	r[1]	N	p
Laying date	r_s = 0.16	39	n.s.
Clutch size	r_s = -0.11	39	n.s.
# chicks hatched/pair	r_s = -0.05	30	n.s.
# chicks fledged/pair	r_s = 0.06	38	n.s.
Food solicitation (mean $pair^{-1}$ h^{-1})	r = 0.57	39	< 0.01
Rate successful copulations (mean $pair^{-1}$ h^{-1})	r = 0.41	39	< 0.05
Rate total copulations (mean $pair^{-1}$ h^{-1})	r = 0.29	39	n.s.

[1] r_s - Spearman rank correlation
r - Pearson correlation

Table 4-3

The effect of prior feeding on the likelihood of copulation success during the 14 days preceding egg-laying in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.

	Copulations	
	Success	**Attempt**
Feeding occurred		
(N)	(41)	(15)
Row %	73	27
Column %	40	22
No feeding		
(N)	(61)	(53)
Row %	54	46
Column %	60	78

Chi-squared = 6.08, df = 1, $p < 0.05$

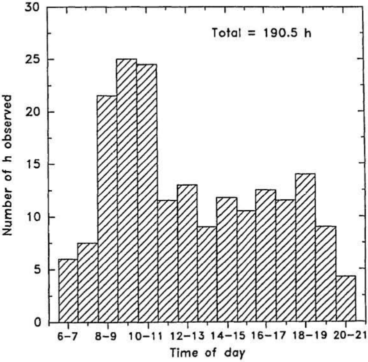


Figure 4–1 – Number of h of observation in relation to time of day, Cape St. Mary's, Newfoundland, 1990.

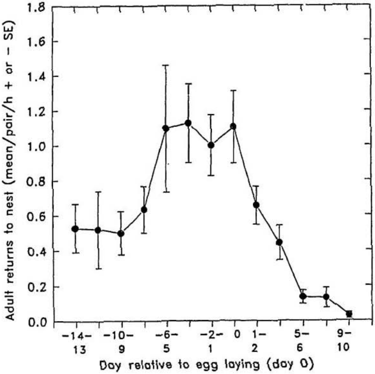


Figure 4-2 – Seasonal changes in adult returns to the nest (mean/pair/h) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.

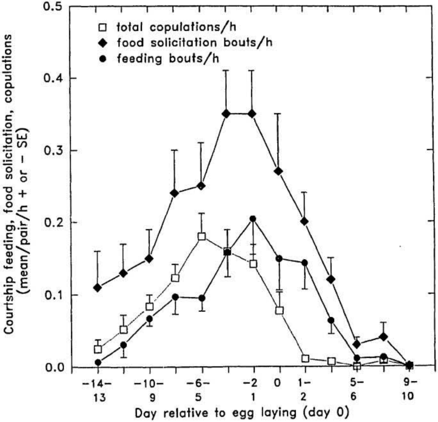


Figure 4-3 - Seasonal changes in bouts of courtship feeding, food solicitation and copulations (mean/pair/h) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.

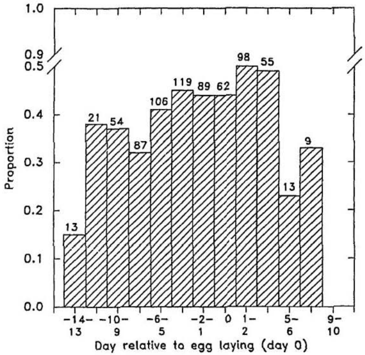


Figure 4-4 – Seasonal changes in the proportion of bouts of food solicitation followed by courtship feeding in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. Sample sizes of courtship feeds indicated.

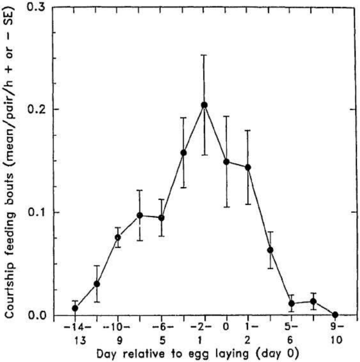


Figure 4-5 – Seasonal changes in courtship feeding bouts (mean/pair/h) in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.

