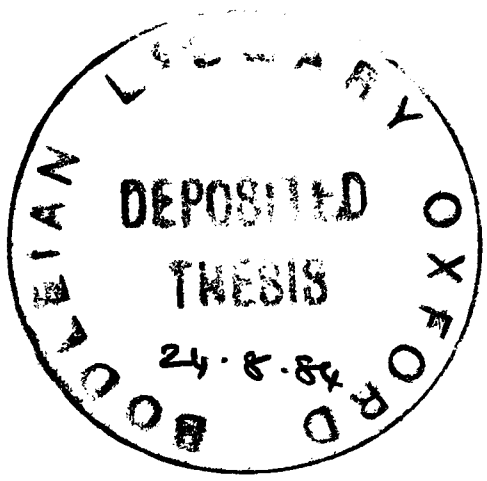
# THE COMPARATIVE BREEDING BIOLOGY, FEEDING ECOLOGY AND BIOENERGETICS OF ADELIE AND CHINSTRAP PENGUINS.




A thesis

submitted to the

Faculty of Biological and Agricultural Sciences

of the

University of Oxford

in supplication for the

Degree of Doctor of Philosophy

by

Gavin Lishman

Wolfson College

December 1983



Frontispiece

View looking north along the east coast of Signy Island showing Adélie and chinstrap penguin colonies in the centre and early summer sea ice in the distance.

# ABSTRACT

The comparative breeding biology, feeding ecology and bioenergetics of Adélie and chinstrap penguins. Gavin Lishman, Wolfson College. Thesis for the degree of Doctor of Philosophy, Michaelmas Term, 1983.

Adélie Pygoscelis adeliae and chinstrap P. antarctica penguins are the two most numerous Antarctic seabird species and play a major role as consumers in the marine ecosystem. Their ecological adaptations to breeding and feeding and influence on marine resources at Signy Island, South Orkney Islands were examined during the 1980/81 and 1981/82 breeding seasons.

Adélies possess adaptations to harsh conditions and a short breeding season. They breed one month before chinstraps, lay two eggs, the first larger and heavier, and incubate for up to 14 days at a time. Chicks are brooded until aged c. 18 days, when they may form crêches, and fledge at c. 61 days. First hatched chicks grow faster than seconds. Chinstrap breeding is less constrained by environmental conditions. Their eggs are not dimorphic, parents incubate for up to 10 days at a time, chicks crêche later, at c. 24 days and fledge earlier, at c. 53 days. Both chicks grow at the same rate.

The diet of both species is mainly krill, though Adélies often catch more juvenile than adult krill, the latter probably being more available when chinstraps are breeding. Different feeding ranges, suggested by lower Adélie feeding frequencies, may also affect krill size caught. Feeding methods are probably similar. Krill rise to the surface at night, when both species probably feed, and 90 % of chinstrap foraging dives are to shallower than 45 m. Adult food consumption was equivalent to 600 g of krill per day, the fasting energy consumption c. 1.2 % of body weight per day and total estimated breeding energy consumption 1.7 - 2.0 x $10^5$ kJ. Lack of food for chicks was indicated, since chicks were less than c. 50 % of adult weight at fledging. This may have been due to the combined impact of the greatly increased penguin breeding population. Together, Adélies and chinstraps comprise over 85 % of the South Orkney avian biomass and are perhaps responsible for c. 80 % of krill consumption by birds.

TABLE OF CONTENTS


| | | Page |
|---|---|---|
| CHAPTER ONE | INTRODUCTION | 1 |
| Aims | | 2 |
| Background | | 4 |
| The study site | | 6 |
| a. General description | | 6 |
| b. Environmental conditions | | 10 |
| CHAPTER TWO | BREEDING BIOLOGY | 15 |
| Introduction | | 16 |
| Methods | | 16 |
| Preparation of study nests | | 16 |
| Daily observations | | 22 |
| Data analysis | | 23 |
| Results | | 26 |
| 1. Pre-laying | | 26 |
| a. Return to the colony after the winter | | 26 |
| b. Pairing | | 26 |
| c. Pre-laying attendance times | | 26 |
| 2. Laying | | 29 |
| a. Dates and laying synchrony | | 29 |
| b. Laying intervals | | 29 |
| c. Observation of laying | | 29 |
| 3. Eggs | | 35 |
| 4. Incubation | | 35 |
| a. Incubation shifts | | 35 |
| b. Incubation period | | 40 |

Page

5. Hatching 40

a. Dates 40

b. Hatching intervals 44

6. The crèche period 44

7. Fledging 44

8. Breeding success 49

a. Breeding success of normal nests 49

1. Basic data 49

2. Factors affecting breeding success 52

2.1. Direct - Predation 52

2.2. Indirect 57

2.2.1. Nest desertion 57

2.2.2. Weather and ice conditions 57

3. Correlations with breeding success 59

3.1. Colony size and nest position 59

3.2. Laying date 59

3.3. Egg and chick differences 59

b. Breeding success of increased clutch nests 59

Discussion 61

1. Pre-laying 61

a. Return to the colony 61

b. Pairing 62

2. Laying 63

a. Synchrony 63

b. Intervals 64

c. Eggs 64

3. Incubation 65

4. Hatching 66

5. The crèche period 69

Page

6. Fledging 70

7. Breeding success 71

a. Basic data 71

b. Factors affecting breeding success 73

1. Direct - Predation 73

2. Indirect 74

2.1. Nest desertion 74

2.2. Weather and ice conditions 75

c. Correlations with breeding success 75

1. Colony size and nest position 75

2. Laying date 76

Conclusions 77

CHAPTER THREE DIET 78

Introduction 79

Methods 79

Data collection 79

Data analysis 80

Results 84

Diet composition 84

1. Fish 84

2. Amphipods 87

3. Krill 87

a. Mean length 87

b. Length distribution 89

c. Total weight of krill in the stomachs 94

d. Krill number 98

Page

e. Relationship between amount of digestion and time since last feed 98

f. Culmen dimensions 98

Discussion 104

1. Diet composition 104

2. Krill 104

Conclusions 115

CHAPTER FOUR FEEDING ECOLOGY 116

Introduction 117

Methods 117

Data collection 117

Data analysis 119

1. Meal size 119

2. Feeding frequency 120

3. Feeding behaviour 120

a. Time of return from foraging trips by adults 120

b. Foraging distance 121

c. Diving depth 122

Results 122

1. Meal size 122

2. Feeding frequency 131

3. Feeding behaviour 133

a. Time of return from foraging trips by adults 133

b. Foraging distance 137

c. Diving depths 142

Discussion 144

1. Meal size 144

2. Feeding frequency 146

| | | Page |
|---|---|---|
| 3. Feeding behaviour | | 147 |
| a. Time of feeding and foraging distance | | 147 |
| b. Diving depths and performance | | 151 |
| Conclusions | | 154 |
| CHAPTER FIVE | CHICK GROWTH | 157 |
| Introduction | | 158 |
| Methods | | 160 |
| Data collection | | 160 |
| Data analysis | | 161 |
| Results | | 164 |
| Discussion | | 182 |
| a. Overall growth pattern | | 182 |
| b. Variations in growth pattern | | 190 |
| Conclusions | | 198 |
| CHAPTER SIX | BIOENERGETICS | 200 |
| Introduction | | 201 |
| Methods | | 202 |
| Preparation of study nests | | 203 |
| Data collection | | 203 |
| Data analysis | | 203 |
| Results | | 205 |
| 1. Weight loss during pre-laying attendance and incubation fasts | | 205 |
| 2. Energy supply during pre-laying attendance and incubation fasts | | 215 |
| Discussion | | 219 |
| 1. Weight loss | | 219 |

Page

2. Energy supply 220

Conclusions 221

CHAPTER SEVEN FOOD CONSUMPTION AND ENERGY REQUIREMENTS 223

Introduction 224

Methods 226

1. Energy consumption 226

a. Adults 226

b. Chicks 227

2. Consumption of krill by Adelies and chinstraps 229

Results 230

1. Adults 230

a. Brooding fasts 230

b. Foraging 230

c. Total energy consumption and food requirements 233

2. Chicks 235

3. Consumption of krill by Adelies and chinstraps 235

Discussion 240

1. Adults 240

2. Chicks 244

3. Consumption of krill by Adelies and chinstraps 245

Conclusions 246

CHAPTER EIGHT DISCUSSION 248

The Spheniscidae 249

1. General similarities 249

2. Species groups with different adaptations 250

a. Emperor and king penguins 250

Page

b. Other penguins 252

1. Macaroni penguins 252

2. Gentoo penguins 252

Adelies and chinstraps 253

1. Differences between Adélies and chinstraps 254

a. Breeding 254

b. Feeding 254

2. Reasons for differences 256

a. Environmental conditions 256

b. Food availability 257

c. Competition 258

3. Differences in Adélie and chinstrap breeding and feeding strategies between this study and previous ones 259

ACKNOWLEDGEMENTS 263

REFERENCES 265

APPENDICES 292

LIST OF TABLES


| | | Page |
|---|---|---|
| 1.1. | The mean monthly temperature and wind speed during the summer months of 1980/81 and 1981/82. | 11 |
| 2.1. | Pre-laying attendance periods of Adelies and chinstraps. | 28 |
| 2.2. | Mean and sample size of Adélie and chinstrap laying dates. | 32 |
| 2.3. | Intervals between the laying of first and second eggs. | 34 |
| 2.4. | Adélie and chinstrap egg measurements, 1981/82. | 36 |
| 2.5. | Egg weights and weight loss (1981/82). | 37 |
| 2.6. | Incubation shift lengths. | 38 |
| 2.7. | Incubation period of first and second eggs. | 41 |
| 2.8. | Hatching dates. | 43 |
| 2.9. | Intervals between the hatching of first and second eggs. | 45 |
| 2.10. | Mean date of the start of the crèche period. | 46 |
| 2.11. | Chick age (d) at the start of the crèche period. | 47 |
| 2.12. | Fledging periods and fledging dates of Adélies and chinstraps. | 48 |
| 2.13. | Breeding success in Adélie and chinstrap study and control colonies. | 50 |
| 2.14. | Percentage mortality from each egg and chick category and the lifespans of the lost eggs and chicks. | 51 |
| 2.15. | The number and proportion of the original sample of nest desertions in total and of those resulting from the non-return of the mate during incubation, the mean lengths of normal incubation shifts and the lengths of shifts prior to desertion | 58 |
| 2.16. | Hatching weights of first and second Adélie and chinstrap chicks. | 60 |

Page

3.1. The percentage composition (± sd.) of stomach contents calculated from the number and weight of each prey type present. 85

3.2. The percentage of stomachs containing krill, fish and amphipods. 86

3.3. The mean length (mm) of krill taken by Adelies and chinstraps. 88

3.4. The mean length (mm) of krill taken by Adélies and chinstraps in each year. 91

3.5. A comparison of the mean length (mm) of krill taken by Adélies and chinstraps when calculated from the number and weight of krill in each length class. 93

3.6. The mean percentage number and weight of krill in each juvenile length class (< 31 mm length) found in Adélie and chinstrap stomachs. 95

3.7. Comparison between years of the weight (g) of krill brought ashore during part of the chick rearing period of both species. 97

3.8. Number of krill per sample. 99

3.9. Comparison of Adélie and chinstrap culmen depths and lengths. 103

4.1. A comparison of feeding frequencies during the guard period calculated from daily and three-hourly weighings. 134

4.2. Feeding frequencies calculated from daily weighings. 135

4.3. Estimates of travelling times between the colony and the foraging area and the total distance foraged. 140

4.4. Details of the foraging trips of the chinstrap penguins studied. 144

| | | Page |
|---|---|---|
| 4.5. | Feeding frequencies (adult visits per day) recorded during Adélie and chinstrap studies. | 148 |
| 4.6. | Energy consumption and weight and number of krill caught during foraging trips. | 155 |
| 5.1. | Parameters of chick growth from hatching to fledging. | 169 |
| 5.2. | Comparison between Adélies and chinstraps in 1981/82 and between Adélies in 1980/81 and 1981/82 of mean chick weight at 5-10 day intervals throughout most of the chick rearing period in each year. | 176 |
| 5.3. | Parameters of chick growth during the exponential growth phase. | 180 |
| 5.4. | A comparison of the weight of control and study chicks assumed to be of the same age. | 181 |
| 5.5. | The slopes and regression coefficients of Adélie and chinstrap culmen and flipper growth. | 188 |
| 5.6. | A comparison of adult and chick culmen and flipper growth. | 189 |
| 5.7. | Asymptotes of chicks from studies of Adélies and chinstraps. | 194 |
| 5.8. | Ratios of chick asymptote to adult weight for Adélies and chinstraps at King George and Signy Is. | 196 |
| 6.1. | The calculated and theoretical values of energy consumption during pre-laying and incubation fasts (first analysis method). | 213 |
| 6.2. | The ratios of calculated and predicted metabolic rates. | 214 |
| 6.3. | The weight of adults at the start and finish of pre-laying and incubation fasts, the mean length of each fast and the mean percentage of body weight last during each fast. | 216 |

Page

7.1. The weight of adults on return from foraging trips made during the chick rearing period. 227

7.2. Estimates of energy consumption calculated from theoretical values for brooding fasts. 231

7.3. Estimates of energy consumption calculated from theoretical values for foraging at sea. 232

7.4. Estimates of the total energy consumption and total krill requirements during the breeding season. 234

7.5. Estimates of the total chick food intake during the fledging period. 236

7.6. An estimate of the weight of krill available from parents during the fledging period. 237

7.7. A comparison of total chick food intake and the amount of food available from the parents. 238

7.8. The proportional biomass and krill and food consumption of birds breeding in the South Orkneys. 239

8.1. Breeding and feeding adaptations characteristic of four groupings of penguin species. 251

8.2. Summary of major differences and similarities between Adélies and chinstraps breeding at Signy Island in 1980/81 and 1981/82. 255

LIST OF FIGURES


| | | Page |
|---|---|---|
| 1.1. | The distribution of the main sites of breeding Adélie and chinstrap penguins. | 5 |
| 1.2. | A map of the South Orkney Islands. | 7 |
| 1.3. | Penguin breeding sites on Signy Island. | 8 |
| 1.4. | A comparison of the size and shape of Adélie and chinstrap penguin colonies on Gourlay Peninsula in 1952 and 1979. | 9 |
| 1.5. | The variation of the mean daily air temperature during the summer months of 1980/81 and 1981/82. | 12 |
| 1.6. | The variation of the mean daily wind speed (knots) during the summer months of 1980/81 and 1981/82. | 13 |
| 1.7. | The amount of pack ice recorded around Signy during the 1980/81 and 1981/82 breeding seasons. | 14 |
| 2.1. | A map of the Gourlay Peninsula penguin colonies, indicating the colonies that were studied. | 18 |
| 2.2. | Adélie penguin: the position of a band on the flipper (after Sladen, 1958) and the type of band used. | 20 |
| 2.3. | Adélie penguin in canvas bag, facilitating sexing and weighing. | 21 |
| 2.4. | The date of first arrival in relation to latitude of the breeding locality. | 27 |
| 2.5. | The distribution of Adélie egg laying dates. | 30 |
| 2.6. | The distribution of chinstrap egg laying dates. | 31 |
| 2.7. | The laying date of the first egg in relation to latitude of the breeding site. | 33 |
| 2.8. | Duration of pre-laying attendance between arrival at the nest site and egg laying and incubation shifts, between | 39 |

laying and hatching of the second egg, in Adélie and chinstrap penguins.

2.9. The distribution of Adélie and chinstrap hatching dates. 42

2.10. Variation with time in the percentage present in the colony and the cumulative percentage mortality of the original number of eggs and chicks in each sample and in the mortality rate of eggs and chicks for Adélies in 1980/81. 53

2.11. Variation with time in the percentage present in the colony and the cumulative percentage mortality of the original number of eggs and chicks in each sample and in the mortality rate of eggs and chicks for Adélies in 1981/82. 54

2.12. Variation with time in the percentage present in the colony and the cumulative percentage mortality of the original number of eggs and chicks in each sample and in the mortality rate of eggs and chicks for chinstraps in 1980/81. 55

2.13. Variation with time in the percentage present in the colony and the cumulative percentage mortality of the original number of eggs and chicks in each sample and in the mortality rate of eggs and chicks for chinstraps in 1981/82. 56

3.1. A comparison of the krill length/weight relationships derived by Lockyer (1973) and that calculated from krill in the stomachs of penguins caught at Signy I. 83

3.2. The mean length of krill taken in relation to time of year. 90

3.3. The distribution of krill caught by penguins. 92

3.4. Variation with time in the weight of stomach contents as a percentage of adult weight. 96

Page

3.5. The relationship between the logarithm of the digestion index and logarithm of krill length for the top sections of 27 Adelie and 32 chinstrap stomachs. 100

3.6. The relationship between culmen depth and mean krill length consumed for the two sexes in each species. 101

3.7. The relationship between culmen length and mean krill length consumed. 102

3.8. Length-frequency distributions of krill caught by Adélies and chinstraps at the South Orkneys in 1980/81 and by net hauls to the north-west of the South Orkneys in 1980/81. 109

3.9. Length-frequency distributions of krill caught by Adélies and chinstraps and by net hauls in Admiralty Bay, South Shetland Is. 111

3.10. Length-frequency distributions of krill in Adélie and chinstrap stomachs during three stages of their breeding seasons in 1980/81. 113

3.11. Length-frequency distributions of krill in Adélie and chinstrap stomachs during three stages of their breeding seasons in 1981/82. 114

4.1. The relationship between chick age and meal size given to Adélie chicks in 1980/81. 123

4.2. The relationship between chick age and meal size given to Adélie chicks in 1981/82. 125

4.3. The relationship between chick age and meal size given to chinstrap chicks in 1980/81. 127

4.4. The relationship between chick age and meal size given to chinstrap chicks in 1981/82. 128

Page

4.5. A comparison of the relationships between chick age and the combined meal size given to both twins and singles of both species in both years. 132

4.6. Timing of feeds, as indicated by frequency of adults visiting or changing over at the nest. 136

4.7. The percentage frequency of feeds delivered to Adélie study nests with chicks over several 24 hour periods during the crèche period. 138

4.8. The number of adult Adélies recorded entering colony A41 during a 24 hour period, expressed as absolute numbers and as a percentage of the 712 birds nesting in the colony. 139

4.9. The estimated foraging ranges of Adélies and chinstraps from Signy and their relationship with the sea-bottom topography around the South Orkney Is. 141

4.10. Diving depths of the chinstrap penguin. 143

4.11. Suggested activity pattern during a foraging trip by a penguin which has arrived at the colony at 1800 h. 150

5.1. The relationship between the mean weight and age of Adélie chicks in 1980/81. 165

5.2. The relationship between the mean weight and age of Adélie chicks in 1981/82. 166

5.3. The relationship between the mean weight and age of chinstrap chicks in 1980/81. 167

5.4. The relationship between the mean weight and age of chinstrap chicks in 1981/82. 168

5.5. The fitted growth curves of Adélie first, single and surviving chicks in 1980/81. 170

Page

5.6. The fitted growth curves of Adélie and chinstrap single chicks in 1981/82. 171

5.7. The fitted growth curves of Adélie single and first plus surviving chicks in 1980/81. 172

5.8. The relationship between mean weight and age of Adélie and chinstrap chicks of all categories. 174

5.9. The fitted growth curves of Adélie and chinstrap chicks of all categories, using the pooled weights for each species in each year. 175

5.10. Growth curves fitted to the exponential growth phase of Adélie chicks in 1980/81. 177

5.11. Growth curves fitted to the exponential growth phase of Adélie chicks in 1981/82. 178

5.12. Growth curves fitted to the exponential growth phase of chinstrap chicks in 1981/82. 179

5.13. The change in culmen depth with age of chinstrap chicks in 1981/82. 183

5.14. The change in culmen length with age of Adélie chicks in 1981/82. 184

5.15. The change in culmen length with age of chinstrap chicks in 1981/82. 185

5.16. The change in flipper length with age of Adélie chicks in 1980/81. 186

5.17. The change in flipper length with age of chinstrap chicks in 1981/82. 187

6.1. The weight loss of fasting Adélies in 1980/81 (second analysis method). 206

Page

6.2. The weight loss of fasting chinstraps in 1980/81 (second analysis method). 207

6.3. The weight loss of fasting chinstraps in 1981/82 (second analysis method). 208

6.4. The weight loss of fasting Adélies in 1980/81 (third analysis method). 209

6.5. The weight loss of fasting chinstraps in 1980/81 (third analysis method). 210

6.6. The weight loss of fasting chinstraps in 1981/82 (third analysis method). 211

6.7. The weight loss of the Pectoralis major muscle during the breeding season. 217

6.8. Body weight loss and proportional Pectoralis major weight loss. 218

7.1. The variation during the breeding season of krill consumption by Adélies and chinstraps at Signy I. 241

7.2. The consumption of krill by Adélies and chinstraps combined at Signy I. 242

7.3. The variation during the breeding season of food consumption by all seabirds breeding at the South Orkney Is. 243

# LIST OF APPENDICES


| | | Page |
|---|---|---|
| 1.1. | The variation of the ice conditions around Signy I during the summer months of 1980/81. | 292 |
| 2.1. | The dimensions and descriptions of all the colonies used in this study. | 294 |
| 2.2. | The dates of first arrival at breeding sites. | 295 |
| 2.3. | Laying dates and intervals from Adélie and chinstrap breeding sites. | 297 |
| 2.4. | Hatching dates from Adélie and chinstrap breeding sites. | 299 |
| 2.5. | Breeding success data of Adélie and chinstrap penguins from main studies. | 300 |
| 3.1. | Length-frequency distribution of the number of krill from each length class. | 301 |
| 3.2. | Length-frequency distribution of the number of krill from each length class found in stomachs of each sex from each sample. | 302 |
| 3.3. | Length-frequency distribution of the weight of krill in each length class found in each sample. | 304 |
| 3.4. | A comparison of the percentage distributions of the number and weight of krill from each length class found in each sample. | 305 |
| 3.5. | The mean adult weight, krill weight and proportional krill weight of each sample. | 306 |
| 4.1. | The variation with chick age of the mean meal size (± 1 sd.) given to Adélie chicks in 1980/81. | 308 |
| 4.2. | The variation with chick age of the mean meal size (± 1 sd.) given to Adélie chicks in 1981/82. | 311 |

Page

4.3. The variation with chick age of the mean meal size (± 1 sd.) given to chinstrap chicks in 1980/81. 313

4.4. The variation with chick age of the mean meal size (± 1 sd.) given to chinstrap chicks in 1981/82. 314

4.5. The mean meal size and frequency of feeds to chicks during the guard and crêche periods. 318

6.1. The mean weight loss and energy consumption of adults during pre-laying attendance and incubation (first analysis method). 319

6.2. The mean weight loss and energy consumption of adults during incubation (second analysis method). 320

6.3. The mean weight loss and energy consumption of adults during incubation (third analysis method). 321

8.1. Synthesis of the available information on the breeding biology, feeding ecology, distribution and demography of the Spheniscidae. 322

# Chapter One

## Introduction

## Aims

There have been many studies of the breeding biology and feeding ecology of sympatrically breeding, closely-related species which have attempted to identify factors important in promoting or maintaining ecological isolation (Lack, 1971). Rather few such studies of seabirds have been made, but notable are those by Bedard (1969 a and b) on auks; Berruti (1979) on sooty albatrosses; Harris (1969 a) on storm petrels in the Galapagos Islands; Hunter (1983) on giant petrels; Nelson (1978) on the Sulidae and Tickell and Pinder (1975) and Prince (in press) on black-browed and grey-headed albatrosses.

In the Antarctic, the breeding distributions of the Adelie penguin Pygoscelis adeliae and the chinstrap penguin Pygoscelis antarctica overlap extensively in the area of the Antarctic Peninsula and adjacent island groups, including the South Orkney Islands (lat.60°43'S., long.45°38'W.). These are near the northern limit of the breeding distribution of Adélie penguins, but near the centre of that of the chinstrap penguin. The many previous studies of the Adélie penguin include those by Sladen (1958) at Signy I, South Orkney Islands and Hope Bay, Antarctic Peninsula Sapin-Jaloustre (1960) at Adélie Land (lat.66°49'S., long.141°24'E.), Taylor (1962) at Cape Royds, Ross Sea and Ainley and others (1983) at Cape Crozier. In contrast, the chinstrap penguin has been little studied. The most notable exception has been the work of Trivelpiece and Volkman at King George I, South Shetland Is, who have carried out the only comparative study of Adélie and chinstrap diet (Volkman, Presler and Trivelpiece, 1980), chick growth (Volkman and Trivelpiece, 1980), nest-site competition (Trivelpiece and Volkman, 1979), nest-site selection (Volkman and Trivelpiece, 1981) and reproductive ecology (Trivelpiece, 1981).

There have been several attempts to quantify the amount of food consumed by seabirds through measurements of the energetic costs of

activities and the timing of events during and outside the breeding season. Croxall and Prince (1982) attempted to assess the consumption of food by seabirds breeding at South Georgia, and Croxall and others (in press c) make the first attempt at such an evaluation for all the breeding populations of seabirds and seals in the Scotia Sea.

Adélie and chinstrap penguins comprise 90 % of the avian biomass of the Scotia Sea, excluding South Georgia, (Croxall and others, in press c) and are important consumers of food resources. Estimates of their world breeding populations indicate at least 2.5 million pairs of Adélies and at least 6 million pairs of chinstraps (Croxall and others, in press b; Ainley and O'Connor, in press). Estimates of the effect on the resources of the Southern Ocean by this number of penguins have been based on few empirical data on the energetic costs of activities during and outside the breeding season.

This study, being only the second comparative study of Adélie and chinstrap penguins, has two main aims :

1. to demonstrate how two closely-related species of Southern Ocean penguin are ecologically adapted to breeding in the Antarctic and to breeding sympatrically. This will be achieved by comparing and contrasting the breeding and feeding strategies of Adélies and chinstraps.

2. to estimate and compare the food consumption of Adélies and chinstraps and compare this with the food consumption of other birds breeding in the South Orkneys.

As a contribution to these, the more specific aims are:

a) to describe the breeding biology of both species, with particular attention being paid to the timing and duration of each activity undertaken in the breeding season and to breeding success.

b) to describe the composition of the diet, the amount and type of prey consumed and the variation and the frequency of food supply to chicks.

c) to describe the growth pattern of Adélie and chinstrap penguin chicks.

d) to describe the energy consumption of fasting adults and use these and other values to estimate total energy consumption and feeding requirements during a breeding season.

## Background

Adélie and chinstrap penguins are small Antarctic and sub-Antarctic penguins (710-760 mm high and 3.5-4.5 Kg in weight) which breed colonially, often in immense numbers (see Plates 1 and 2). Both species only come ashore for extended periods in order to breed and to moult. At other times, they are to be found amongst pack ice, though this may apply more to Adélies than chinstraps. The main breeding localities of the two species are shown in Figure 1.1. The Adélie breeding distribution ranges from Bouvet I (lat.54°23'S., long.03°24'E.) to Ross I (lat.77°30'S., long.168°00'E.), but over 40 % of the total population breed in the Ross Sea area. The chinstrap breeding distribution ranges from Heard I (lat.53°06'S., long.73°30'E.) to Balleny I (lat.66°55'S., long.163°20'E.), but over 90 % breed on the islands of the Scotia Arc (Sladen, 1964; Watson, 1975; Croxall and Kirkwood, 1979; Ainley and O'Connor, in press).

This study was carried out at Signy Island, South Orkney Islands during the austral summers of 1980/81 and 1981/82. The environmental conditions during the two breeding seasons studied were very different, with prolonged pack ice presence in 1980/81 and its relative absence in 1981/82. Although it would have been desirable to have carried out work during two very similar breeding seasons, to ensure replication of results, it was nevertheless useful to be able to ensure replication of penguin ecology varied under very different environmental conditions.

PLATE I



Chinstrap penguin and
week old chick



Adélie penguin and three week old chick



PLATE 2. Aerial view of Gourlay Peninsula, Signy Island with Adélie penguin colonies showing clearly as dark patches.

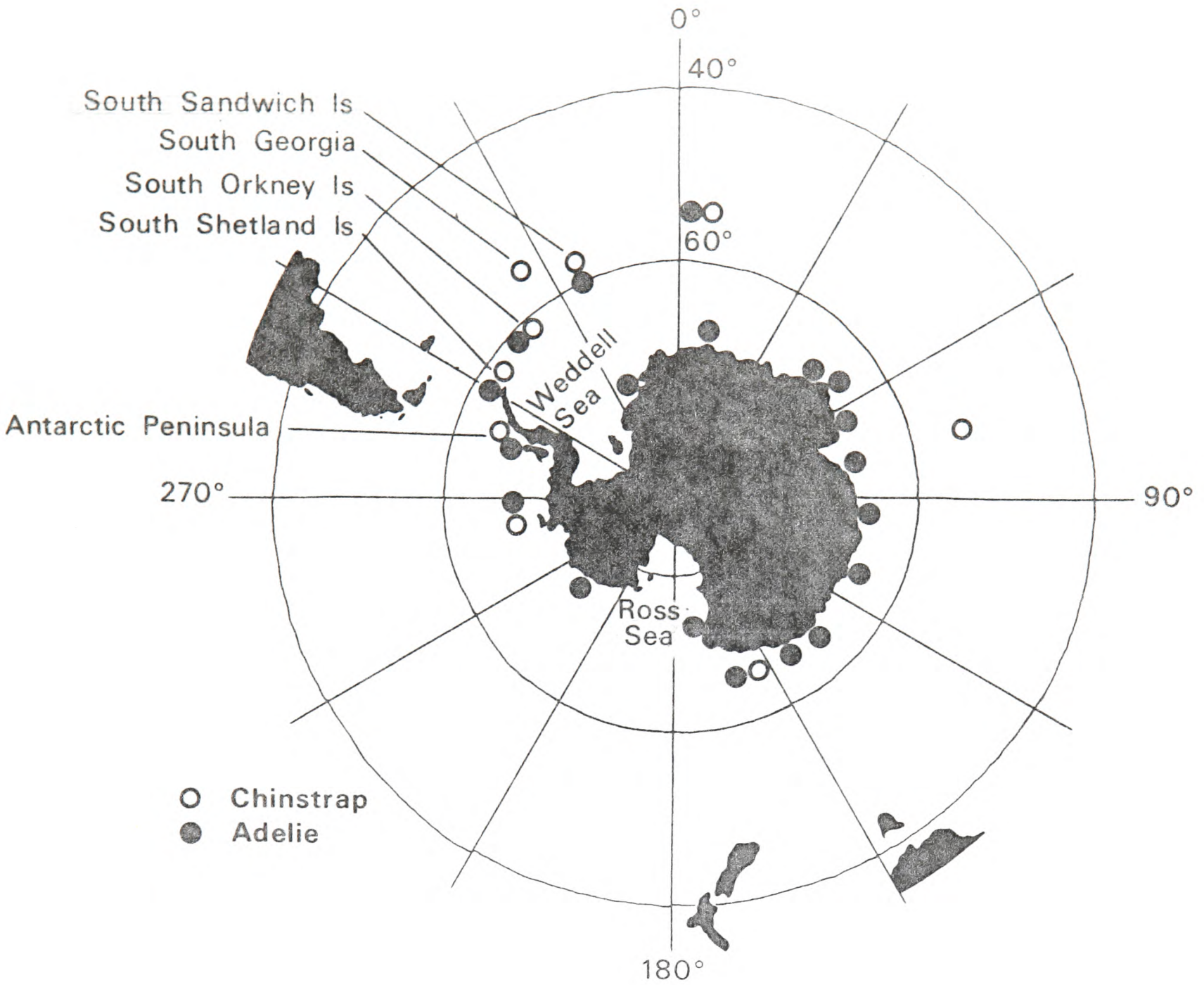



Figure 1.1. The distribution of the main rookeries of breeding Adélie and chinstrap penguins (after Watson, 1975). (Note: there are 27 Adélie rookeries on the coast of the Ross Sea.)

## The study site

### a. General description

The South Orkney Islands (Figure 1.2) form part of the Scotia Arc and lie on the boundary of the Scotia and Weddell Seas, about 550 km south of the Antarctic convergence. The nearest landmass is Clarence I, South Shetland Is, which is about 450 km away. To the north of the largest island, Coronation I, there is a confluence of the Antarctic circumpolar current and the Weddell sea current. This confluence is about 60 km from Signy I by the most direct sea route. Signy I (Figure 1.3) is the fourth largest and most southerly island of the group, with an area of 20 $km^2$, measuring 8 km and 5 km at its maximum axes. Approximately three-quarters of the island is permanently or semi-permanently snow or ice covered. The ice and snow-free areas comprise nearly all the coastal regions and are largely covered by lichens and mosses.

Adélie, chinstrap and gentoo Pygoscelis papua penguins and the occasional macaroni Eudyptes chrysolophus penguin breed in the areas indicated on Figure 1.3. In 1978/79, estimates of the numbers of breeding Adélie and chinstrap penguins were 37 000 and 80 000 pairs, respectively. These figures represent increases of 300 % and over 800 % over the past 30 years, which are attributed to enhanced food availability resulting from declining populations of large baleen whales (Sladen, 1964; Conroy, 1975; Laws, 1977; Volkman and Trivelpiece, 1980; Croxall and others, 1981). Few past records of the size and position of the Signy penguin colonies exist, but comparison (Figure 1.4) of the maps drawn in 1952 and 1979 (Croxall and Kirkwood, 1979) shows how the increase in penguin numbers has affected colony size and configuration in the Gourlay Peninsula area of the island. Chinstrap colonies have increased in size and numbers and there has been considerable colonization of completely new areas. Most Adélie colonies have increased in size, though it is possible that there has been some

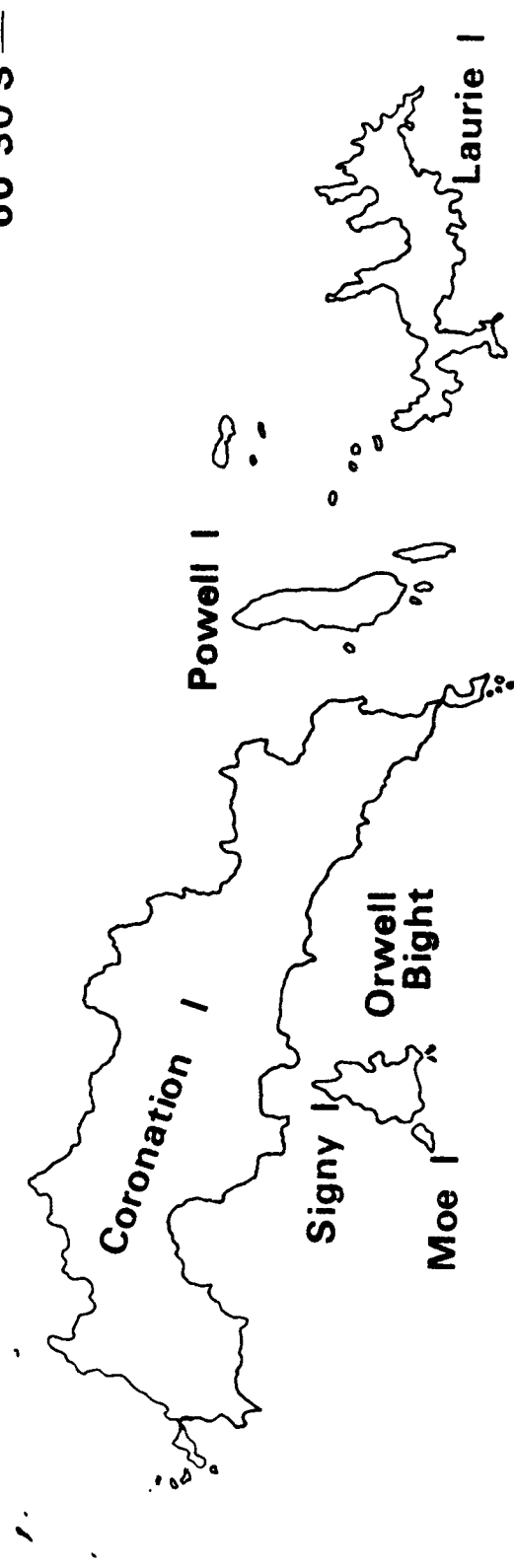



Figure 1.2. A map of the South Orkney Islands.

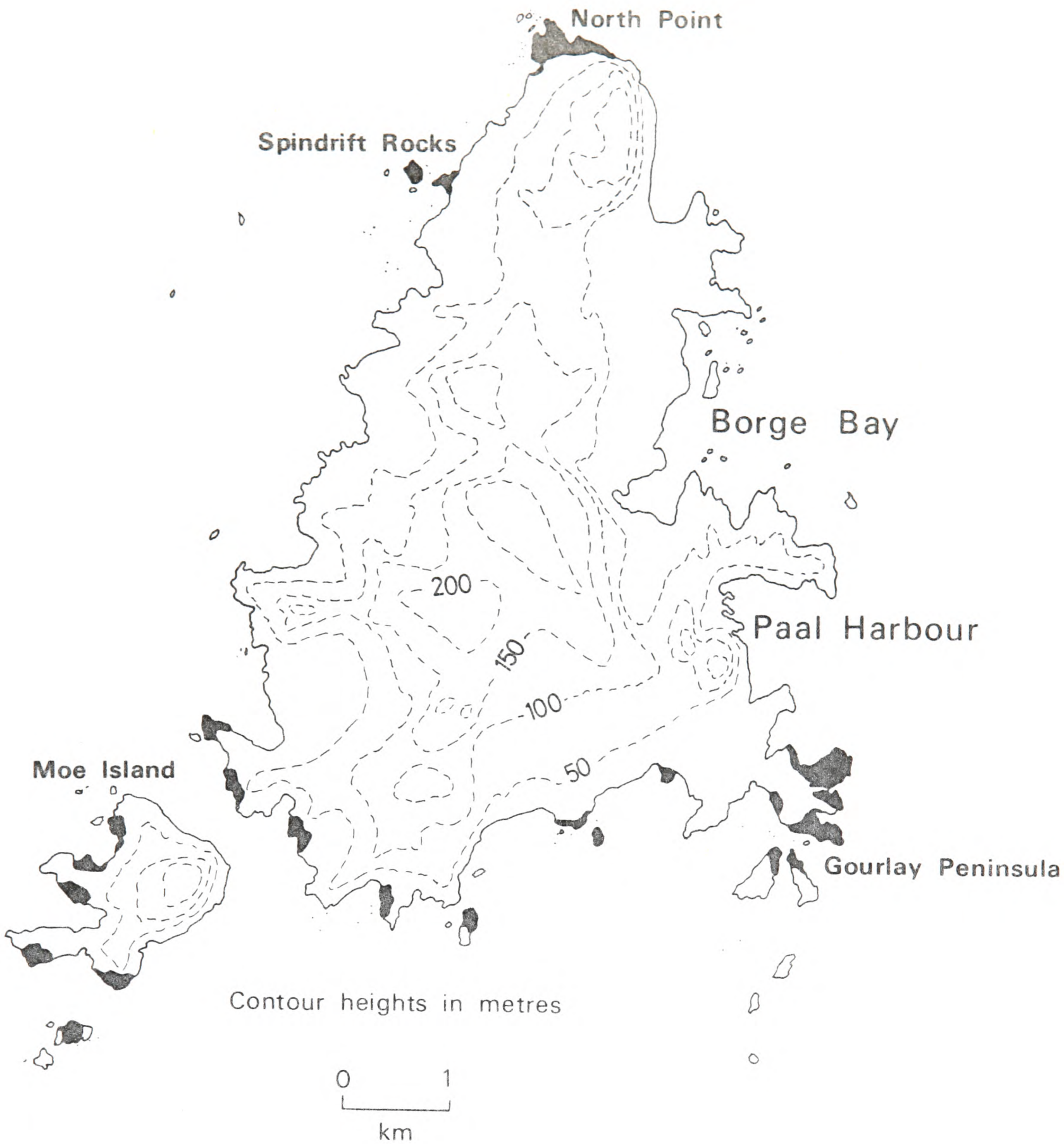



Figure 1.3. Penguin breeding sites on Signy Island.




Figure 1.4. A comparison of the size and shape of Adélie and chinstrap penguin colonies on Gourlay Peninsula in 1952 and 1979.

displacement of Adélies from nest-sites by chinstraps, as at King George I, South Shetland Is (Trivelpiece and Volkman, 1979). Recent estimates (since 1979) of selected colonies on Gourlay Peninsula show no consistent overall change in numbers, though it is possible that this may be detectable over a longer period.

b. Environmental conditions

The weather at Signy I during the summer months of the 1980/81 and 1981/82 breeding seasons was characterized by little sunshine, cool temperatures (Table 1.1 and Figure 1.5), moderate to high winds (Table 1.1 and Figure 1.6) and frequent precipitation.

In 1980/81, the pattern of ice presence was very different from that in 1981/82. The 1981/82 breeding season was relatively ice-free. All pack and fast ice moved away from the South Orkneys during November 1981. In 1980/81, the ice did not move away completely until the beginning of February 1981. It remained solid (fast) until the middle of December and then broke into pieces (pack) which drifted in an open or tight formation, depending on wind conditions, in the region of the islands until February 1981. The amount of pack ice around Signy during the two breeding seasons is shown in Figure 1.7, and the full details of the ice conditions at the start of the 1980/81 breeding season are given in Appendix 1.1.

Fast ice presents no real barrier to penguin movement, though it is possible that Adélies are more able to cross it than chinstraps. Pack ice is broken up fast ice which can be up to 4 or 5 m high, has a very irregular surface and is constantly moving. It appeared that at times neither Adélies nor chinstraps could cross it. A wide coastal belt of such ice could therefore totally prevent movement of adults to or from the colonies.

| | Mean monthly temperature (°C) | | Mean monthly wind speed (knots) | |
|---|---|---|---|---|
| Month | 1980/81 | 1981/82 | 1980/81 | 1981/82 |
| October | -3.9 | -7.2 | 16.4 | 14.0 |
| November | -2.0 | -1.1 | 13.7 | 18.0 |
| December | 0.0 | 0.2 | 8.1 | 15.0 |
| January | 0.7 | 2.3 | 12.6 | 14.1 |
| February | 1.7 | 2.1 | 14.0 | 11.2 |
| March | 1.2 | | 14.3 | |

Table 1.1. The mean monthly temperature and wind speed during the summer months of 1980/81 and 1981/82. (B.A.S. data).