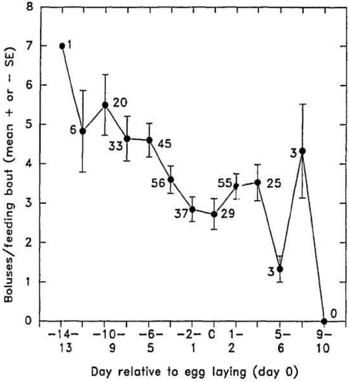


Figure 4-6 – Seasonal changes in the mean number of boluses/feeding bout in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. Sample sizes of total feeds indicated.

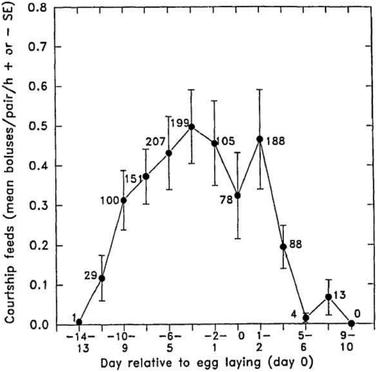


Figure 4–7 – Seasonal changes in courtship feeds (mean boluses/pair/h) in Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. Sample sizes of total boluses indicated.

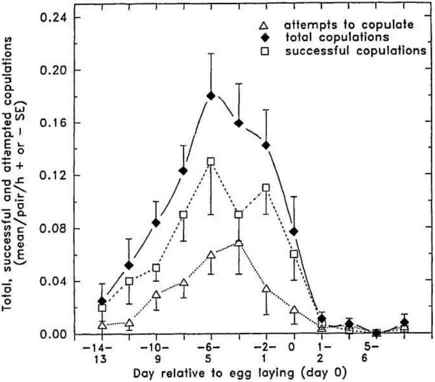


Figure 4−8 − Seasonal changes in successful copulations (cloacal contact), attempts to copulate (mount, no cloacal contact), and total copulations (successes + attempts) (mean/pair/h) in Black−legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.

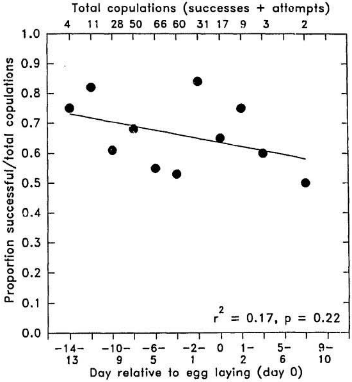


Figure 4-9 - Seasonal changes in the proportion of all copulations involving cloacal contact in Black-legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.

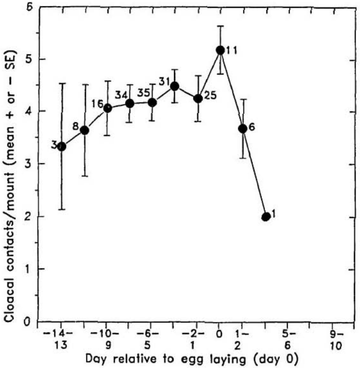


Figure 4–10 – Seasonal changes in cloacal contacts /mount (mean number) in Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990. Sample sizes of successful copulations indicated.

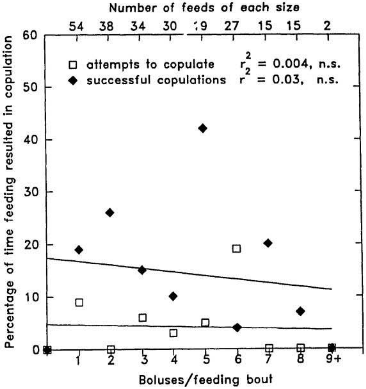


Figure 4–11 – The influence of multiple boluses on the success of subsequent copulations in Black–legged Kittiwakes at Cape St. Mary's, Newfoundland, 1990.

4.6 REFERENCES

Altmann, J. (1974). Observational study of behavior: sampling methods Behaviour, 49, 227-265.

Birkhead, T.R. (1979). Mate guarding in the Magpie Pica pica. Animal Behaviour, 27, 866-874.

Birkhead, T.R. and A.P. Moller. (1992). Sperm Competition in Birds. Academic Press: London.

Brown, R.G.B. (1967). Courtship behaviour in the Lesser Black-backed Gull, Larus fuscus. Behaviour, 29, 122-153.

Chardine, J. (1983). Aspects of the breeding behaviour of the kittiwake (Rissa tridactyla) before laying. Unpublished Ph.D. thesis, University of Durham, England.

Chardine, J. (1987). The influence of pair-status on the breeding behaviour of the Kittiwake Rissa tridactyla before egg-laying. Ibis, 129, 515-526.

Gilbert, A.B. (1971). The female reproductive effort. In: Physiology and Biochemistry of the Domestic Fowl, Vol.3 (ed. by D.J. Bell and B.M. Freeman), pp. 1153-1162. Academic Press: London.

Hatch, S.A. (1983). Mechanism and ecological significance of sperm storage in the Northern Fulmar with reference to its occurrence in other birds. Auk, 100, 593-600.

Hunt, G.L. Jr. (1980). Mate selection and mating systems in seabirds. In: Behaviour of Marine Animals, Vol. 4 (ed. by J. Burger, B. Olla and H. Winn), pp. 113-151. Plenum Press: New York.

Jandel Corp. (1990). Sigmaplot, Version 4.01. Jandel Scientific: Corte Madera, California.

Krebs, J.R. (1970). The efficiency of courtship feeding in the Blue Tit Parus caeruleus. Ibis, 112, 108-110.

Lack, D. (1940). Courtship feeding in birds. Auk, 57, 169-178.

Martin, P. and P. Bateson. (1986). Measuring Behaviour: An Introductory Guide. Cambridge University Press: Cambridge.

Morris, R.D. (1986). Seasonal differences in courtship feeding rates of male common terns. Canadian Journal of Zoology, 64, 501-507.

Niebuhr, V. (1981). An investigation of courtship feeding in Herring Gulls, Larus argentatus. Ibis, 123, 218-223.

Nisbet, I.C.T. (1973). Courtship feeding, egg-size and breeding success in Common Terns. Nature, 241, 141-142.

Nisbet, I.C.T. (1977). Courtship-feeding and clutch size in Common Terns Sterna hirundo. In: Evolutionary Ecology (ed. by B. Stonehouse and C.M. Perrins), pp. 101-109. Macmillan Press Ltd.: London.

Paludan, K. (1955). Some behaviour patterns of Rissa tridactyla. Vidensk. Medd. fra Dansk. Naturh. Foren., 117, 1-21.

Roudybush, T.E., C.R. Grau, M.R. Petersen, D.G. Ainley, K.V. Hirsch, A.P. Gilman, and S.M. Patten. (1979). Yolk formation in some Charadriiform birds. Condor, 81, 293-298.

Royama, T. (1966). A re-interpretation of courtship feeding. Bird Study, 13, 116-129.

Sokal, R.R. and F.J. Rohlf. (1981). Biometry, 2nd edition. W.H. Freeman: San Francisco.

SPSS Inc. (1988). SPSS-X User's Guide, 3rd edition. Chicago.

Sturkie, P.D. (1965). Avian Physiology. Cornell University Press: New York.

Tasker, C.R. and J.A. Mills. (1981). A functional analysis of courtship feeding in the Red-billed Gull, Larus novaehollandiae scopulinus. Behaviour, 77, 221-241.

Taylor, I.R. (1979). Prey selection during courtship feeding in the Common Tern. Ornis Scandinavica, 10, 142-144.

Chapter 5

GENERAL DISCUSSION

The central aim of this study was an examination of the adjustments in parental investment made by Black-legged Kittiwakes in response to fluctuating environmental conditions. Capelin is an important food of breeding seabirds in Witless Bay and clear evidence of delayed spawning and decreased biomass of capelin in 1991 was obtained by other researchers. The availability of food was predicted to be the key factor affecting various aspects of breeding biology, and apparent food shortages in 1991 were the hypothesized cause of the breeding failure experienced by kittiwakes in that year.

Kittiwakes exhibit the central features of a K-selected species (Pianka 1970), adult survival is generally high and annual reproductive output is low (Wooller and Coulson 1977). High juvenile mortality tends to favour adult birds conserving resources for themselves rather than their offspring and thus surviving longer, and investing in only a few well-provided-for young whose chances of survival are consequently enhanced. That kittiwakes are adapted to maximize adult survival rates means that individual birds in a particular year will reduce their investment in reproduction or abandon breeding altogether if the risks to their survivorship are too great.