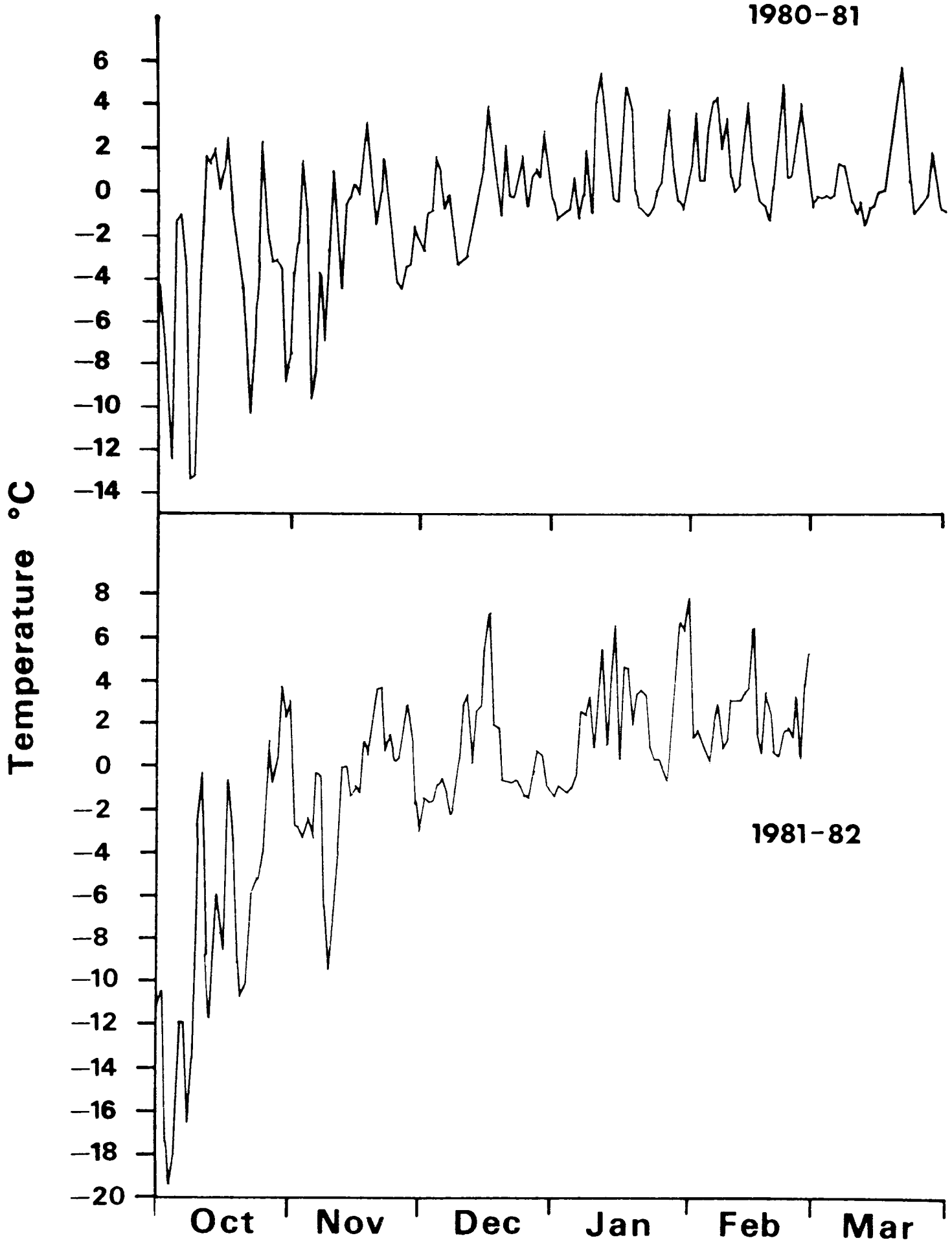



Figure 1.5. The variation of the mean daily air temperature during the summer months of 1980/81 and 1981/82. (B.A.S. data)

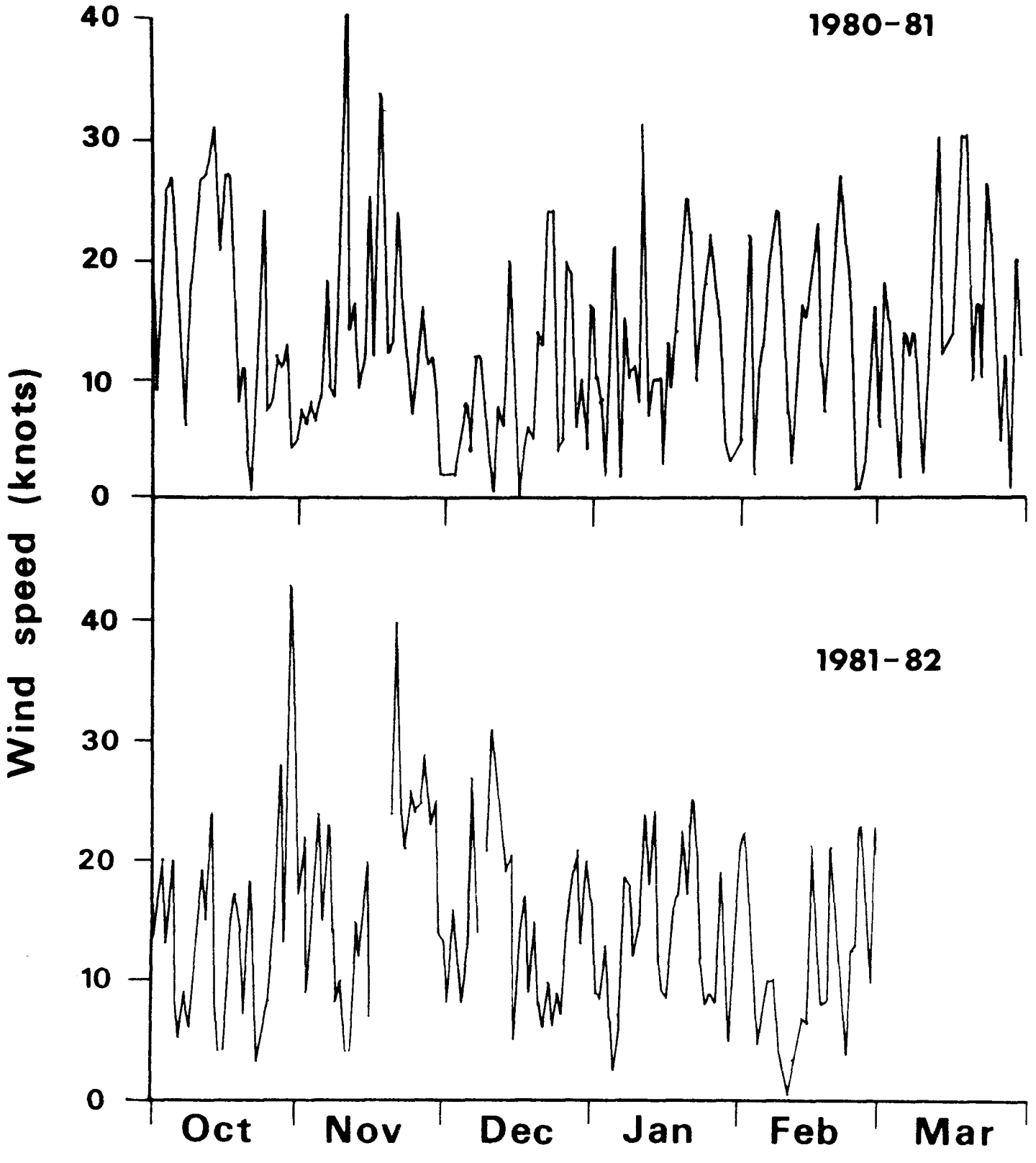



Figure 1.6. The variation of the mean daily wind speed (knots) during the summer months of 1980/81 and 1981/82. (B.A.S. data)

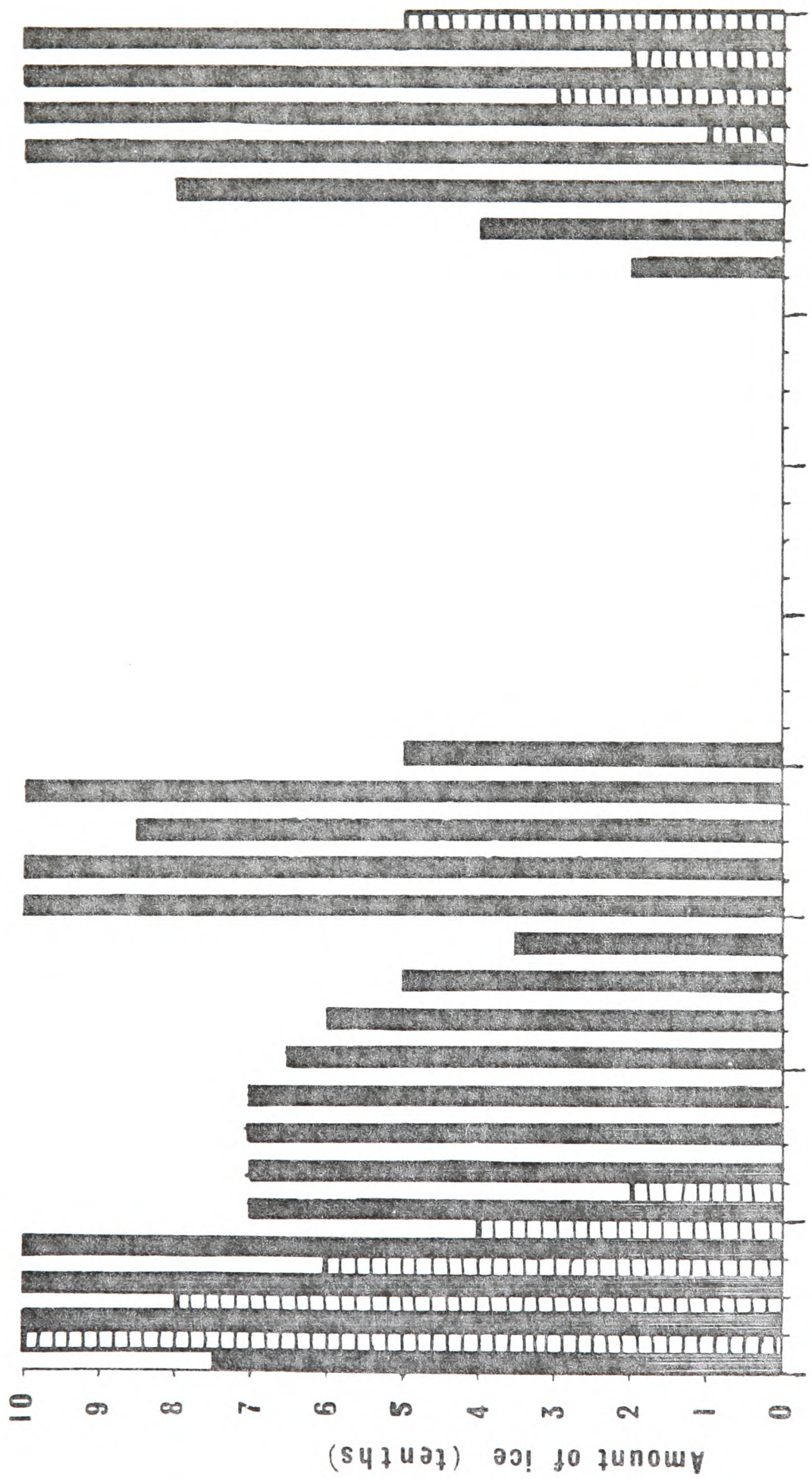



Figure 1.7. The amount of pack ice recorded around Signy during the 1980/81 and 1981/82 breeding seasons. (B.A.S. data)

# Chapter Two

## Breeding biology

# INTRODUCTION

A study of the breeding biology of a species is fundamental to the interpretation of its ecological adaptations. Adélie penguin breeding biology has been the subject of much research, including extensive general studies by Levick (1914) at Cape Adare, Sladen (1958) at Signy I and Hope Bay, Sapin-Jaloustre (1960) at Adélie Land, Taylor (1962) and Yeates (1968) at Cape Royds, Spurr (1975a) at Cape Bird and Ainley and others (1983) at Cape Crozier and intensive studies of particular aspects by Stonehouse (1963), Penney (1964), Oelke (1975), Yeates (1975), Mougin (1968), Tenaza (1971), Ainley and LeResche (1973), Derksen (1977), Ainley (1978), Davis (1980; 1982 a; 1982 b), and Ainley and DeMaster (1980).

In contrast, the breeding biology of the chinstrap penguin has been studied in detail only by Trivelpiece (1981) at King George I, South Shetland Is, which was also the only comparative study of both species at one breeding site.

With the aim of determining the ways in which Adélies and chinstraps are ecologically adapted to breeding in the Antarctic and to sympatric breeding at Signy I, this chapter presents data on their breeding biology at Signy I and interprets the intra- and interspecific differences within and between the two breeding seasons studied.

# METHODS

## Preparation of study nests

One colony of each species was selected, for the establishment of a study group of 60 nests, according to the following criteria:

1) reasonably isolated, to minimise interference from birds at other colonies.

2) easily accessible, for daily nest checks and for continuous observations from a hide erected nearby.

3) of medium size (100-1000 nests) and established for some years, to reduce the proportion of young, less experienced birds that might be particularly susceptible to disturbance during fieldwork.

Adélie colony 41 (A41) and chinstrap colony 80 (C80) both fulfilled these criteria. The size of each colony, and the position of each study nest with respect to the colony edge and the nearest nest, were recorded. The position of all the colonies mentioned in this thesis is given in Figure 2.1 and details of the size, shape and terrain of each colony summarised in Appendix 2.1.

The groups of 60 nests were chosen to lie in a narrow band across the centre of the colony from edge to edge to ensure a potential cross-section of age and experience. However, birds that panicked and fled the colony when approached were not selected.

Study nests were normally established when two birds had paired at the nest site and started courtship behaviour. Adélie nests were chosen on 22/10/80 (by R.A.Price) and 21/10/81, chinstrap nests were chosen on 1/12/80 (the earliest possible date after my arrival at Signy) and 23/11/81.

As the substrate was unsuitable for stakes, nests were marked by a numbered tag attached with wire to a stone placed nearby. Adélies ignored these markers, but chinstraps often removed them to use as nest material, necessitating frequent replacement.

Prior to incubation, birds were paint marked for identification, but flipper banding, which caused more disturbance to the birds, was carried out during incubation when the parents showed less tendency to flee the nest site if disturbed. The bands were of a design first used by Cooper and Morant (1981). When closed and fitted, the band was pear-shaped, measured 32 x 17 mm and the join between the two ends was adjacent to the

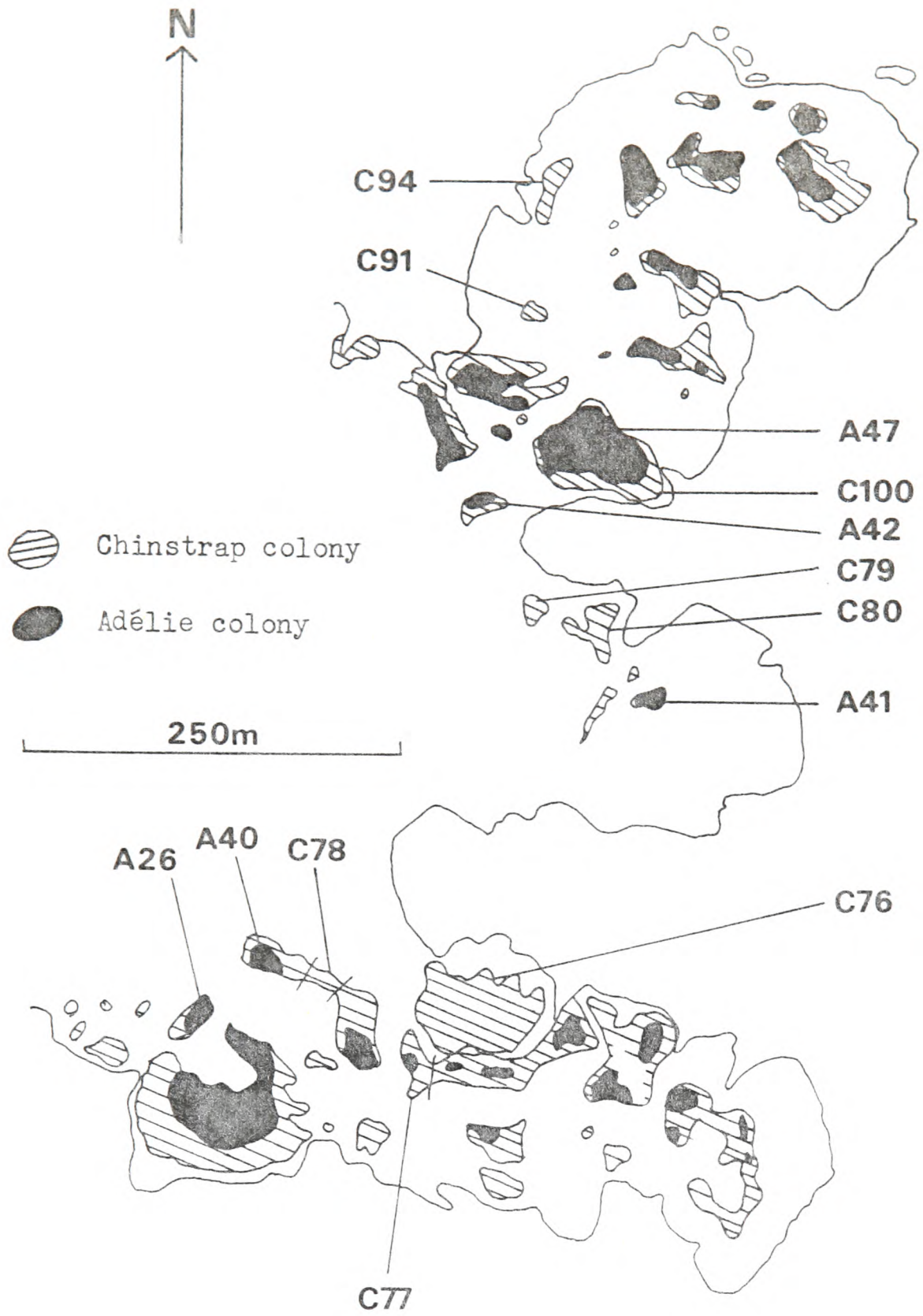



Figure 2.1. A map of the Gourlay Peninsula penguin colonies, indicating the colonies that were studied.

body (Figure 2.2). Numbers on the bands could easily be read from about 25 m using binoculars.

As the birds were banded single-handed, a technique different from that described by Sladen and Penney (1960) was used. The right hand is placed on the bird's head, gripping it gently and covering the eyes. It rarely struggled, even though its flippers and feet were free. The left hand is passed under the penguin, gripping each leg firmly between the fingers. The bird is then lifted up with the palm of the hand and the head placed under the left arm leaving the weight of the body supported horizontally along the left forearm. If the legs are gripped firmly, the bird does not struggle. The right flipper (which receives the band) is left free so the band can be easily applied with the right hand by first squeezing the band around the flipper and finally closing it with pliers. Banding usually took less than 30 seconds and the method used did not cause any desertions.

The sex of the study birds was determined whenever possible. The nine methods of sexing Adélies (Sladen, 1958) depend on marking and subsequent observation of breeding birds and are not totally reliable. Cloacascopy (Sladen and LeResche, 1970; Sladen, 1978) is the only reliable method available. With practice, it is quick and easy and causes no harm to the bird. The handling method used was similar to that already described except that, as both hands are needed to insert the cloacascope, the bird was placed head down into a conically shaped canvas bag (Figure 2.3) and held between the knees while sitting on a rock. Particularly nervous birds were not handled and were sexed by comparing their behavioural traits with birds already sexed by cloacal inspection. Few chinstraps were sexed, in 1980/81 because of an already high desertion rate caused by ice conditions, and in 1981/82 to reduce desertion in the only field season when a complete record of chinstrap breeding biology could be obtained.

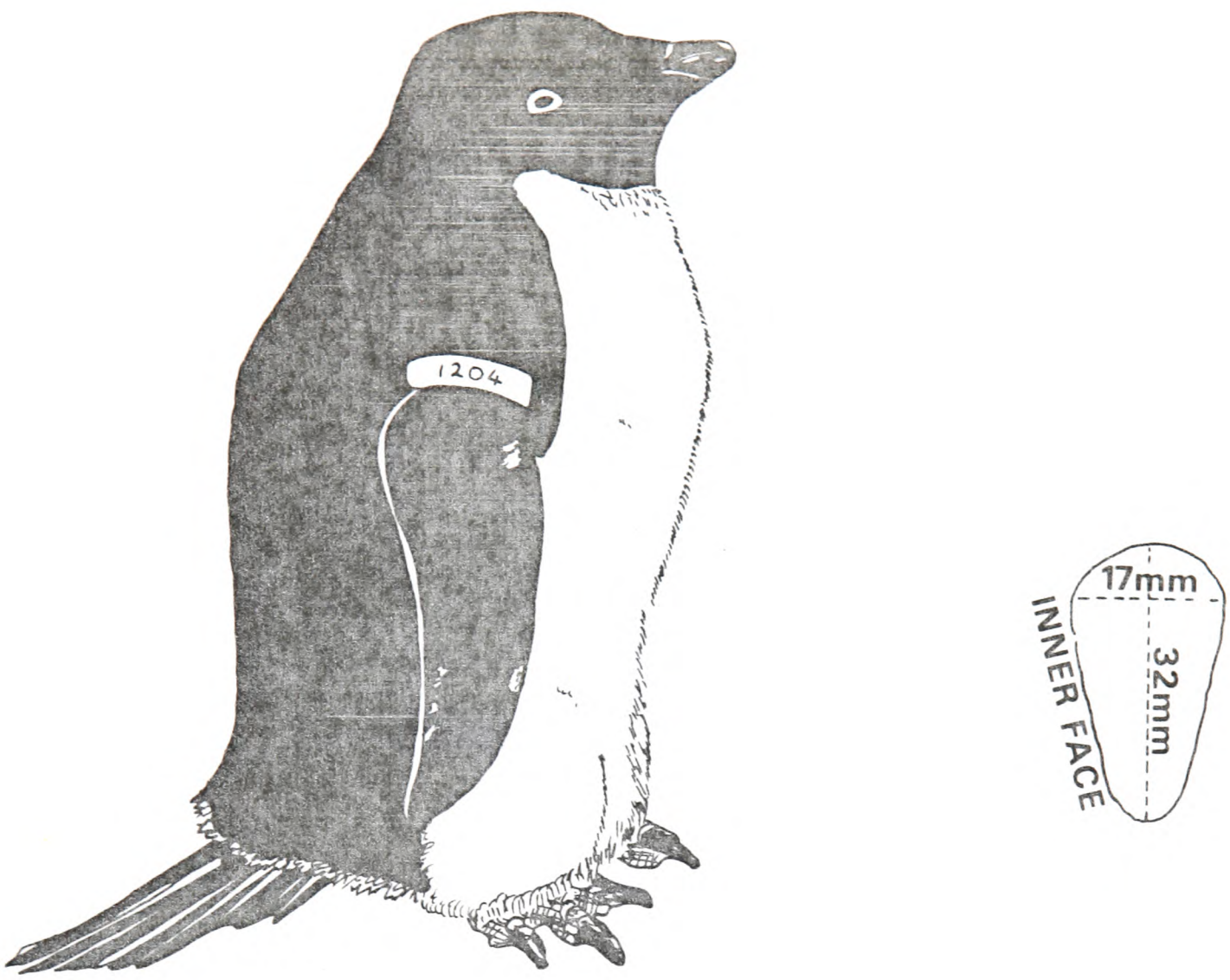



Figure 2.2. Adélie penguin : the position of a band on the flipper (after Sladen, 1958) and the type of band used.

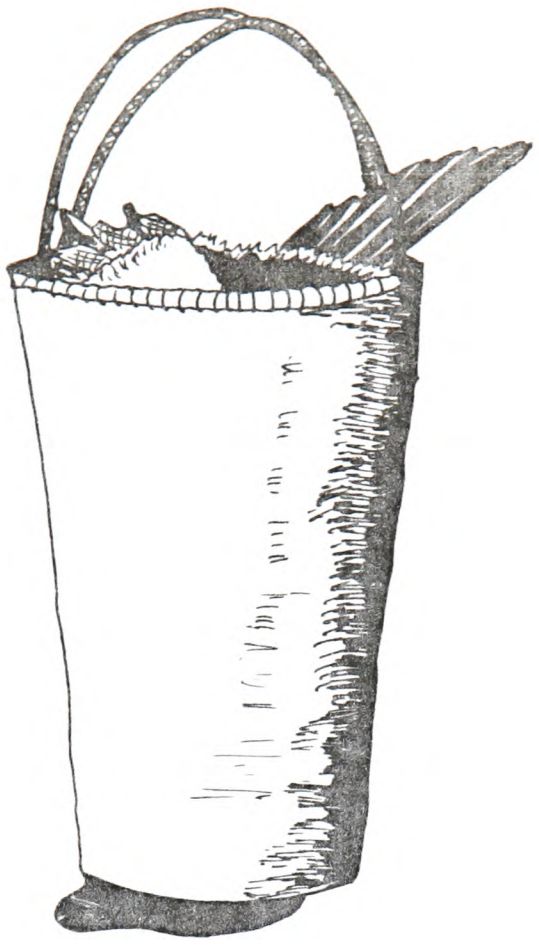


Figure 2.3. Adélie penguin in canvas bag, facilitating sexing and weighing.

Daily observations

Nests were checked daily between 0900 and 1200 local time. The identity of each bird at the nest was noted and on the day of laying the eggs of each clutch were weighed and measured and then colour marked to distinguish them. As incubating birds usually lifted themselves just off their eggs when approached, checks of clutch size were normally made without touching the birds. Eggs were reweighed a few days before hatching.

When chicks hatched, they were also colour coded. Just before the start of the crèche period, they were paint marked and had leg rings fitted. When their flippers were large enough, the chicks were flipper-banded and the leg rings were removed.

In 1980/81, chinstrap breeding was seriously disrupted by the heavy pack ice present around the island for much of the summer. By preventing partners returning to relieve their mates, it was almost certainly the cause of the many desertions by incubating adults. As nest failures increased, additional nests were brought into the sample in an attempt to maintain an acceptable sample size to record all the aspects of breeding biology. However, the ice was particularly difficult for penguins to cross at and after the time of chick hatching. This, together with unusually cold, wet and windy weather, resulted in heavy mortality during the first week after hatching. After only four weeks, all but two chicks in the sample had died and observations ceased.

To investigate variations in breeding capability, the breeding success of birds commencing with natural clutches of one and two eggs and artificial clutches of three eggs was studied. Of the Adélie three egg clutches, none were raised to hatching so, for both Adélies and chinstraps, three chick broods were created at hatching. Chicks were chosen so that the weights of the three chicks in the artificial broods differed by similar amounts. The transferred chick was always the youngest and

lightest of the three. The progress of these broods was followed in the same way as natural broods.

Data analysis

The laying date, interval between laying of eggs in the same clutch, egg volume and weight loss, incubation period, hatching date, hatching interval within a clutch and fledging date of eggs and chicks from all the study nests were recorded. The mean and standard deviation for the different egg and chick categories in each colony were compared intra- and inter-specifically and between years. Since nests were only visited daily, all these values (except egg volume) are open to an error of ± 1 day.

Egg volumes were calculated in 1981/82 using Volume = $0.5\ ab^2$, where a = egg length and b = maximum egg diameter (Reid, 1965). Egg weight at laying was calculated as a percentage of female bodyweight to see whether there was a difference between the two species. Female bodyweight was recorded in another colony and taken as the mean weight at the end of the Adélie female pre-laying attendance period of 27 females (see Table 6.3) and, since no similar chinstrap data are available, the mean weight at the start of the first chinstrap incubation shift of 15 females from another colony (see Table 6.3) plus the mean of the combined weight of the two eggs laid. The rate of egg weight loss was calculated from the difference between the recorded weights and the time between weighings and assuming a linear rate of weight loss throughout incubation. The resulting figure and the incubation period were used to estimate total weight loss during incubation and this was expressed as a percentage of the original weight.

The time between arrival at the nest site and laying (pre-laying attendance), the average length of each incubation shift and the total time invested by each parent in incubation were calculated from the records of attendance at the nest before and during incubation. Shifts that did not

culminate in relief by a partner without egg loss or desertion taking place were not used.

Parents did not sit tightly on the nest and incubate the eggs properly until the last egg in the clutch had been laid. The actual incubation period was, therefore, equal to the time between laying and hatching of the second or only egg in the clutch, although the time taken for all eggs to hatch was calculated. The second male shift by both species started just before hatching, and was judged to have ended when the female returned to the nest to feed the chicks for the first time.

The fledging period comprises the guard and crèche periods. During the guard period, an adult is constantly at the nest, first brooding the chicks and later standing beside them. The chicks are fed by the brooding adult until its mate returns or until it has regurgitated all of its stomach contents to the chicks. At the start of the crèche period, chicks are left on their own in the colony and parents return only to feed them. The age of chicks and the date at the start of the crèche period were recorded and compared.

The length of the chick fledging period was considered to be the time elapsed between hatching and leaving the colony for the sea. Some chicks that had left the colony were still fed by parents on the shoreline, even though they were fully moulted and had walked to the sea. In becoming independent, chicks probably go through three or four phases: completion of moult in the colony, leaving the colony, the first trip to the sea, and possibly a last feed by the parents on the shoreline. Here, the date a chick was last seen in the colony was taken as the fledging date.

Nest failure during incubation and the guard period was often caused by predation or environmental conditions, but also by desertion of the nest by the incubating or brooding bird before its mate had returned.

Breeding success of the study birds was determined at several stages: number of eggs laid per pair, number of eggs hatched per pair, the

percentage of eggs laid that hatched and the percentage of eggs hatched that fledged. The overall breeding success was expressed as the number of chicks that fledged per pair, irrespective of the number of eggs laid, and the number of chicks fledged as a percentage of the number of eggs laid.

For comparison of the percentages of eggs and chicks lost and the average lifespan of those eggs and chicks that were lost, eggs were divided into four categories: single, first, second and third eggs. If laid, third eggs were always replacements in a two egg clutch. Chicks were divided into five categories: single, first, second and surviving chicks from clutches where either the first or second egg had been lost during incubation.

The average survival of first and second eggs and chicks and the average total mortality in a two egg clutch were calculated for each day of the breeding season.

Several Adélie and chinstrap colonies at Signy I are visited three times each year to record the number of breeding pairs, the number of chicks hatched and the number fledged. These counts can be used as controls to measure the effect on the breeding success of the study birds of daily visits to their colonies. The control counts were not usually made on the exact day when all laying, all hatching etc. had taken place, but by adjusting the number of eggs, chicks, etc. recorded in the study nests to the number present on the dates that these were recorded in the control colonies, a direct comparison of breeding success was obtained. It was assumed that the timing and duration of breeding events in the control and study colonies were the same.

Many aspects of Adélie and chinstrap breeding biology were also recorded in the colonies used for studies of feeding ecology and bioenergetics. These data have been included in some of the calculations of mean laying date, laying interval, incubation shift lengths, incubation periods, mean hatching date and mean hatching intervals.

# RESULTS

## 1. Pre-laying

### a. Return to the colony after the winter

In 1981, the first Adélie was seen on 28 September and the first chinstrap on 5 November. The rate of build up of numbers of chinstraps seemed greater than Adélies, although this was not quantified. Many similar data exist for Signy and other localities (Appendix 2.2), and there is a significant correlation between the date of return of Adélies and the position (in degrees latitude south) of the breeding site (Figure 2.4).

### b. Pairing

In consecutive years, many pairs remain the same and use the same nest site (Ainley and others, 1983). At Signy, 53 % (55) of Adélies banded in 1980/81 returned in 1981/82. Of these, 20 pairs remained the same and, of the 20 pairs, 18 used the same nest. Chinstraps are not as faithful as Adélies to nest site or mate since only 31 % (51) of chinstraps banded in 1980/81 returned in 1981/82 and of these, 10 pairs were the same, and of the 10 pairs, 6 used the same nest.

During pairing and copulation, adults perform many rituals and displays. Adélie breeding behaviour has been well studied (Murray, 1909; Levick, 1915; Falla, 1937; Sladen, 1954; 1958; Sapin-Jaloustre, 1960; Taylor, 1962; Stonehouse, 1963; Penney, 1964; 1968; LeResche and Sladen, 1970; Ainley, 1975; Spurr, 1975b; 1977; Ainley and others, 1983), but that of chinstraps, although similar in many respects, has been little investigated.

### c. Pre-laying attendance times

These are given in Table 2.1. The attendance of both sexes is significantly longer for Adélies than chinstraps ($P < 0.001$).

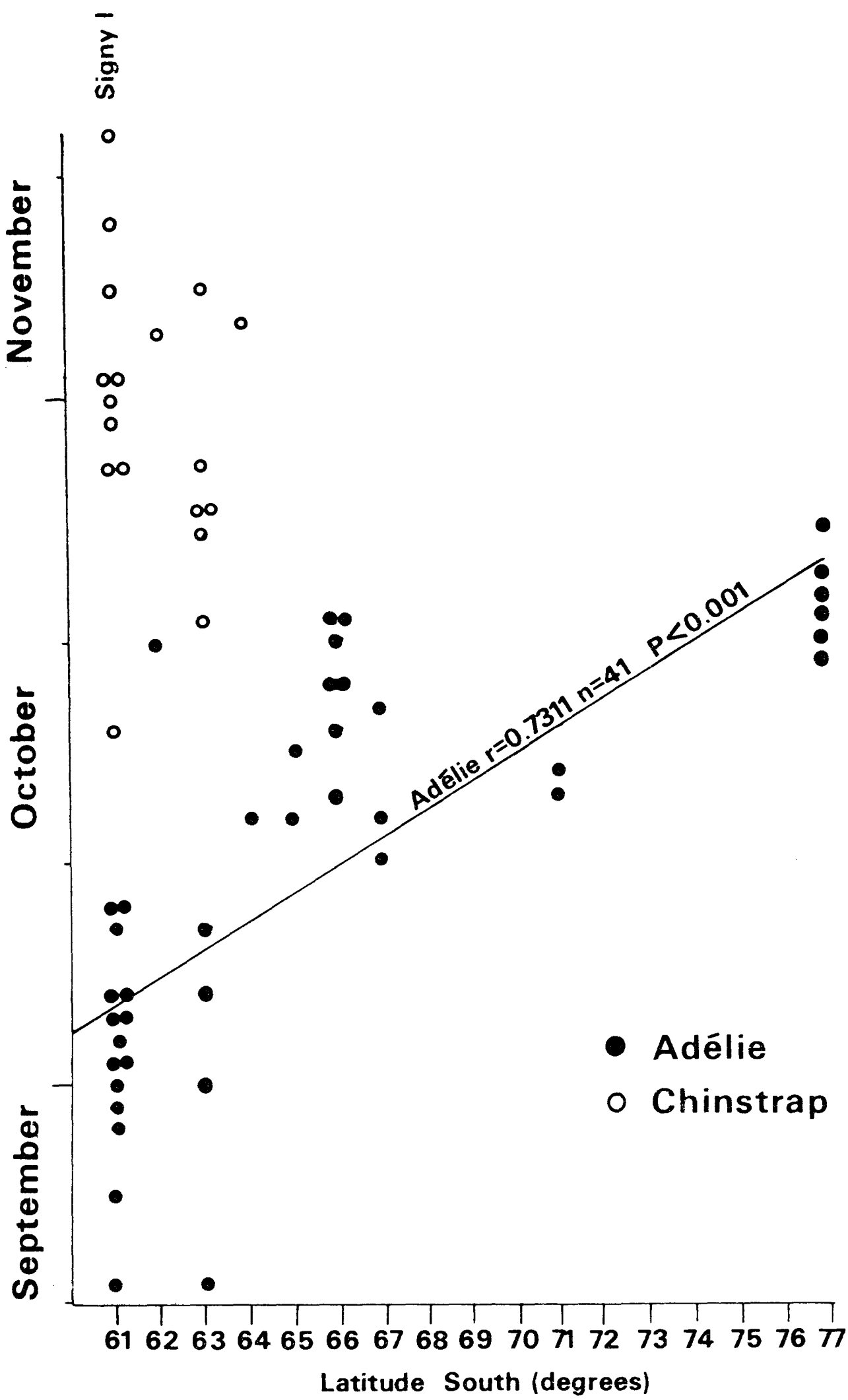



Figure 2.4. The date of first arrival in relation to latitude of the breeding locality. (Full details are given in Appendix 2.2.).

| Species | Sex | Pre-laying attendance period (d) | | |
|---|---|---|---|---|
| | | Mean | sd. | No |
| Adélie | Male | 18.0 | 3.6 | 26 |
| | Female | 17.6 | 2.6 | 19 |
| Chinstrap | Male | 14.3 | 2.0 | 21 |
| | Female | 13.3 | 2.9 | 17 |

Table 2.1. Pre-laying attendance periods of Adélies and chinstraps. (This was recorded in 1981/82 for birds banded in 1980/81 and was taken as the time between arrival at the nest site and egg-laying.)

2. Laying

a. Dates and laying synchrony

The distribution and range of laying dates are given in Figures 2.5 and 2.6 and summarized in Table 2.2. In 1980/81, chinstrap laying was much later than in 1981/82. This is because the sample was not established until after laying had begun in C80, which precluded the use of earlier laying birds. Previous data from Signy and elsewhere (Figure 2.7 and Appendix 2.3) show that Adélies lay later further south, but there is considerable year-to-year variation at the same site. Although the range is small, and there are few data, chinstrap laying dates appear to be relatively uninfluenced by latitude.

Synchrony of clutch initiation was analysed by comparing the standard deviation of the first egg laying date and the time taken for all the pairs in a sample to lay one egg. There was no discernable difference in laying synchrony by the two species.

b. Laying intervals

The laying interval between first and second eggs is about 3 days in both species (Table 2.3) but occasionally reaches 6 days. Only in 1980/81 was the laying interval for chinstraps significantly longer than that for Adélies ($P<0.002$).*

c. Observation of laying

There was a single observation made of an Adélie penguin laying an egg. This is the first such record, despite many hours of observations in penguin colonies during this and other studies. When first seen, the bird was in the incubating position and making periodic mewing sounds which

* All tests of significance used in this thesis are t-tests unless stated otherwise.

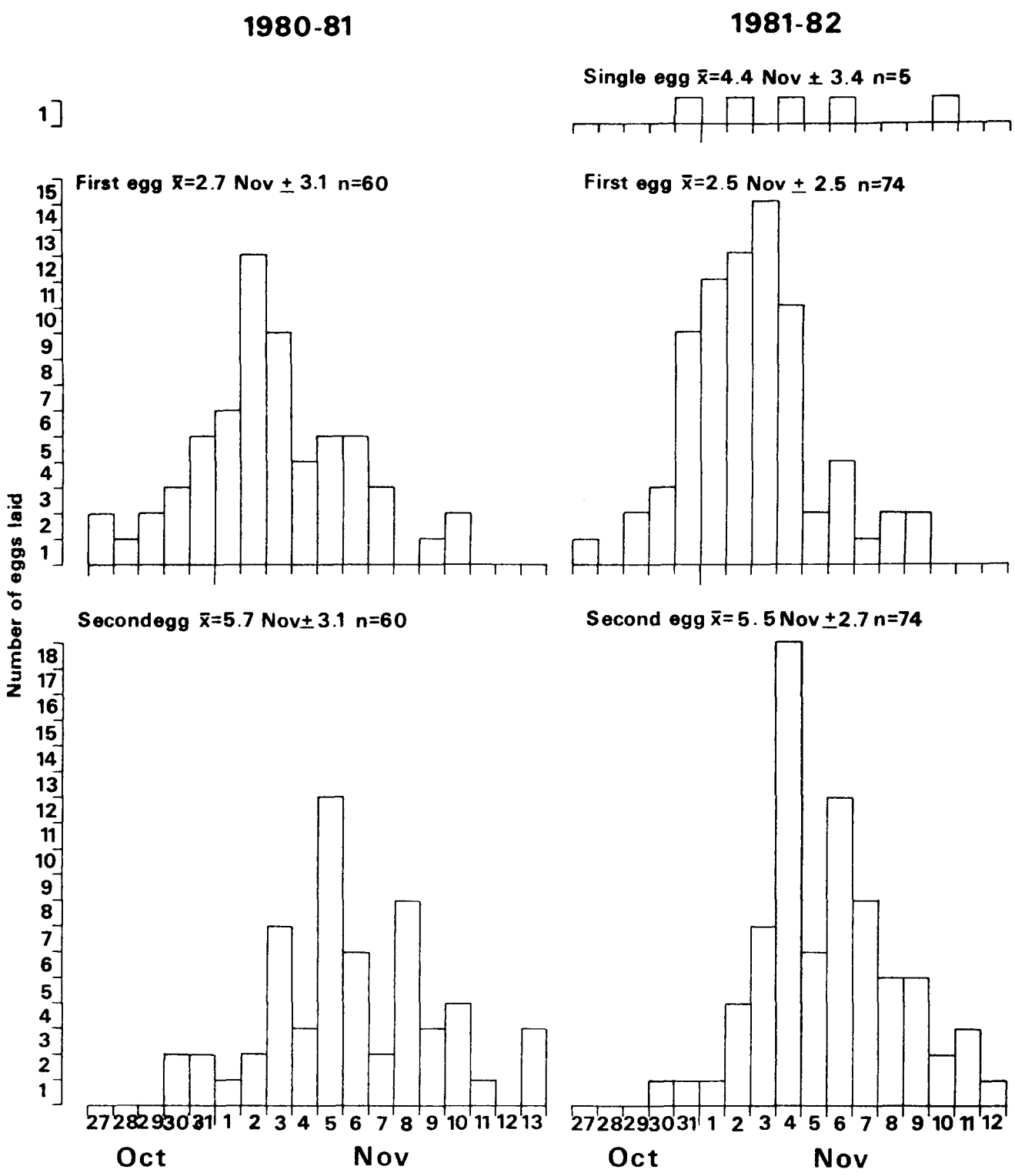



Figure 2.5. The distribution of Adélie egg laying dates. (In each case the mean laying date ± 1 standard deviation and the sample size are given.)