From the results of this study it is clear that kittiwakes make adjustments in their behaviour in the direction of increased adult survivorship to compensate for apparent food shortages during the breeding season. Timing of breeding was later, there was a greater amount of non-breeding, clutch sizes were smaller, egg volumes were reduced, and chick survivorship and growth rates were lower in 1991, the year with the most severe apparent food shortages.

Perrins (1970) contends that although there is selection for birds to lay as early in the season as possible, they may not be able to do so until there is enough food available, or until they have accumulated sufficient body reserves to withstand the nutritional demands of egg production. Insufficient body reserves may also be implicated in the reduced clutch size and egg volume demonstrated by kittiwakes in 1991. Little is known of the winter diet of Black-legged Kittiwakes breeding in Newfoundland, so they may have suffered food shortages the previous winter as well. The ultimate adjustment in favour of increased adult survivorship and reduced investment in reproduction is to abandon breeding altogether, as occurred in 1991 to a greater extent than previous years.

Courtship feeding can be an important activity in the pre-laying period for improving females' physical condition. In a comparison of two colonies, Nisbet (1977) found the mean laying date to be earlier in the colony which had the greater rate of courtship feeding, and courtship feeding rate was positively correlated with clutch size and egg volume (Nisbet 1973). The nutritional importance of courtship feeding was supported in the current study through the phenology of this event in relation to egg laying and the substantial amount of food female kittiwakes received at the peak of courtship feeding. However, there was no significant relationship between courtship feeding rate and timing of breeding, clutch size, or hatching and fledging success. Productivity was very high at Cape St. Mary's in 1990 and although there was inter-pair variability in feeding rates, food supplies may have been more than the necessary minimum for all pairs. As stress can heighten the differences between high and low quality pairs and amplify the relationship between behavioural differences and reproductive success, it would have been instructive to have repeated the courtship feeding study at Gull Island in 1991.

An examination of inter-observer reliability was made in the context of the courtship feeding study and the results of these analyses were considered when interpreting the courtship feeding results. Two of the seven variables, adults returns to the nest and copulations, were scored reliably. Characteristics which distinguished these two variables from those not scored reliably were either their frequency of occurrence (when a behviour occurs infrequently, a few disagreements constitute a larger proportion of the whole) or their conspicuousness. The remaining variables were affected by either systematic error or random error which influenced conclusions differently depending on the questions asked. The difficulties discovered here in obtaining adequate observer agreement reinforce the importance of adequate observer training and the necessity for trial studies to clarify choice of variables and sample sizes needed.

The aspects of seabird breeding biology most sensitive to environmental changes (eg. reduced food supplies) are probably diet and adult activity budgets, as assessed here in courtship feeding and chick feeding rates and adult attendance patterns during incubation and chick rearing. Some ambiguities and inadequacies in these results indicate areas for future research. Studies of kittiwake diet should include estimations of bolus mass, the ability of kittiwakes to exploit different food types as necessitated by environmental conditions, fish surveys within the foraging range of the colony to directly assess food availability, and assessment of the nutritive value of different food types. More in-depth studies of adult activity budgets may be able to tease out the relative importance of predation pressure and hunger in determining adult attendance patterns. Closely related to this is the issue of what constitutes 'normal' variability in breeding parameters both between seasons at the same colonies, and between colonies in different areas. More information is also needed on how closely related species (e.g. Herring and Black-backed gulls) cope with the same environmental conditions.

For a K-selected species such as the kittiwake, a few years of breeding failure will have a small effect on population size over the long term because the annual survival rates of adult birds are high (82%, Coulson and Wooller 1976) and chicks fledged in a particular year will continue to recruit for the following 3-8 years (Wooller and Coulson 1977). With complete breeding failure, the numbers would then decrease by 18% annually, equivalent to the adult mortality rate (Coulson and Wooller 1976). However, sustained decline in breeding success will affect the population. It is not clear how long kittiwakes on Gull Island have been suffering reduced breeding success, but for all variables compared, productivity in 1990 and 1991 had decreased from values obtained by Maunder and Threlfall (1972) in 1969 and 1970. This decrease was already evident in 1988 in reduced fledging success and clutch size (J.M. Porter pers. comm.). An examination of recruitment to

Witless Bay kittiwake colonies may be another fruitful area for future research.

The wealth of variability exhibited by Black-legged Kittiwakes in this study show them to be ideal subjects for examining the adaptive significance of behaviour. Colonial seabirds, with their numbers and relative ease of access, provide particularly valuable opportunities for further testing of theories related to reproductive biology.

5.1 References

Coulson, J.C. and R.D. Wooller. (1976). Differential survival rates among breeding Kittiwake Gulls Rissa tridactyla (L.). Journal of Animal Ecology, 45, 205-213.

Maunder, J.E. and W. Threlfall. (1972). The breeding biology of the Black-legged Kittiwake in Newfoundland. Auk, 89, 789-816.

Nisbet, I.C.T. (1973). Courtship-feeding, egg-size and breeding success in Common Terns. Nature, 241, 141-142.

Nisbet, I.C.T. (1977). Courtship feeding and clutch size in Common Terns, Sterna hirundo. In: Evolutionary Ecology (ed. by B. Stonehouse and C. Perrins), pp.101-109. University Park Press: Baltimore, Maryland.

Perrins, C.M. (1970). The timing of bird's breeding seasons. Ibis, 112, 242-255.

Pianka, E.R. (1970). On r- and k-selection. American Naturalist, 104, 592-597.

Wooller, R.D. and J.C. Coulson. (1977). Factors affecting the age of first breeding of the Kittiwake Rissa tridactyla. Ibis, 119, 339-349.

Appendix A

COMMON AND SCIENTIFIC NAMES OF SPECIES MENTIONED IN THE TEXT

BIRDS

Leach's Storm-Petrel	*Oceanodroma leucorhoa* (Vieillot)
Brown Pelican	*Pelecanus occidentalis californicus* L.
Northern Gannet	*Sula bassanus* (L.)
Lesser Snow Goose	*Chen caerulescens* (L.)
Herring Gull	*Larus argentatus* Pontoppidan
Lesser Black-backed Gull	*Larus fuscus* L.
Great Black-backed Gull	*Larus marinus* L.
Black-legged Kittiwake	*Rissa tridactyla* (L.)
Red-legged Kittiwake	*Rissa brevirostris* (Bruch)
Red-billed Gull	*Larus novaehollandiae scopulinus* Stephens
Common Tern	*Sterna hirundo* L.
Roseate Tern	*Sterna dougallii* Montagu
Razorbill	*Alca torda* L.
Common Murre	*Uria aalge* (Pontoppidan)
Thick-billed Murre	*Uria lomvia* (L.)
Atlantic Puffin	*Fratercula arctica* (L.)
domestic chicken	*Gallus gallus* var. *domesticus* (L.)
Common Raven	*Corvus corax* L.
House Wren	*Troglodytes aedon* Vieillot
Chipping Sparrow	*Spizella passerina* (Bechstein)

FISH

Atlantic herring	*Clupea harengus* L.
Northern anchovy	*Engraulis mordax* Girard
capelin	*Mallotus villosus* (Muller)
Atlantic cod	*Gadus morhua* L.
Atlantic mackerel	*Scomber scombrus* L.

PLANTS

black spruce	*Picea mariana* Engelm.
balsam fir	*Abies balsamia* (L.) Mill.

MAMMALS

domestic cat	*Felis domestica* L.

Appendix B

PERSONAL COMMUNICATIONS

1. Dr. John Chardine
Research Scientist, Marine Ecology
Canadian Wildlife Service
P.O. Box 21276
St. John's, Newfoundland
A1A 5B2

2. Dr. Susan Goldberg
Director, Psychiatric Research
The Hospital for Sick Children
555 University Ave.
Toronto, Ontario
M5G 1X8

3. Dr. Jon Lien
Professor, Psychology Department
Memorial University of Newfoundland
St. John's, Newfoundland
A1B 3X9

4. Dr. Julie Porter
Research Scientist
Department of Fisheries and Oceans
St. Andrews, New Brunswick
E0G 2X0

Appendix C

BLACK-LEGGED KITTIWAKE COURTSHIP DISPLAYS

As Paludan (1955) is not widely available, his descriptions of Black-legged Kittiwake courtship displays are quoted here in a condensed form.