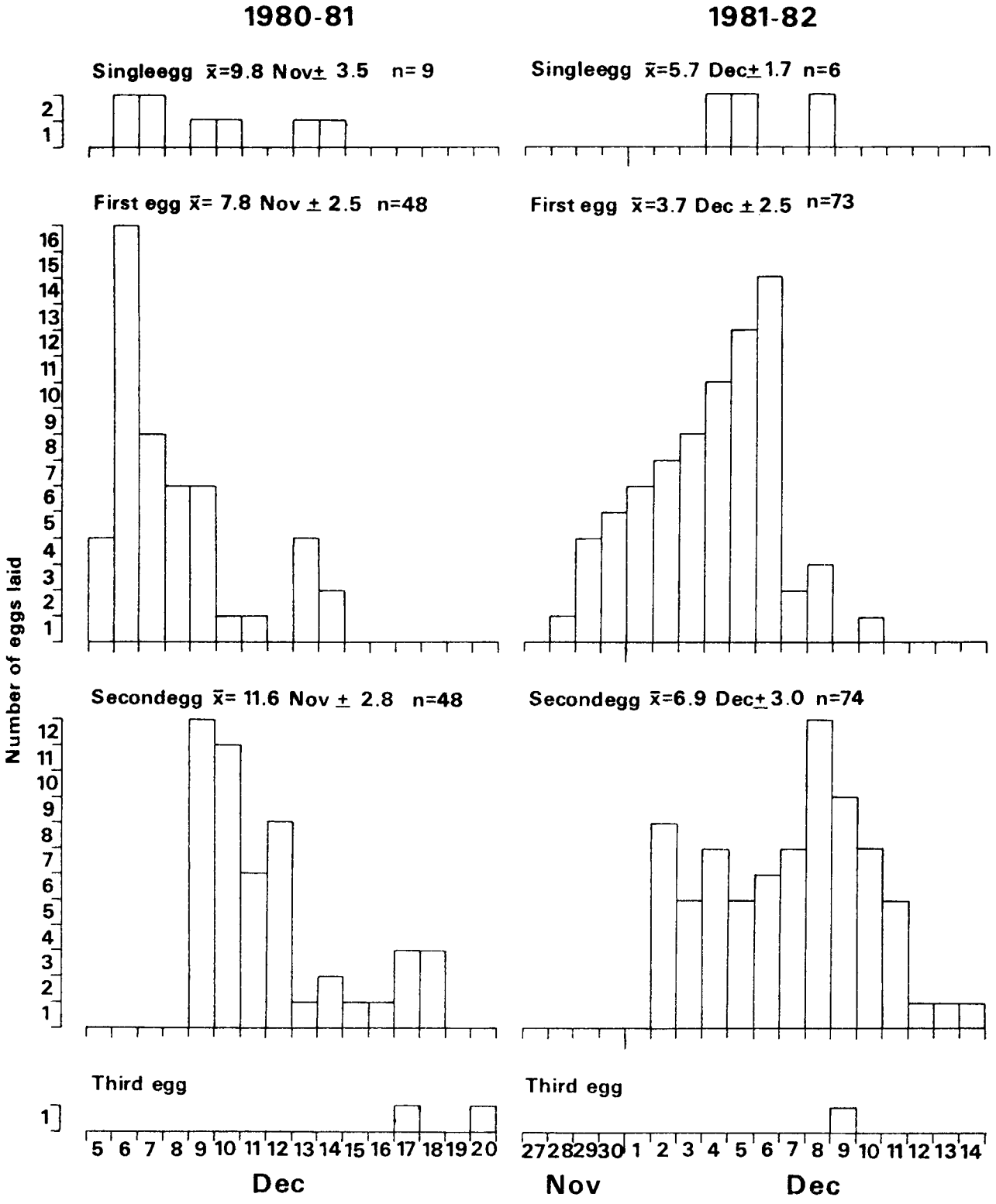



Figure 2.6. The distribution of chinstrap egg laying dates. (In each case, except for third eggs, the mean laying dates ± 1 standard deviation and the sample size are given.)

| Species | Year | Egg category | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Single | No | First | No | Second | No | Third | No |
| Adélie | 1980/81 | 07/11 | 2 | 03/11 | 60 | 06/11 | 60 | 11/11 | 2 |
| | 1981/82 | 04/11 | 5 | 03/11 | 74 | 06/11 | 74 | | |
| Chinstrap | 1980/81 | 10/12 | 8 | 08/12 | 48 | 12/12 | 48 | 18/12 | 2 |
| | 1981/82 | 06/12 | 6 | 04/12 | 73 | 07/12 | 73 | 09/12 | 1 |

Table 2.2. Mean and sample size of Adélie and chinstrap laying dates. (Laying dates of Adélie single and third eggs in 1980/81 were recorded in another colony.)

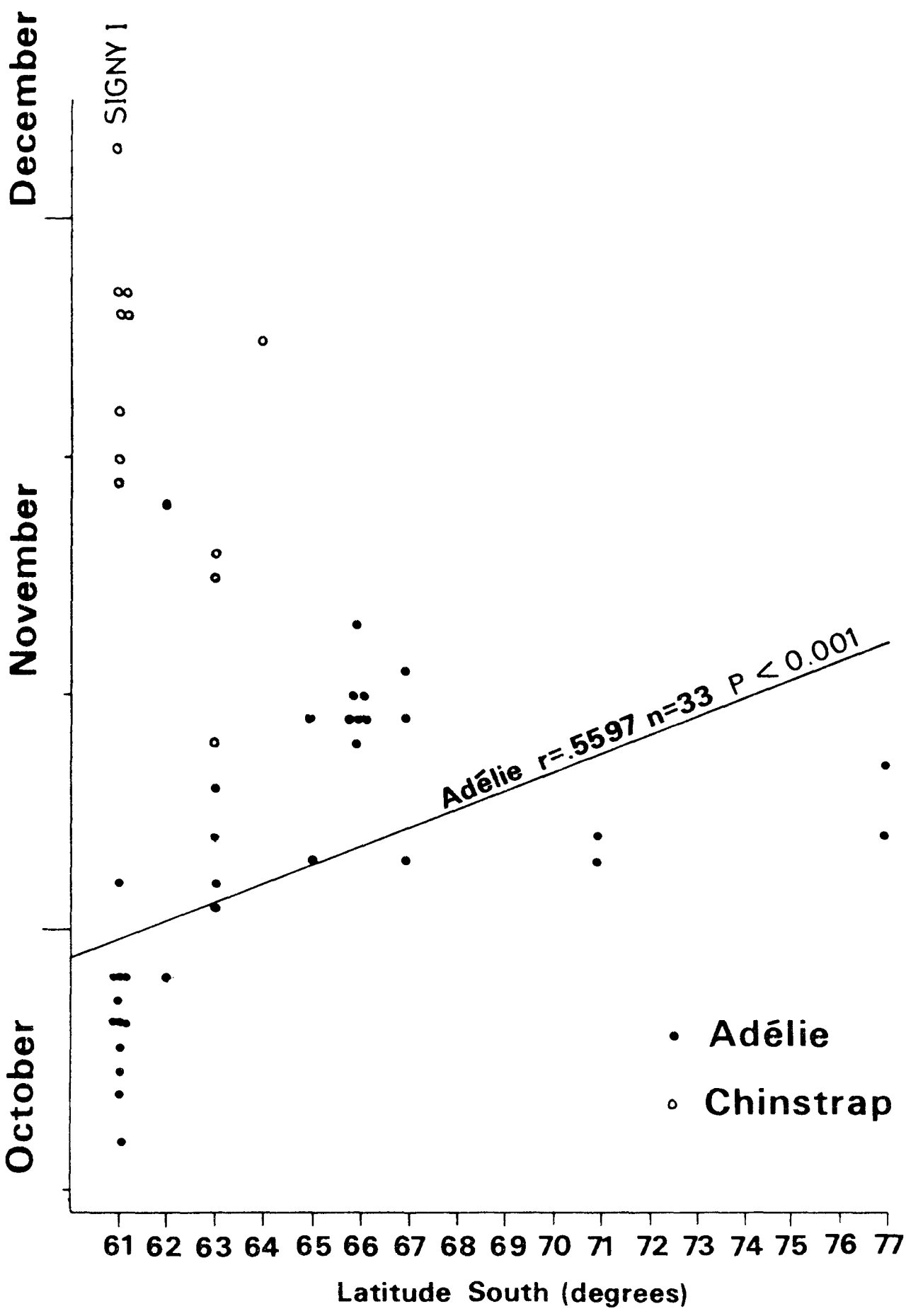



Figure 2.7. The laying date of the first egg in relation to latitude of the breeding site. (Full details are given in Appendix 2.3.).

| Year | Interval (d) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Adélie | | | | Chinstrap | | | |
| | Mean | sd. | range | No | Mean | sd. | range | No |
| 1980/81 | 3.1 | 0.7 | 1-4 | 130 | 3.4 | 0.8 | 1-4 | 91 |
| 1981/82 | 3.1 | 0.7 | 2-6 | 72 | 3.2 | 1.1 | 0-6 | 134 |

Table 2.3. Intervals between the laying of first and second eggs.

coincided with contractions of the posterior half of the body. After about a minute, the contractions stopped, the bird lifted itself off the nest and the egg dropped about 10 cm into the nest. Both parents looked at the egg and then the male started incubating. When laid, the egg was pale green, perhaps because bile was involved in shell production.

3. Eggs

Egg volumes and dimensions are given in Table 2.4. All chinstrap eggs have the same mean volume, but Adélie first eggs are on average significantly larger than single or second eggs and all Adélie eggs have greater mean volumes than chinstrap eggs of any category ($P<0.001$). Adélie egg measurements from other studies (Clarke, 1906; Taylor, 1962; Mougin, 1968; Yeates, 1968) show that first egg volume is larger than the second by a similar margin to that reported here. This is presumably also true of egg weights, although there are few data available from other studies.

Egg weight and weight loss and egg weight as a percentage of female bodyweight are given in Table 2.5. Adélie first eggs are on average heavier than second eggs and all chinstrap eggs ($P<0.001$). The incubation periods of eggs of the same category of both species is the same (see next section) but chinstrap eggs lose slightly more of their weight during incubation than Adélie eggs ($P<0.001$). The weight loss of Adélie eggs at Cape Bird was 13 % of initial mass (Rahn and Hammel, 1982) which was less than but similar to that recorded here (15.7-16.0 %).

4. Incubation

a. Incubation shifts

The lengths of all the incubation shifts are given in Table 2.6 and a visual representation of the partition of the pre-laying attendance and incubation shifts by each sex is given in Figure 2.8.

| Species | Measurement | | Single eggs | First eggs | Second eggs |
|---|---|---|---|---|---|
| Adélie | Volume | Mean | 99.2 | 106.1 | 100.4 |
| | $cm^3$ | sd. | 4.3 | 8.2 | 8.3 |
| | | No | 5 | 73 | 73 |
| | | Range | 93.3-104.4 | 89.2-126.1 | 80.6-119.0 |
| | Length | Mean | 67.3 | 69.2 | 68.4 |
| | mm | sd. | 1.7 | 2.6 | 2.9 |
| | | No | 5 | 73 | 73 |
| | | Range | 64-68 | 61-75 | 59-76 |
| | Maximum | Mean | 54.0 | 55.3 | 54.2 |
| | diameter | sd. | 0.9 | 1.6 | 1.6 |
| | mm | No | 5 | 73 | 73 |
| | | Range | 53-55 | 52-59 | 51-58 |
| Chinstrap | Volume | Mean | 92.0 | 91.9 | 92.1 |
| | $cm^3$ | sd. | 0.9 | 7.3 | 7.0 |
| | | No | 3 | 51 | 56 |
| | | Range | 91.3-93.3 | 82.5-116.9 | 76.8-108.2 |
| | Length | Mean | 66.3 | 67.1 | 67.0 |
| | mm | sd. | 1.9 | 2.5 | 2.3 |
| | | No | 3 | 51 | 56 |
| | | Range | 65-69 | 62-72 | 62-73 |
| | Maximum | Mean | 52.7 | 52.3 | 52.4 |
| | diameter | sd. | 0.5 | 1.6 | 1.6 |
| | mm | No | 3 | 51 | 56 |
| | | Range | 52-53 | 49-57 | 49-56 |

Table 2.4. Adélie and chinstrap egg measurements, 1981/82. (Mean values were obtained by calculating the volume of each individual egg and then taking the mean of these.)

| | First egg | | | | Second egg | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | sd. | range | No | Mean | sd. | range | No |
| **Adélie** | | | | | | | | |
| Laying wt. (g) | 120.8 | 9.6 | 101-145 | 79 | 113.2 | 9.4 | 85-133 | 69 |
| Percent female wt.[1] | 3.3 | | | | 3.1 | | | |
| Wt. loss/day ($gd^{-1}$) | 0.54 | 0.23 | 0.04-1.07 | 68 | 0.53 | 0.21 | 0.16-1.00 | 53 |
| Total wt. loss (g) | 18.9 | | | | 18.1 | | | |
| Percent wt. loss | 15.7 | | | | 16.0 | | | |
| **Chinstrap** | | | | | | | | |
| Laying wt. (g) | 113.6 | 8.7 | 94-140 | 52 | 112.2 | 7.7 | 96-130 | 55 |
| Percent female wt.[2] | 3.1 | | | | 3.1 | | | |
| Wt. loss/day ($gd^{-1}$) | 0.55 | 0.10 | 0.40-0.80 | 54 | 0.56 | 0.12 | 0.30-0.90 | 55 |
| Total wt. loss (g) | 19.8 | | | | 19.0 | | | |
| Percent wt. loss | 17.4 | | | | 16.9 | | | |

Notes: [1] 3631 g ; [2] 3610 g

Table 2.5. Egg weights and weight loss (1981/82).

| Species | Year | | First male shift (d) | First female shift (d) | Second male shift (d) |
|---|---|---|---|---|---|
| Adélie | 1980/81 | Mean | 12.6 | 14.0 | 5.1 |
| | | sd. | 1.7 | 2.0 | 2.2 |
| | | No | 123 | 112 | 104 |
| | | Range | 9-17 | 10-19 | 1-12 |
| | 1981/82 | Mean | 13.7 | 12.8 | 5.4 |
| | | sd. | 1.7 | 2.1 | 2.3 |
| | | No | 77 | 73 | 74 |
| | | Range | 9-18 | 8-18 | 1-12 |

| Species | Year | | First female shift (d) | First male shift (d) | Second female shift (d) | Second male shift (d) |
|---|---|---|---|---|---|---|
| Chinstrap | 1980/81 | Mean | 6.1 | 11.2 | 9.6 | 7.6 |
| | | sd. | 2.0 | 2.8 | 1.4 | 1.6 |
| | | No | 67 | 45 | 21 | 29 |
| | | Range | 3-12 | 6-18 | 7-12 | 4-10 |
| | 1981/82 | Mean | 6.0 | 9.8 | 7.8 | 4.9 |
| | | sd. | 2.4 | 2.9 | 2.3 | 1.6 |
| | | No | 128 | 103 | 98 | 90 |
| | | Range | 1-14 | 5-18 | 4-15 | 1-09 |

Table 2.6. Incubation shift lengths. (Those of Adélies in 1980/81 and chinstraps in 1981/82 were obtained from more than one colony.)

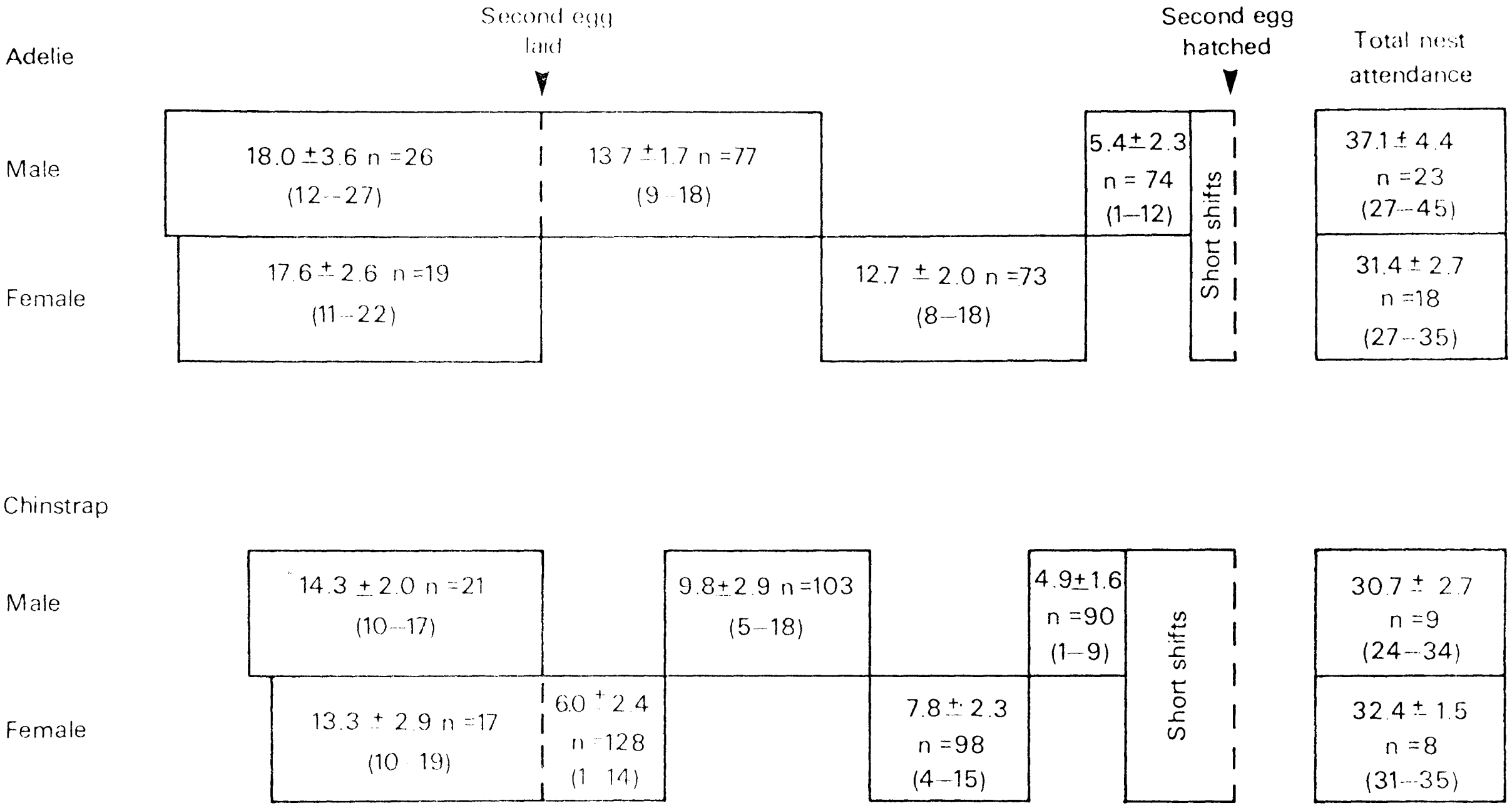



Figure 2.8. Duration of pre-laying attendance, between arrival at the nest site and egg laying, and incubation shifts, between laying and hatching of the second egg, in Adélie and chinstrap penguins. (Within each box, the values are mean ± 1 sd. and sample size with ranges with parentheses; the short shifts by either sex of both species did not follow any pattern but were less than three days in duration; total nests attendance, between initial date of arrival at the nest and hatching of the second egg, was measured for birds that hatched eggs successfully and where the date of arrival was recorded; some incubation shift data were obtained from more than one colony.)

The pattern of incubation shifts by the two species was different. First shifts of chinstraps were by females but those of Adélies were by males. Shifts subsequently alternated between males and females. For each sex, total nest attendance by Adélies was greater than by chinstraps ($P<0.005$). Adélie males spent more time at the nest in pre-laying attendance and incubation than females ($P<0.001$), but there was no difference in the lengths of the first incubation shifts by each sex. There was also no difference between the sexes for chinstraps. Assuming pre-laying attendance by each sex was the same in both years, the total nest attendance by Adélies of each sex was the same in both years but, with the exception of the first female shift, chinstraps of each sex were in pre-laying attendance and incubating for longer in 1980/81 than 1981/82 ($P<0.002$).

b. Incubation period

Incubation periods of first and second eggs are given in Table 2.7. First eggs are only partially incubated before the second egg is laid, which causes both eggs to hatch almost simultaneously.

Chinstrap first eggs took slightly longer to hatch than Adélie first eggs in both years, but all other first eggs and all second eggs had the same incubation period.

5. Hatching

a. Dates

The distribution and range of hatching dates of eggs from the study colony are given in Figure 2.9. The late hatching dates of chinstrap eggs in 1980/81 are a consequence of unavoidably establishing the sample later in that year. The mean $\pm$ 1 sd. of the hatching dates of eggs from the study colony and several other colonies are given in Table 2.8.

| | | Incubation period (d) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Adélie | | | | Chinstrap | | | |
| Year | Egg | Mean | sd. | range | No | Mean | sd. | range | No |
| 1980/81 | First | 35.6 | 1.5 | 33-40 | 84 | 36.4 | 1.1 | 33-39 | 21 |
| | Second | 33.5 | 1.1 | 32-38 | 70 | 33.4 | 1.0 | 31-38 | 28 |
| 1981/82 | First | 35.3 | 1.2 | 33-39 | 60 | 36.2 | 1.3 | 33-39 | 65 |
| | Second | 33.9 | 1.2 | 32-38 | 40 | 33.9 | 1.1 | 31-38 | 71 |

Table 2.7. Incubation period of first and second eggs.