1. The kittiwaking ceremony (greeting ceremony)
   Figure C-1

> When a Kittiwake returns to the nest the mates greet each other in a characteristical way which might be called the greeting ceremony.... When the greeting ceremony is fully developed both parents join in it with the same eagerness. They remain standing in the nest, normally facing each other directly but the angle may vary considerably, the longitudinal axes of the bodies may even be parallel, with heads pointing in the same direction. The transition between head and the somewhat curved neck is angular. The beak is widely open, the tongue projecting like a bent bow from the bottom part of the mouth cavity....
>
> Showing signs of great excitement the mates carry out a series of quick nodding movements during which the necks may be crossing, now the neck of one mate being above and now that of the other. Simultaneously the kittiwake sound is uttered.... The call is often given by the returning as well as by the sitting mate before landing takes place.
>
> The ceremony is subject to considerable modification when brooding has commenced. Normally the returning mate will still emit the kittiwake sound, but far from always it is returned by the brooding bird which may even ignore it and continue brooding without interruption. According to the different stages of the nests appreciable differences in the ceremony are noticed ranging from the "hysterical" kittiwaking and neck-twisting seen in the busily nest-building pair to the less intense greeting displayed in nests where incubation has commenced.
>
> Although the kittiwaking ceremony is of prime importance as a greeting ceremony on a partner's return

> to the nest I have seen it displayed by birds which have for some time been together on the nest. The reason for this phenomenon could not be analyzed in detail, however, the kittiwake call uttered by the neighbouring pairs can act as a releaser. On one occasion a male was heard to utter a couple of "kittiwakes", jumping on to the back of the female only to alight quickly again as the female showed no response to this nor to his "kittiwaking". In a case like this we may be dealing with a displacement activity released by the conflict between his desire for coition and the total lack of response in the female. (pp. 3-4)

2. <u>Head-bobbing</u> (head-tossing)
   Figure C-2

> During this ceremony the female bends the legs a little, keeping the body almost horizontal and the neck drawn in. In this posture it performs bobbing movements of the head, the beak describing an up- and down-ward arc. The ups and downs are carried out in the same, slow, tempo, the beak never ascending to a vertical position. During the ascension a further, slight, retraction of the neck takes place. It has not been possible to perceive any sound during the performance of the ceremony.
>
> In most cases the female alone performs, sometimes pressing closely up to the male's breast or it proceeds to the begging ceremony which can also be performed intermittently during the head-bobbing. This, in connection with the submissive posture of the female, makes it tempting to consider the head-bobbing part of the female's begging for food. However, other features lend to the head-bobbing a more independent status. In the first place the male may join in the head-bobbing and it seems odd to assume that both partners show signs of submission or that the male takes part in the begging which otherwise is specific for the female. In the second place the head-bobbing may occur during the late incubation period, even with chicks in the nest, while all begging and food-offering stops when the last egg of the clutch has been laid. (pp. 5-6)

3. Food-begging and feeding of the female

Figures C-3 and C-4

> Following the return of one or the other mate and the ensuing kittiwake ceremony the female often starts begging, that is if the pair is in the pre-egg stage. The food-begging may have been preceded or intermittently interrupted by head-bobbing, however, this is far from always the case.
>
> The female adopts a submissive posture, conspicuously directing her chief interest towards the beak of the male, pecking at or biting round it. She may also rub her beak against the male's breast and throat. In most cases it calls forth the desired reaction: a swelling of his throat indicates the upward passage of a food-pellet. When it has arrived in the pharynx he opens the beak, and eagerly the female eats of the pellet which does not normally proceed any further. Once I have seen a little of the pellet spilling over into the nest but at once it was picked up carefully....
>
> The process of regurgitation in the male Kittiwake is somewhat different from that of the Herring Gull and the Lesser Blackback. In the Kittiwake the prelude as well as the food-offering takes place on the nest while in the other two species it takes place in the territory outside the nest. While uttering a wailing meh the male Blackback withdraws a little and in an apparent state of nausea he bends his neck, the beak pointing towards the ground, and regurgitates whereafter the female eats the food either off the beak of the male or from the ground. In the male Kittiwake no nausea-like state is noticed and no sound is produced. Quietly he remains standing keeping body and neck in almost normal position, only when the food pellet arrives in the pharynx the opened beak is lowered somewhat against the breast. (pp. 7-8)

4. Copulation

Figure C-5

> The pre-coition display is subject to numerous modifications. In some cases the coition is preceded by several of the ceremonies already mentioned, in others it takes place almost without any prelude. The ceremonies normally performed are left out, the sexual urge rises in the male, he takes a glance at the mate's back and suddenly mounts. In such cases an unsuccessful

copulation will be the normal result because the female's drive is too weak. However, quite normal copulations were seen to take place in this way.

Under normal circumstances the copulation is more complicated. The characteristical sequence of events may be as follows. The male or female returns to the nest where it is greeted by the mate's kittiwaking accompanied by some choking. Now the female commences head-bobbing and the male joins in it. The female's head-bobbing gradually changes into food-begging; it pecks at and bites round the male's beak submissively pressing closely up to his breast. These stimuli show a distinct effect in the male who regurgitates food for the female. Now some head-bobbing may follow before the male jumps on to the female's back. At first he steps a little to and fro until he gains his balance and settles down in the right position with the feet on the female's shoulders. Then follow the coitions during which his tail is pressed downwards, now to the right and now to the left of the female's tail which is somewhat raised, while he waves the wings to maintain the balance....The female rests in the nest spreading her wings a little while supporting them against the rim of the nest. Sometimes she turns her head nibbling at the plumage of the male's throat or at his beak. During this display they mutually show their beaks and the contrasting colours of the epithelial lining of the mouth cavity which may act as a further stimulus in this situation. Normally 5-7 coitions are carried out, but once at least 12 were counted. When they have been completed the male remains for a moment on the female's back, shakes his plumage and flies away or alights.

During the copulation the female almost invariably rests on the nest. Only two exceptions were observed. Once she rested on the rim of the nest and in another case on a boulder close to the nest. In either case the pair had apparent difficulties in finding their balance. (pp. 10-11)

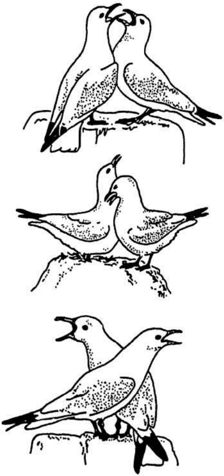


Figure C-1 Greeting ceremony in the Black-legged Kittiwake. (Cramp 1983)

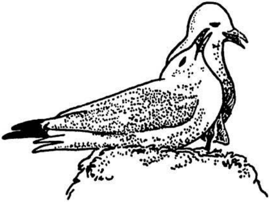


Figure C-2 Head-tossing in the Black-legged Kittiwake. (adapted from Paludan 1955)

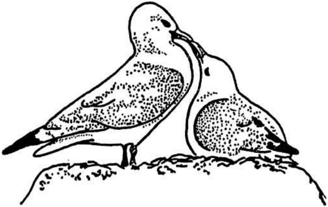


Figure C-3 Food begging in the Black-legged Kittiwake. (adapted from Paludan 1955)

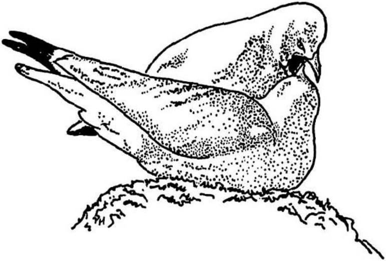


Figure C-4 Courtship feeding in the Black-legged Kittiwake. (adapted from Paludan 1955)

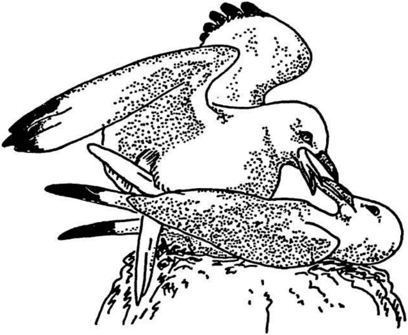


Figure C-5 Copulation in the Black-legged Kittiwake. (Cramp 1983)

REFERENCES

Cramp, S. (ed.) (1983). Handbook of the Birds of Europe, the Middle East and North Africa. Volume 3. pp. 863-875. Oxford University Press: Oxford.

Paludan, K. (1955). Some behaviour patterns of Rissa tridactyla. Verdansk. Medd. Dansk. Naturh. Forem. **117**, 1-21.