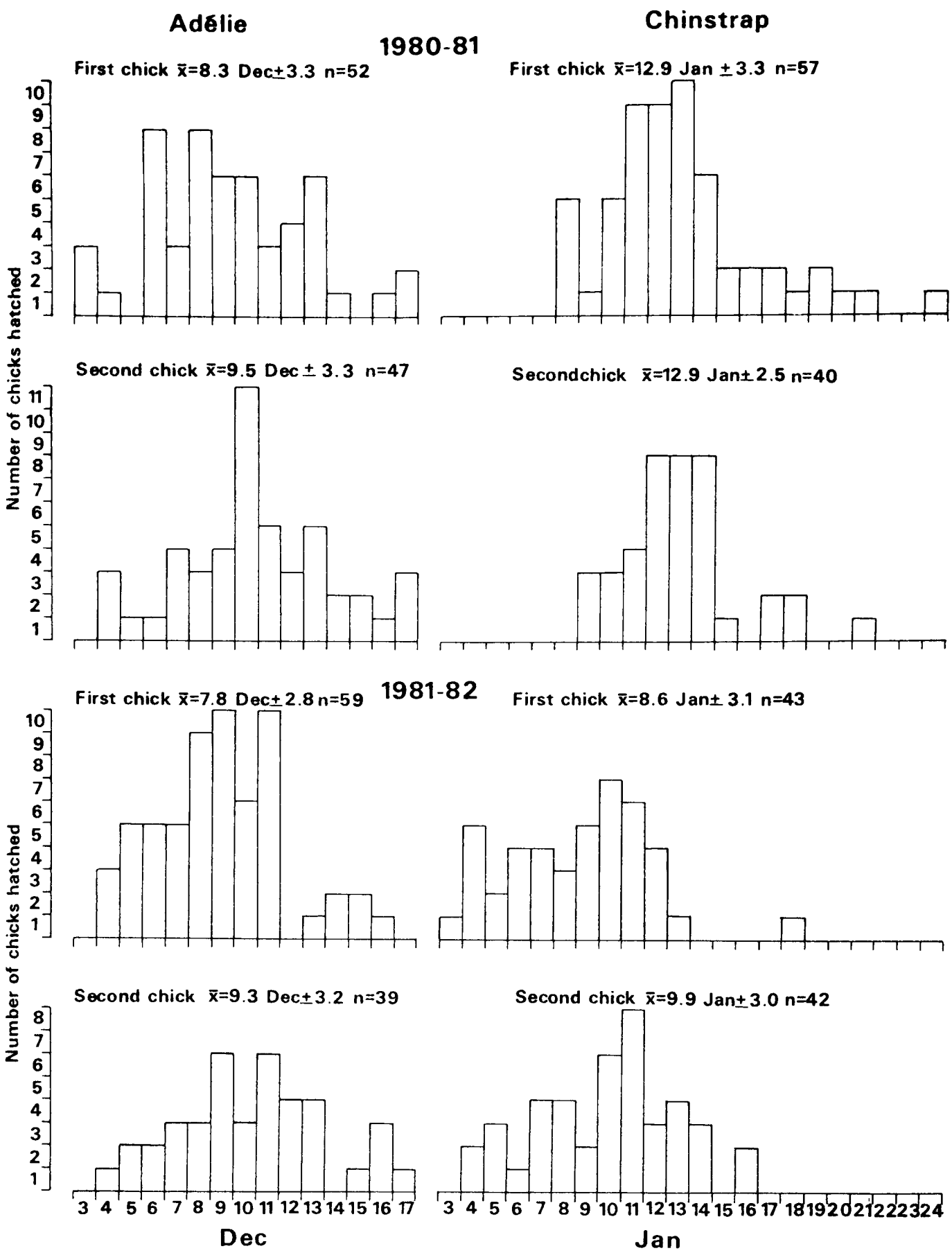



Figure 2.9. The distribution of Adélie and chinstrap hatching dates.

| Species | Year | First chick | | | Second chick | | |
|---|---|---|---|---|---|---|---|
| | | Mean | sd. | No | Mean | sd. | No |
| Adélie | 1980/81 | 8.9/12 | 3.0 | 86 | 9.8/12 | 3.1 | 69 |
| | 1981/82 | 7.8/12 | 2.8 | 59 | 9.3/12 | 3.2 | 39 |
| Chinstrap | 1980/81 | 12.4/01 | 3.8 | 105 | 13.5/01 | 3.6 | 81 |
| | 1981/82 | 7.9/01 | 3.2 | 79 | 9.2/01 | 3.5 | 72 |

Table 2.8. Hatching dates. (Data from several other colonies are included in all categories except for Adélies in 181/82.)

In 1980/81, there was no significant difference between the hatching date of the first and second egg, but in 1981/82, all first eggs hatched earlier than second eggs ($P<0.02$).

Hatching dates from previous years at Signy and other sites are in Appendix 2.4. As with laying dates, Adélie hatching dates are later at the more southerly breeding sites. Only Signy data are available for chinstraps, but it is unlikely that the pattern for hatching differs from that for laying dates, i.e. the dates are uninfluenced by latitude.

b. Hatching intervals

These are given in Table 2.9. For both species, the interval was greatest in 1981/82 ($P<0.001$) and in that year the interval was greater for Adélies than chinstraps ($P<0.02$).

6. The crèche period

The dates and the ages of chicks at the start of the crèche period are given in Tables 2.10 and 2.11, respectively. Adélie chicks formed crèches at an earlier age (16-19 d) than chinstrap chicks (23-29 d), and single chicks of both species formed crèches when 2.4-5.7 d older than first or second chicks. Chinstrap crèches normally only comprised three or four chicks whereas Adelie crèches usually comprised 10-20 chicks. The date of onset of chinstrap crèche tended to be less synchronous within the study nests than the onset of Adélie crèche. Some chinstrap adults stayed with their chicks for up to 36 d, compared with a maximum for Adélies of 28 d.

7. Fledging

Fledging periods and dates are given in Table 2.12. In 1981/82, fledging periods of Adélies were on average 8 d longer than those of chinstraps ($P<0.001$). 1980/81 fledging periods could not be accurately recorded, but were at least 56 d for the nine Adélie chicks that fledged (no chinstrap chicks in the 1980/81 sample survived to fledging).

| Year | Hatching interval (d) | | | | | |
|---|---|---|---|---|---|---|
| | Adélie | | | Chinstrap | | |
| | Mean | sd. | No | Mean | sd. | No |
| 1980/81 | 0.98 | 0.86 | 63 | 0.65 | 0.65 | 40 |
| 1981/82 | 1.86 | 1.19 | 29 | 1.28 | 0.94 | 70 |

Table 2.9. Intervals between the hatching of first and second eggs. (Data from several other colonies are included in the 1980/81 Adélie and 1981/82 chinstrap categories.)

| Year | Crēche period start date | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Adélie | | | | Chinstrap | | | |
| | Mean | sd. | range | No | Mean | sd. | range | No |
| 1980/81 | 26.9/12 | 1.5 | 26/12-03/01 | 46 | | | | |
| 1981/82 | 30.3/12 | 3.5 | 26/12-09/01 | 50 | 6.0/02 | 3.8 | 28/01-11/02 | 26 |

Table 2.10. Mean date of the start of the crēche period. (No chinstrap chicks reached crēche age in 1980/81.)

| Species | Year | | Chick category | | |
|---|---|---|---|---|---|
| | | | Singles | Firsts | Seconds |
| Adélie | 1980/81 | Mean | 19.1 | 16.7 | 15.8 |
| | | sd. | 1.7 | 2.1 | 2.2 |
| | | No | 22 | 24 | 21 |
| | | Range | 15-23 | 13-20 | 14-21 |
| | 1981/82 | Mean | 21.0 | 18.3 | 18.0 |
| | | sd. | 2.3 | 3.1 | 2.1 |
| | | No | 43 | 6 | 4 |
| | | Range | 17-28 | 14-24 | 16-21 |
| Chinstrap | 1981/82 | Mean | 28.7 | 24.0 | 23.0 |
| | | sd. | 4.0 | 3.6 | 3.3 |
| | | No | 19 | 6 | 3 |
| | | Range | 22-36 | 20-30 | 19-27 |

Table 2.11. Chick age (d) at the start of the crèche period.

| | | | Fledging period | | | Fledging dates | | |
|---|---|---|---|---|---|---|---|---|
| | Chick | No | Mean | sd. | range | Mean | sd. | range |
| Adélie | First | 21 | 60.3 | 2.4 | 54-64 | 06/02 | 3.0 | 04-15/02 |
| | Second | 8 | 61.3 | 2.9 | 55-64 | 07/02 | 4.0 | 04-15/02 |
| Chinstrap | First | 15 | 53.7 | 3.0 | 49-59 | 01/03 | 2.0 | 25/2-02/03 |
| | Second | 8 | 52.5 | 3.1 | 48-56 | 01/03 | 2.4 | 24/2-02/03 |

Table 2.12. Lengths of chick fledging periods (days) and dates of fledging in 1981/82.

8. Breeding success

a. Breeding success of normal nests

1. Basic data

Estimates of breeding success from the study and control colonies and the effect of disturbance on breeding success in the study colony are given in Table 2.13.

The daily visits to the study colonies had a varying effect on breeding success. In 1980/81, the percentage of eggs that fledged as chicks was 31 % less for Adélies but only 1.2 % less for chinstraps than in the control colonies. In 1981/82 this figure was 46.5 % less and 18.5 % less for Adélies and chinstraps, respectively. A comparison of the difference between the study and control colonies of the percentage of eggs hatched and the percentage of eggs fledged shows that, with the exception of chinstraps in 1981/82, the effect on breeding success of daily visits to the study colony was less during incubation than during chick rearing.

Breeding success data from this and previous studies are compared in Appendix 2.5. Breeding success fluctuates greatly between sites and years, but Signy Adélie control colony breeding success is only just outside the range of values. Chinstrap data are less comparable as few previous data exist.

The percentages of egg and chick losses and lifespans in days of the lost eggs and chicks are given in Table 2.14. In both years, there were similar losses of first and second eggs, but there were greater losses of single eggs. Chinstrap egg losses were higher than Adélie egg losses in both years and higher in 1980/81 than in 1981/82. Nearly all lost eggs survived for about 20 days, with the exception of Adélie eggs in 1980/81, which survived for about 14 days.

Second chicks nearly always had the highest mortality and the mortality of survivors was usually lower than that of pairs of chicks. The mortality of chicks of both species was highest in 1980/81, but chinstrap

| Adélie | 1980/81 | | | | 1981/82 | | | |
|---|---|---|---|---|---|---|---|---|
| | Study colony | | Control | % decrease | Study colony | | Control | % decrease |
| | actual | adjusted | colony | in study colony | actual | adjusted | colony | in study colony |
| No pairs | 60 | 60 | 394 | | 27 | 26 | 456 | |
| No eggs | 120 | 120 | (788) | | 49 | 43 | (754) | |
| No chicks | 98 | 80 | 647 | | 35 | 27 | 612 | |
| % eggs hatched | 82 | 67 | 82 | (15) | 71 | 63 | 81 | (18) |
| Chicks hatched/pair | 1.6 | 1.3 | 1.6 | | 1.3 | 1.0 | 1.3 | |
| No chicks fledged | 9 | 9 | 303 | | 11 | 13 | 578 | |
| % chicks fledged | 9.2 | 11.3 | 46.8 | | 31.4 | 48.1 | 94.4 | |
| Chicks fledged/pair | 0.15 | 0.15 | 0.77 | | 0.41 | 0.48 | 1.27 | |
| % chicks/egg | 7.5 | 7.5 | 38.5 | 31 | 22.4 | 30.2 | 76.7 | 46.5 |

| Chinstrap | 1980/81 | | | | 1981/82 | | | |
|---|---|---|---|---|---|---|---|---|
| | Study colony | | Control | % decrease | Study colony | | Control | % decrease |
| | actual | adjusted | colony | in study colony | actual | adjusted | colony | in study colony |
| No pairs | 60 | 46 | 294 | | 64 | 55 | 343 | |
| No eggs | 105 | 85 | (543) | | 123 | 103 | (642) | |
| No chicks | 39 | 6 | 106 | | 55 | 38 | 431 | |
| % eggs hatched | 37 | 7 | 20 | (13) | 45 | 37 | 67 | (30) |
| Chicks hatched/pair | 0.6 | 0.1 | 0.5 | | 0.9 | 0.7 | 1.3 | |
| No chicks fledged | 1 | 1 | 13 | | 23 | 23 | 262 | |
| % chicks fledged | 2.6 | 16.7 | 15.1 | | 41.8 | 60.5 | 60.8 | |
| Chicks fledged/pair | 0.016 | 0.02 | 0.04 | | 0.36 | 0.42 | 0.76 | |
| % chicks/egg | 1.0 | 1.2 | 2.4 | 1.2 | 18.7 | 22.3 | 40.8 | 18.5 |

Table 2.13. Breeding success in Adélie and chinstrap study and control colonies.
Note: The number of eggs laid in the control colonies has been calculated using the adjusted numbers of pairs and eggs in the study colonies. (see page 25 for explanation of how these data were adjusted.)

| Species/ Year | Egg status | Mortality % | Mortality No | Lifespan Mean | Lifespan sd. | Lifespan range | Lifespan No | Chick status | Mortality % | Mortality No | Lifespan Mean | Lifespan sd. | Lifespan range | Lifespan No |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Adélie | First | 15 | 9 | 14.8 | 6.5 | 6-24 | 4 | First | 86 | 38 | 25.9 | 14.5 | 4-55 | 38 |
| 1980/81 | Second | 22 | 13 | 12.7 | 9.2 | 2-33 | 7 | Second | 100 | 44 | 16.5 | 11.4 | 2-53 | 44 |
| | | | | | | | | Survivor | 69 | 7 | 35.1 | 17.3 | 6-60 | 7 |
| Adélie | First | 15 | 6 | 21.1 | 11.6 | 2-35 | 7 | First | 67 | 8 | 22.4 | 18.1 | 0-47 | 8 |
| 1981/82 | Second | 28 | 11 | 17.7 | 11.1 | 1-34 | 7 | Second | 83 | 10 | 18.0 | 13.3 | 0-42 | 10 |
| | Single | 50 | 2 | 19.5 | 4.5 | 15-24 | 2 | Single | 33 | 1 | 50.0 | - | - | 1 |
| | | | | | | | | Survivor | 53 | 4 | 14.5 | 5.0 | 4-20 | 4 |
| Chinstrap | First | 60 | 29 | 17.5 | 11.6 | 0-36 | 27 | First | 100 | 41 | 8.2 | 4.0 | 1-20 | 41 |
| 1980/81 | Second | 60 | 29 | 18.0 | 10.0 | 1-34 | 25 | Second | 100 | 41 | 8.0 | 4.1 | 1-17 | 41 |
| | Single | 75 | 6 | 9.5 | 7.6 | 2-25 | 6 | Single | 75 | 3 | 5.3 | 0.9 | 4-6 | 3 |
| | | | | | | | | Survivor | 92 | 11 | 7.3 | 3.1 | 1-13 | 11 |
| Chinstrap | First | 45 | 34 | 21.0 | 8.6 | 5-36 | 25 | First | 57 | 13 | 18.9 | 12.4 | 4-44 | 13 |
| 1981/82 | Second | 43 | 32 | 19.4 | 8.1 | 4-35 | 24 | Second | 96 | 22 | 11.3 | 6.8 | 1-27 | 22 |
| | Single | 60 | 3 | 21.0 | 6.4 | 16-30 | 3 | Single | 100 | 1 | 18.0 | - | - | 1 |
| | | | | | | | | Survivor | 63 | 5 | 15.4 | 10.0 | 1-38 | 5 |

Table 2.14. Percentage mortality from each egg and chick category and the lifespan of the lost eggs and chicks. (Sample sizes represent the actual numbers of eggs and chicks that were lost and the percentages represent the proportion of the original sample that was lost.)

chick mortality was higher than that of Adélies in both years. The lifespans of all dead chicks were the same, with the exception that, in 1980/81, Adélie survivors lived longer than second chicks ($P<0.01$) and chinstrap chicks did not live for as long as in 1981/82.

As each breeding season progressed, survival and mortality and the mortality rate changed as shown in Figures 2.10-2.13. Survival of first eggs was generally higher than that of second eggs, but the rate of decrease in egg numbers was the same for both eggs in both years, i.e.the rates of hatching were the same.

Survival of first chicks was always higher than that of second chicks, except for chinstrap chicks in 1980/81, which all had an equally low survival rate. Chick survival was lowest in 1980/81 for both species.

Chinstrap losses were greatest in 1980/81 when they sustained complete reproductive failure. Adélie losses were mainly during the guard period and were also high in that year, but some chicks did survive to fledging. The post-hatching period was the time of heaviest mortality for both species in both years.

## 2. Factors affecting breeding success

### 2.1. Direct

#### Predation

Sub-Antarctic (or brown) skuas Catharacta lonnbergi and greater sheathbills Chionis alba take poorly attended eggs and chicks in or near the breeding colonies. Continual observations of the study nests were not possible, so the proportion of egg and chick losses which were directly due to predation could not be quantified. An observation was made of co-ordinated predation by a pair of skuas. One bird pulled a peripherally nesting adult Adélie off its nest by its tail feathers while its partner took an egg from in front of the penguin. Both skuas then shared the egg next to the nest.

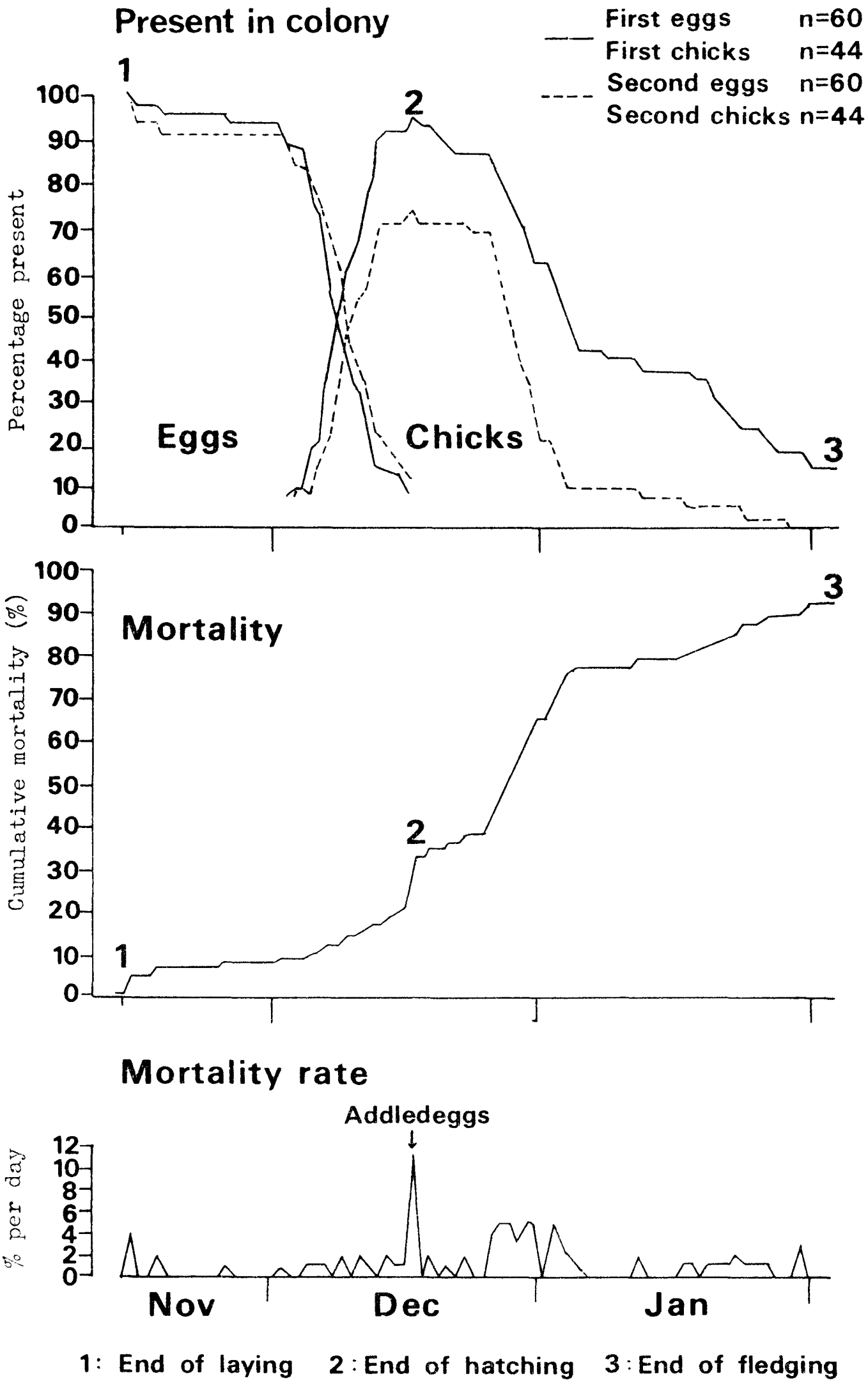



Figure 2.10. Variation with time in the percentage present in the colony and the cumulative percentage mortality of the original number of eggs and chicks in each sample and in the mortality rate of eggs and chicks for Adélies in 1980/81.

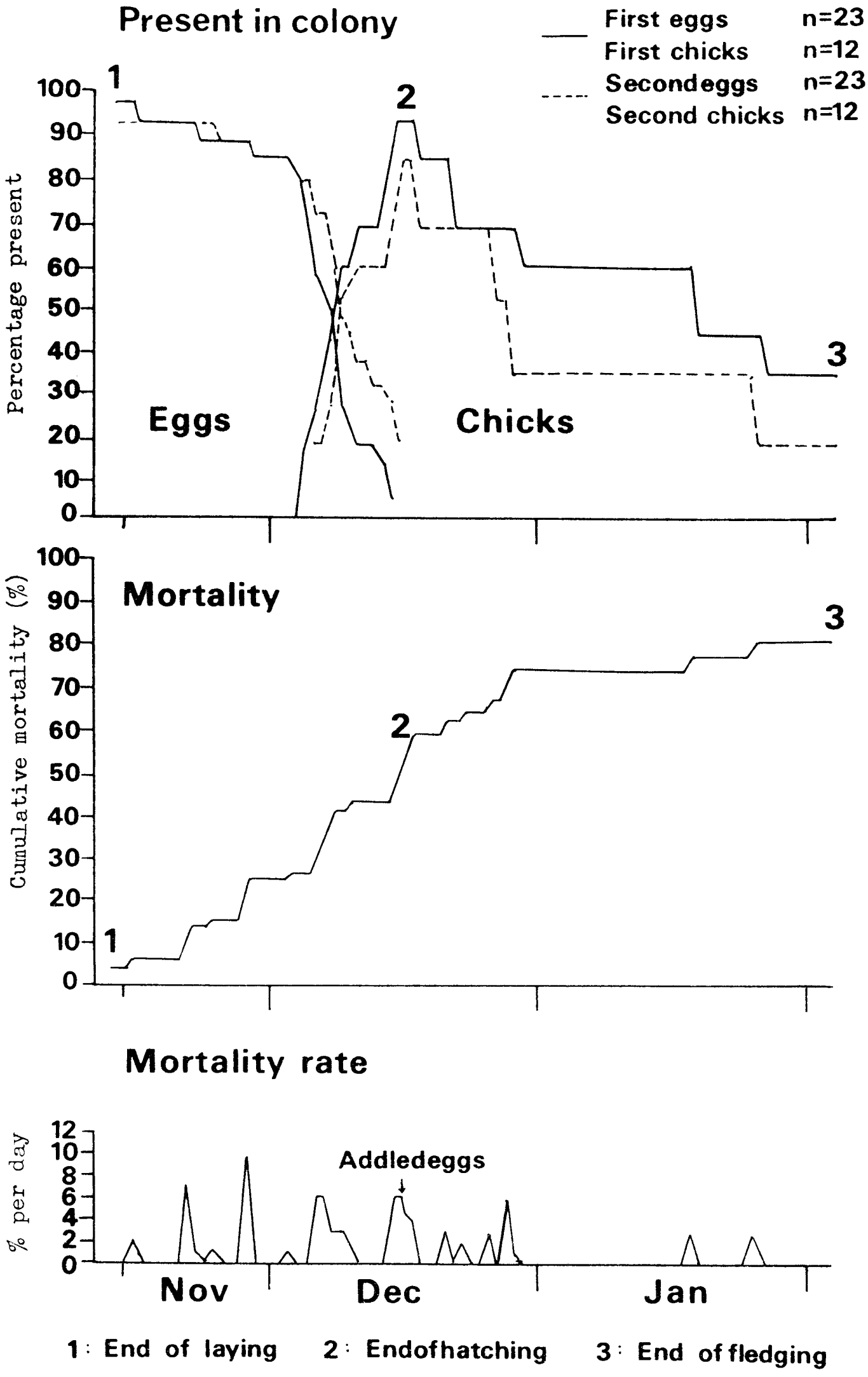



Figure 2.11. Variation with time in the percentage present in the colony and the cumulative percentage mortality of the original number of eggs and chicks in each sample and in the mortality rate of eggs and chicks for Adélies in 1981/82.

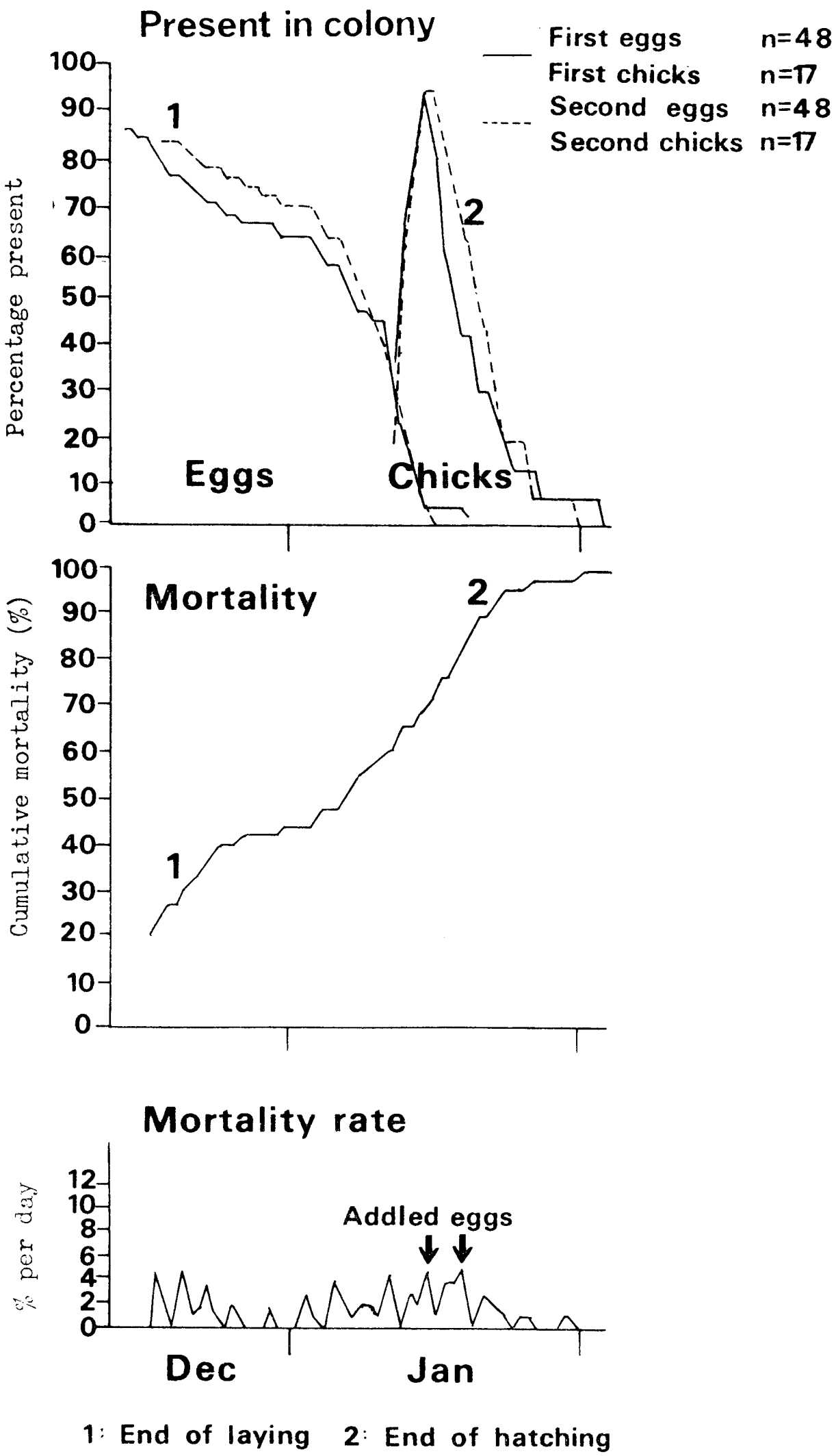



Figure 2.12. Variation with time in the percentage present in the colony and the cumulative percentage mortality of the original number of eggs and chicks in each sample and in the mortality rate of eggs and chicks for chinstraps in 1980/81.

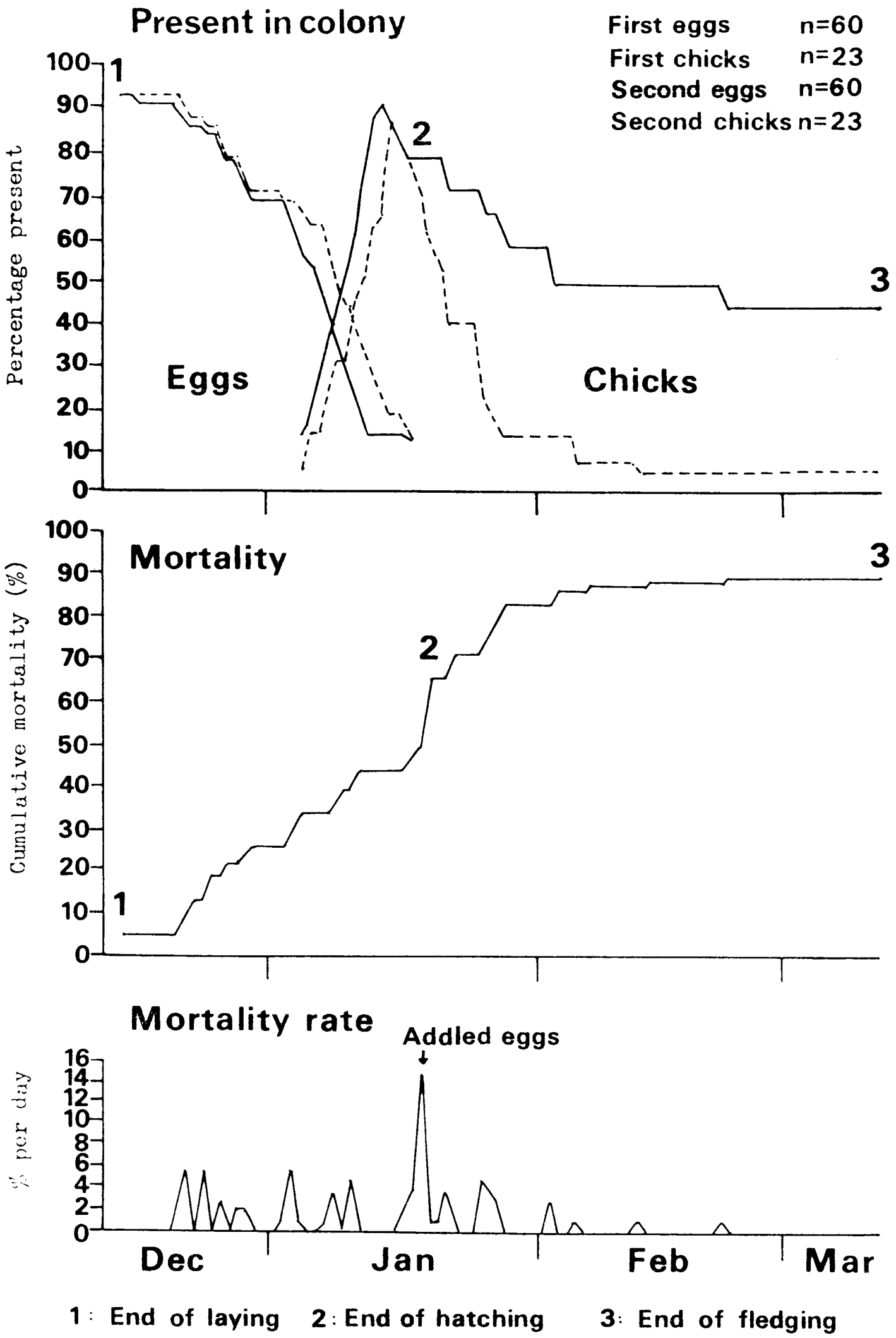



Figure 2.13. Variation with time in the percentage present in the colony and cumulative percentage mortality of the original number of eggs and chicks in each sample and in the mortality rate of eggs and chicks for chinstraps in 1981/82.

## 2.2. Indirect

### 2.2.1. Nest desertion

The act of nest desertion did not cause mortality, but eggs and chicks left at the nest were taken by skuas or sheathbills or chicks died of starvation if neither parent returned to the colony.

In both years, more chinstraps deserted their nests than Adélies (1980/81: 43.4 % vs. 6.7 % ; 1981/82: 24.2 % vs. 2.5 %) and there were more desertions in 1980/81 than in 1981/82 (Table 2.15). Some birds fasted for considerable periods before deserting the nest. Female chinstraps deserting after a first incubation shift of 16 days would also have attended the nest for an additional 13 days before laying (mean pre-laying attendance period, see Table 2.1) and thus these birds would have fasted for a total of 29 days. Adélie males deserting after 22 days would, likewise, have fasted for 40 days (mean pre-laying attendance of 18 days, see Table 2.1), and maybe longer since these birds would also have travelled over ice to reach the colony at the start of the breeding season.

During the guard period, in the three cases where it was certain that chick death was due to desertion, a female Adélie deserted after 10 days and two males after 16 and 19 days.

Of the chicks that died during the crèche period, in 1980/81 65 (73 %) Adélie chicks died of starvation (no chinstrap chicks survived to the crèche stage) and, in 1981/82, 10 (41 %) Adélie and 6 (20%) chinstrap chicks died of starvation.

### 2.2.2. Weather and ice conditions

Some chick mortality can be indirectly attributed to weather and ice conditions. Mortality was greatest in 1980/81, which was colder than 1981/82 and characterized by very unusual ice conditions, especially in

| Shift | No. of nests | Total no. desertions | | No. due to non-return | | Shift length | Time before deserting (d) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Mean | sd. | range | No |
| | | No | % | No | % | (d) | | | | |
| Adélie 1980/81 | | | | | | | | | | |
| First male | 120 | 6 | 5.0 | 3 | 2.5 | 12.6 | 13.7 | 0.5 | 13-14 | 3 |
| First female | 120 | 2 | 1.7 | 0 | - | 14.0 | - | | | |
| Adélie 1981/82 | | | | | | | | | | |
| First male | 80 | 1 | 1.3 | 1 | 1.3 | 13.7 | 22.0 | | | 1 |
| First female | 80 | 1 | 1.3 | 0 | - | 12.8 | - | | | |
| Chinstrap 1980/81 | | | | | | | | | | |
| First female | 120 | 32 | 26.7 | 15 | 12.5 | 6.1 | 8.9 | 2.2 | 7-16 | 15 |
| First male | 120 | 11 | 9.2 | 11 | 9.2 | 11.2 | 15.4 | 2.0 | 12-18 | 11 |
| Second female | 120 | 9 | 7.5 | 7 | 5.8 | 9.6 | 15.0 | 2.9 | 10-19 | 7 |
| Chinstrap 1981/82 | | | | | | | | | | |
| First female | 143 | 3 | 2.1 | 1 | 0.7 | 6.0 | 11.0 | | | 1 |
| First male | 143 | 30 | 21.4 | 28 | 20.0 | 9.8 | 13.8 | 2.3 | 10-18 | 28 |
| Second female | 143 | 1 | 0.7 | 1 | 0.7 | 7.8 | 11.0 | | | 1 |

Table 2.15. The number, and proportion of the original sample, of nest desertions in total and of those resulting from the non-return of the mate during incubation, the mean lengths of normal incubation shifts and the lengths of shifts prior to desertion.

January 1981, when there was also a period of severe weather. Adélie chicks were nearly fledged by this time, and mainly resisted the harsh conditions, but chinstrap chicks were hatching and at their most vulnerable and suffered high mortality.

3. Correlations with breeding success

3.1. Colony size and nest position

No correlations were found between colony size, nest position and nearest-nest distance and breeding success of either Adélies or chinstraps.

3.2. Laying date

No correlation was found between first egg laying date and the eventual survival of eggs or chicks in a clutch.

3.3. Egg and chick differences

It was hypothesized that second eggs and chicks which were lighter than the first egg or chick at laying or hatching might have a shorter survival time than those of the same weight as first eggs or chicks. No correlation was found between weight difference and subsequent lifespan of second chicks, although Adélie first chicks tended to be heavier than second chicks at hatching (Table 2.16).

b. Breeding success of increased clutch nests

Nine three-egg Adélie clutches were created but none survived for more than 15 days (mean = 7.9 ± 5.3 days). Of the 20 created at hatching, there were only two nests in which three eggs hatched, and both these remained as broods of three chicks for five days.

Seven three-chick chinstrap broods were created, but none survived as broods of three chicks for longer than 18 days (mean = 7.6 ± 4.5 days, range = 4-18 days).

| Species | Year | Chick hatching weight | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | First | | | | Second | | | |
| | | Mean | sd. | range | No | Mean | sd. | range | No |
| Adélie | 1980/81 | 85.5 | 13.0 | 61-128 | 53 | 81.0 | 10.3 | 64-112 | 45 |
| | 1981/82 | 85.4 | 29.5 | 61-117 | 38 | 81.3 | 10.2 | 66-108 | 17 |
| Chinstrap | 1980/81 | 66.0 | 9.8 | 47-93 | 52 | 66.0 | 8.6 | 49-84 | 39 |
| | 1981/82 | 77.4 | 8.1 | 62-98 | 40 | 77.7 | 11.4 | 58-110 | 40 |

Table 2.16. Hatching weights of first and second Adélie and chinstrap chicks.

# DISCUSSION

## 1. Pre-laying

### a. Return to the colony

Adélies breed mainly in regions surrounded by sea ice for most of the winter. The pattern of ice dispersal from each site at the end of the winter is usually very similar from year to year, but more southerly breeding sites are the last to become ice-free. Adélies must therefore cross the ice to reach the breeding colony, which takes considerably longer than swimming. Chinstraps arrive later in the year than Adélies and tend to breed in areas where there is less ice in winter so their return is less hindered. This allows a shorter journey time and, as shown here, it is more likely that all the birds will arrive more quickly. The time of arrival will affect all the subsequent events of the breeding season, so laying and hatching dates of Adélies are also later at the more southerly breeding sites.

The presence of ice may be expected by Adélies returning to many of the breeding sites further south than Signy. In such circumstances, it is likely that these birds are adapted to begin the breeding cycle when the ice normally disperses. In years when ice is still present at the time when the breeding cycle is due to start, there are two possible consequences. Firstly, the return to the breeding colony of Adélies and chinstraps can be delayed until the ice has dispersed (Penney, 1968; Trivelpiece, 1981). Presumably, the onset of the breeding cycle can also be delayed to some extent, which will delay the timing of subsequent events. Secondly, the subsequent events of the breeding season can be affected, especially if the birds have had to walk over ice for some distance to reach the breeding colony. This can reduce the energy reserves available for egg formation and incubation (Ainley and LeResche, 1973) and, if ice persists, delay relief during incubation and cause nest desertion (Yeates, 1968; this study).

Despite the different ice conditions, both species bred at the same times in the two seasons studied. Adélies bred earlier than chinstraps in both seasons, perhaps as soon as it was possible for them to do so. This involved them walking over ice to reach Signy at the start of each season. The more southerly distribution of Adélies may mean that they are adapted so that their chicks are raised as early as possible and have a chance to develop feeding skills and build up energy reserves before winter and the return of ice. Chinstraps also crossed ice at the start of both seasons so, although they did not attempt to breed as early as Adélies, they displayed a drive to start breeding at a certain time. Sea ice does not usually re-form at Signy until June, much later than at the more southerly Adélie breeding sites. It is possible that chinstraps are adapted to this and therefore breed later than Adélies but at a time which ensures that their chicks can develop fully before winter.

b.Pairing

The main causes of mate change have been cited as breeding failure the previous season (Spurr, 1972), asynchronous return of a pair and non-return of the mate (Ainley and others, 1983). The poorer chinstrap fidelity in 1981/82 may have been due to the non-return of many birds, perhaps caused by heavy adult mortality the previous winter. It is possible that a combination of the effects of the environmental conditions in 1980/81 and the disturbance caused by daily visits to the study colony may have caused chinstrap adults to avoid breeding at the same site the following season. It is perhaps more likely, though, that the desire to breed in the same colony overcomes the effects of such disturbance, which would be relatively short-lived in comparison with the breeding life of this species. The stresses imposed by the conditions of 1980/81 may have prevented birds of both species from obtaining sufficient food to achieve reproductive condition and, in many cases, this may have caused late arrival of birds

(Spurr, 1975a). Birds not retaining the same mate are less likely to lay eggs, unless the change is to a more experienced partner (Penney, 1968; LeResche and Sladen, 1970), but this could not be demonstrated here.

The pair bond was often maintained at the same nest site. It has been previously shown for several other seabird species that mate retention can lead to higher productivity (Coulson, 1966; Mills, 1973; Davis, 1976; Asbirsk, 1979) so it is reasonable to assume that mate retention is selectively advantageous to Adélies and chinstraps. Male Adélies usually defend and retain their old nest sites (Stonehouse, 1963) and this tended to be the case at Signy, but equal numbers of both sexes defended old chinstrap nest sites. This may be a consequence of high partner loss the previous winter. Nest sites might also be retained because high breeding success has been consistently experienced in the past (Asbirsk, 1979). In addition, nest-site retention may reduce time-consuming intraspecific competition at the beginning of the breeding season (Sealy, 1972).

Between 1952 and 1978 at Signy, there has been little evidence of the type of nest-site competition between Adélies and chinstraps where their colonies are adjacent, as described by Volkman and Trivelpiece (1979) (see Figure 1.4). This is probably because there is still adequate room for both species to breed.

2. Laying

a. Synchrony

No difference in laying synchrony was found, which contrasts with the situation at King George I, where Trivelpiece (1981) found that synchrony of Adélies was greater than of chinstraps. It was pointed out that high synchrony among Adélies corresponds with their continental distribution and the short breeding season experienced. The evolution of breeding synchrony as an adaptation to breeding further south is likely, but one would then expect Adélies to be more synchronous than chinstraps at Signy I and this

was not the case. It may also be that laying synchrony is either an adaptation to decrease the risk of predation or a short-term adaptation to environmental conditions (Birkhead, 1977 b; Gochfeld, 1980), especially since Trivelpiece (1981) found that gentoo penguins at King George I bred more synchronously in a year when there was more ice present at the beginning of the breeding season. It was not possible to detect a similar trait for chinstraps from this study because the 1980/81 sample had a biased distribution.

b. Intervals

A delay of about three days between the laying of two eggs in a clutch is probably the time taken for the second egg to form after the laying of the first. It has been suggested that this is the time required for the mobilization and deposition of calcium and phosphorus to form the relatively heavy egg shell (at approximately 13 % of egg weight for Adélies) (Williams, 1981 a, 1981 b). The longer chinstrap laying intervals in 1980/81 may have arisen because the birds were in poor condition after crossing ice to reach the breeding site. Adélies may be better adapted to this and so their laying pattern was unaffected.

A second egg laid after six days may have been formed from a third follicle after the second had failed for some reason. Alternatively, longer laying intervals may be characteristic of young, inexperienced birds.

c. Eggs

Both species lay two eggs and may lay replecement eggs if one is lost. On only two occasions (both chinstrap) were two chicks raised to fledging by a pair. In the two breeding seasons studied, mortality of chicks of both species was high, but it must be assumed that a clutch size of two is an adaptation to the largest number of young for which the parents can

normally provide enough food (Lack, 1954). As well as this, Adélies have a disparity in egg sizes. It is likely that this is part of a brood reduction mechanism (see section 4).

3. Incubation

Adélie incubation shifts were longer than those by chinstraps. This is probably an adaptation to the time taken to walk over sea ice before and after an incubation shift and the time foraging to build up energy reserves depleted by both the incubation shift and the walk. Chinstraps are more likely to be able to swim through open water to enter and leave the colony before and during incubation. This uses less energy so less time is required between incubation shifts to restore energy reserves. The shifts can therefore be shorter. In 1980/81, when sea ice did obstruct chinstrap travel, incubation shifts by them were longer. Variations in ice conditions from year to year are likely to affect incubation shift lengths of both species. At Cape Royds, Yeates (1968) found that Adélie shift lengths are shorter when the ice edge is closer.

Other incubation shift data (Ainley and others, 1983; Bagshawe, 1933; Conroy and others, 1975 a; S.Hunter, personal communication) agree with those reported here, although Bagshawe (1933) mentions an average incubation shift length for chinstraps of 2.8 ± 1.9 days (n = 12), which is quite different. Davis (1982 a) suggests that abnormal incubation shift lengths, and especially very long ones which lead to desertion of the incubating bird, are more frequent in inexperienced pairs. The experience of pairs used in this study is unknown, so this cannot be examined.

Two interspecific differences occurred immediately after egg laying. Adélie males were heavier than females but chinstrap females were slightly heavier than males and the first Adélie incubation shift was by males but that of chinstraps was by the female. In addition, the amount of time invested by each sex in pre-laying attendance and incubation was very

similar for chinstraps, but considerably longer for Adélie males than Adélie females.

Sex-weight differences of Adélies may mean that males have greater energy reserves in the form of fat. This would make them better equipped to incubate after laying and to invest more time in incubation. It is also possible that males incubate for longer because females need to forage more to replace the energy reserves used during ovogenesis (Burger, 1979) as well as those used in incubation and travelling to and from the colony.

Although smaller, the chinstrap sex-weight differences at the end of laying means that, despite energy used in pre-laying attendance, ovogenesis and in walking to the colony at the start of the breeding season, females are more able than males to incubate immediately after laying. The results suggest that chinstrap males return to the colony before females. The extra energy used in spending longer in the colony may account for the sexual dimorphism and incubation pattern after laying.

There is a stage towards the end of incubation at which birds change over at the nest every two or three days and this begins earlier for chinstraps than Adélies. Chinstraps breed later and in relatively ice free areas, so it is fairly certain that one of a pair can present food to chicks at hatching before the chick yolk sacs are depleted. If ice is present, Adélies are unable to make very short trips to sea between incubation shifts. Therefore, to ensure each chick has food at hatching, it pays the adults to leave their return from the last long trip until close to hatching.

4. Hatching

Because first eggs are not properly incubated until second eggs are laid, the two eggs hatch more synchronously than they were laid. Williams (1981 b) found this to be the case for clutches of rockhopper Eudyptes chrysocome and macaroni penguins, except that in many cases the second egg

hatched first. Since first eggs from this study still hatched first, it is likely that they developed to some extent, through partial incubation, before the second eggs were laid.

It is very likely that disparity in egg sizes and hatching intervals comprise a brood reduction mechanism which is better developed in Adélies than chinstraps. Brood reduction gives the larger chick in a brood a better chance of survival if environmental conditions, food availability or inexperience of the breeding pair are such that two chicks cannot be raised. It provides one chick with some advantage over its sibling which may enhance the former's chances of survival. First chicks hatch earlier than second chicks, so they will have been fed and thus are probably larger and fitter than their siblings when these hatch. If the parents are unable to provide adequate food for two chicks then the first chick has an advantage when begging for food which further increases its chances of survival. Although hatching weights of first and second chicks are similar, it is also possible that, by being in a larger egg for longer, first chicks are physically and physiologically more advanced in development when they hatch and are in a better position to compete for food.

The harsher environmental conditions experienced by Adélies may cause them to invest more in their first eggs and have longer hatching intervals than chinstraps to ensure that at least one chick has a chance of survival. Chinstraps breed mainly on Antarctic and Sub-Antarctic islands where conditions are not so severe as those experienced by Adélies mainly breeding further south, and, as the two eggs are of similar size, their chicks from first eggs will have only the advantage gained by hatching three days before their siblings. In adverse conditions, this may still be sufficient to ensure the second chick dies and leaves the first chick with a better chance of surviving to fledging.

If conditions are suitable, the ecologically adapted maximum number of chicks can be raised by a species. Thus, both the Galapagos Spheniscus mendiculus and the gentoo penguin raise two chicks in years when more food is available. Conversely, they may raise no chicks at all in years when there is a food shortage (Boersma, 1976; Croxall and Prince, 1979; Williams, 1980 a). The ability to raise as many chicks as the average clutch size when conditions are favourable is found in many species of birds (Lack, 1954; Ricklefs, 1968 c; O'Connor, 1978). In this study, the greatest hatching intervals were those between Adélie first and second chicks in 1981/82, i.e. in the year with the better conditions. This suggests that the extent of the brood reduction mechanism is not determined by year to year variations in environmental conditions and that Adélies may have a better developed brood reduction mechanism as a permanent adaptation to breeding further south.

Brood reduction has been observed in many species, including other penguins. Two extreme examples are the macaroni and rockhopper penguins in which differential egg mortality has evolved as a brood reduction mechanism. They lay one egg (the first) which is markedly lighter and smaller than the other and often totally disregarded by the parents. Macaroni penguins have never been shown to rear this egg, but for rockhoppers it may function as an insurance against failure or loss of the second egg (Lack, 1968; Howe, 1976; Williams, 1980 b) so that brood reduction only occurs after the preferred egg has survived the first half of the incubation period when egg mortality in macaroni and rockhopper penguins is highest (Gwynn, 1953; Warham, 1963; Williams, 1980 b), or when it has survived to hatching. Tinbergen (1951) has demonstrated similar preferential treatment for large eggs in a clutch in other bird species and several species have been shown invariably to raise only a single chick from a two egg clutch (Miller, 1973; Nelson, 1977; Newton, 1978).

Other adaptations which may act to maximise the reproductive output of a species include the ability of adults to vary clutch size in accordance with a temporary change in local conditions and the ability of chicks to store sufficient resources to survive short term instability of food supply (O'Connor, 1977). Although there is no direct evidence for Adēlies and chinstraps, it may be that single egg clutches are laid by females that have experienced difficulty in feeding at the beginning of a breeding season. On many occasions, chicks were able to survive on stored energy reserves for up to about five days, depending on age, when feeding frequency was low.

5. The crēche period

Examples of chicks of a species forming crēches are found in three genera of penguins : Aptenodytes (Stonehouse, 1953 and 1960), Eudyptes (Pettingill, 1960; Warham, 1974 a and b) and Pygoscelis (Levick, 1914; Roberts, 1940), and in other species, e.g. the common eider Somateria mollissima (Munro and Bedard, 1977 a and b), the pelicans Pelecanus erythrorhynchos and P.onocrotalus roseus (Schaller, 1964; Brown and Urban, 1969) and flamingos, such as Phoeniconaias minor (Brown and Root, 1971). Davis (1980) considered that crēching behaviour has evolved in response to its survival value in protection from predation, but that it also helps to maintain body temperatures under severe environmental conditions. Indeed, in the case of the emperor penguin Aptenodytes forsteri and the king penguin A.patagonicus, crēching is assumed to have evolved primarily as a thermoregulatory device (Roberts, 1940; LeMaho, 1977).

Sladen (1958) defined the start of the crēche period as the time when actual crēches start to form. This is difficult to record accurately since different numbers of chicks could constitute a crēche and the action of crēching very often depends on environmental conditions, levels of predation and the degree of protection given by non-breeding adults that

return to the colony at about this time (the re-occupation period) (Davis 1982 b).

Three factors determine the degree of self-sufficiency chicks must have before they can be left alone by their parents. They must be able to thermoregulate efficiently, which they can usually do from the age of c15 days (Sapin-Jaloustre and Bourliere, 1951; Goldsmith, 1962); chicks and parents must be able to recognise each other, which they can do after 17 days (Thompson and Emlen, 1968); and chicks must be able to re-locate their nests since their parents usually return to feed them there (Spurr, 1975a).

Davis (1982 b) recorded 16 days as the earliest age at which crêche can occur. In this study, some chinstraps were not left alone until 36 days old, so other factors may also be involved in determining the onset of the crêche period.

A single foraging parent cannot provide enough food for two chicks after they reach a certain age since the demand for food constantly outweighs the amount a single parent can supply. The age at which this occurs is determined by a) the combined stomach capacity of the chicks in the brood, b) the amount of food that an adult can obtain in one feeding trip and c) the frequency with which an adult can deliver the food to the brood. Thus, single chicks are brooded for longer than pairs and, in a year such as 1980/81, when there was difficulty in obtaining food, the crêche period started earlier. If chinstrap adults did not travel as far as Adélies to forage, the feeding frequency would be higher, and this would account for a later onset of the chinstrap crêche period.

6. Fledging

It is possible that there was more food available to chinstrap chicks to allow them to have a shorter fledging period than Adélie chicks in 1981/82, although this cannot be tested. Many factors can be involved in determining the length of the chick rearing period. Food availability is certainly

one of them, since it will determine the time taken for the chicks to reach independence, but the length of the breeding season may also be an influence. Adaptation to a short breeding season and extended snow cover of breeding sites by reducing the chick rearing period has been shown for the little auk Plautus alle in Spitsbergen (Stempniewicz, 1981).

7. Breeding success

a. Basic data

It is hardly surprising that breeding success was decreased by disturbance since the study colonies were entered daily to check nests and weigh chicks (see chapter 5). The immediate effects of human disturbance on penguin breeding success have not previously been recorded, but Oelke (1978) suggested that long term human disturbance in the Ross Sea sector caused the Adélie breeding population to decrease by 30-40 %. At Signy, breeding success was more affected by disturbance in 1981/82 than in 1980/81. Breeding success was low in both the study and control colonies in 1980/81 due to the conditions, so it is unlikely that disturbance would have constituted a large proportion of the adverse factors affecting breeding in that year. In 1981/82, disturbance was probably the major factor affecting breeding success, so its effect on the study colonies became more noticeable.

The fact that, in both years, disturbance caused a greater decrease in breeding success during the chick rearing phase than during incubation is perhaps due to the daily handling of chicks and the effect of this on the parent guarding the nest. During incubation most nests were checked from a distance, which probably helped to reduce the disturbance effect.

Although the experimental techniques used for the two species were slightly different, the data for the breeding success of increased clutch nests suggest that, while neither species can rear a third chick, chinstraps are able to do better than Adélies. Both species lay

replacement third eggs, but it is unusual for a third egg to be laid unless one of the other two eggs has already been lost. The adult brood patch can only properly accomodate two eggs, so it is unlikely that three eggs could be incubated successfully until hatching. If three chicks had hatched, successful rearing to fledging would seem unlikely. The ability to lay a third egg if one has been lost early in incubation therefore has a purely replacement function.

More single eggs were lost than those from clutches of two, perhaps because single eggs are laid by relatively inexperienced birds. Greater egg losses in 1980/81 can be attributed to an effect of the ice in that year, but it is difficult to see why both egg and chick mortality of chinstraps was greater than that of Adélies in both years.

This situation contrasts with Sladen (1955), Conroy and others (1975 b) and Trivelpiece (1981) who found that chinstrap mortality was lower than that of Adélies. Trivelpiece (1981) attributes this to the later breeding season, milder environmental conditions and lack of ice as a hindrance to feeding experienced by chinstraps but not by Adélies. At Signy I there was obviously a critical factor which increased chinstrap mortality. It could be that they are generally more susceptible to predation and harsh environmental conditions than Adélies, or perhaps their energy supply was deficient in either quantity or quality. High second chick mortality is probably due to the brood reduction mechanism discussed earlier. It is surprising, however, that mortality of second chicks was not greater for Adélies than chinstraps. Adélie first eggs weighed more than second eggs when laid and, although not significantly different, the mean hatching weight of Adélie second chicks was less than that of first chicks, whereas chinstrap first and second chicks had almost identical hatching weights. It would have been expected, therefore, that a greater investment in the Adélie first chick would have increased the chances of survival of first chicks over second chicks more than for chinstraps.

The advantage of brood reduction is demonstrated by the lower mortality of surviving chicks when compared with that of pairs. The loss of an egg or chick might indicate inexperience of the breeding pair in coping with predation or environmental conditions, but brood reduction may significantly increase the chances of survival of the remaining chick. Brood reduction is therefore very important for Adélies since the environmental conditions they experience in most of their breeding range probably rarely favour the chance of raising two chicks.

Trivelpiece (1981) found that most Adélie and chinstrap egg and chick mortality occurred just after laying and hatching. Similarly, Cairns (1981) found that black guillemot Cepphus grylle chick mortality was highest during the first few days after hatching. Since the lifespans of most lost eggs and dead chicks from this study were usually the same, it is probable that mortality occured at the same stages in the breeding season of both species, such as toward the end of an incubation shift when parents are more likely to leave the nest due to exhaustion of fat reserves, or just after hatching when chicks have exhausted reserves from the yolk sac and need to be fed in order to survive. An additional cause of mortality at this critical stage could be disastrous. The 1980/81 ice conditions delayed the feeding of chinstrap chicks just after they had hatched, resulting in almost complete chick mortality.

b. Factors affecting breeding success

1. Direct

Predation

The impression was gained from observations in the colonies that Adélies mainly suffer predation from skuas, while chinstrap eggs and chicks are mainly taken by sheathbills. The breeding season of the skua coincides with the egg and chick rearing phases of the Adélie breeding cycle and the breeding season of the sheathbill coincides with those of the chinstrap

breeding cycle, so a potential food source is available to both predators when it is most needed. The close association of sheathbill and penguin breeding and the consequent food supply from penguins has been previously shown (Paulian, 1953; Downes and others, 1959; Jones, 1963; Derenne and others, 1976; Burger, 1979) and a similar association has been reported for breeding cormorants Phalacrocorax verrucosus (Paulian, 1953).

Mortality caused by predation of gentoo chicks by skuas apparently ceases when flipper bones have become ossified and chicks can defend themselves (Williams, 1980 a). This is probably the reason why Adélie and chinstrap chick mortality rate due to predation decreased as the chicks got older.

At sea, Adélies and chinstraps are exposed to predation by the Leopard seal Hydrurga leptonyx (Levick, 1915; Murphy, 1936; Hamilton, 1939; Sladen, 1958; Penney and Lowry, 1967; Muller-Schwarze and Muller-Shwarze, 1975; Spellerberg, 1975; Butler and Muller-Shwarze, 1977; personal observations), but the effects are not easily quantified.

2. Indirect

2.1. Nest desertion

There were more desertions by chinstraps than Adélies in both years. There is no obvious reason for this, but it is possible that the chinstrap sample included birds in poorer condition, who would desert the nest before being relieved by their partner (which was the major type of nest desertion), or more inexperienced breeders (perhaps because theirs is a more rapidly expanding population). Davis (1982 a) proposes that a large proportion of nest desertions are due to deviations from an optimum nest-relief pattern and that adult nest-relief is governed by a biological clock which ensures that each bird returns before the fat reserves of its incubating partner or before the yolk sac reserves of newly hatched chicks are depleted. While the latter may be a timed response to stimulation from an egg near to

hatching, the former implies that each bird responds to the condition of its partner when deciding when to return to relieve it at the nest, which seems unlikely.

2.2. Weather and ice conditions

Chick mortality was increased by weather and ice conditions, and chinstraps were more affected than Adélies. Some previous studies have also noted similar effects. Taylor (1962), Stonehouse (1963), Yeates (1968), Ainley and LeResche (1973), Spurr (1975a) and Ainley and others (1983) record a similar effect on Adélies to that shown here and Conroy and others (1975 a) note a similar effect on chinstraps. In the northern hemisphere, Birkhead and Nettleship (1981) found that late ice-breakout decreased breeding success of thick-billed murres Uria lomvia in Northern Canada. Breeding success in this study was reduced in 1980/81 by both disturbance and ice, but Appendix 2.5 shows that the breeding success in the control colonies was also much lower than in a normal year.

c. Correlations with breeding success

1. Colony size and nest position

In this study, no correlation was found between the distance from the nest to the edge of the colony and breeding success. This could be because most of the study nests were 'central' as classified by Penney (1968), i.e. most were immediately surrounded by other nests as opposed to being on the periphery of the colony. Thus, a decrease in breeding success in nests toward the edge of the colony (Patterson, 1965; Nelson, 1966; 1978; Coulson, 1968 ; Penney, 1968; Tenaza, 1971; Spurr, 1974; 1975a; Davis, 1980; Trivelpiece, 1981; Ainley and others, 1983) might not be expected.

No correlation was found between colony size and breeding success, but this is perhaps because the colonies compared did not include very small

ones. These have been shown to produce a lower number of young per breeding pair than large colonies for several species of birds (Darling, 1938; Austin, 1945) including Adélie and yellow-eyed Megadyptes antipodes penguins (Richdale, 1951; Trivelpiece, 1981). In many cases this has been attributed to there being a high proportion of young, inexperienced breeders in the small colonies (Roberts, 1940; Lack, 1954; Coulson and White, 1956; 1960; Trivelpiece, 1981). Trivelpiece did not find the same situation for chinstraps, and this was attributed to their nesting habits. Chinstraps nest mainly on steep, rocky slopes in a less dense formation than Adélies (Muller-Schwarze and Muller-Schwarze, 1975; Volkman and Trivelpiece, 1981) so nesting in the centre of a large colony does not carry the same selective advantages (e.g.reduced predation pressure) as it would for Adélies. Thus, the nests of young, inexperienced chinstraps are likely to be randomly distributed in small and large colonies alike.

2. Laying date

That there was no correlation between laying date and breeding success contrasts with Trivelpiece (1981) who found that pairs of Adélies and chinstraps which had laid their eggs more than four days after the peak of egg laying of each species (classified as late breeders) laid fewer eggs and hatched and crēched fewer chicks than the earlier breeding pairs (classified as synchronous). It is possible that, either the birds from this study were of similar breeding experience and therefore showed little difference in breeding success, despite some asynchrony in laying dates, or that the conditions did not change enough to place any inexperienced birds at a disadvantage as a result of any asynchrony.

# CONCLUSIONS

The important difference between the breeding biology of Adélies and chinstraps at Signy I is that Adélies breed about one month before chinstraps. It is possible that this is primarily an adaptation to breeding further south where the breeding season is shorter and ice can affect the timing of the events of the breeding season. The onset of the Adélie breeding season could thus be determined by the time of ice breakout, but also by adaptation to breed as early as possible in a breeding season. Consequently, Adélies may be better adapted than chinstraps to breeding under extreme environmental conditions. The most important adaptations are long incubation shifts and brood reduction by greater investment in the first egg and long hatching intervals. Chinstraps, with shorter incubation shifts and equal investment in both eggs, may be well adapted to the environmental conditions of the South Orkneys but, although long hatching intervals facilitate brood reduction under extreme conditions, the heavy mortality caused by the conditions of 1980/81 is an indication that this species is not well adapted to an extreme Antarctic climate.

# Chapter Three

## Diet

## INTRODUCTION

The aims of this chapter are to describe the diet of Adélies and chinstraps at Signy I and its variation between and within years, to suggest explanations for differences between the two species and to assess the extent to which these are a significant part of ecological distinctions between the species.

Investigations of the diet and feeding ecology of seabirds can show how they have adapted their breeding strategies to cope with the variable availability of food and in what ways competition for food is avoided.

The only previous comparison of the diet of pygoscelid penguins (at King George I; Volkman and others, 1980) showed that Adélies and chinstraps took the same prey species, but that there were differences in the size of prey caught. These were suggested as being due, in part, to "geographical and temporal differences in feeding areas and habits," but it remained uncertain as to whether differences in diet indicated this or whether the birds were foraging for the most available prey items within the constraints imposed by foraging areas and foraging behaviour.

## METHODS

### Data collection

Five birds were collected during the pre-laying attendance period, then at the start of each incubation shift and each week after hatching. To ensure samples were taken at the start of an incubation shift, 20 pairs of Adélies and their nests were marked and monitored daily and birds were killed when they returned to the nest. It was not always possible to be present when a bird returned, so each sampled bird could have been at the nest for up to 24 hours when taken. This meant that the weight of food brought ashore

might not be correctly recorded since some digestion would have occurred, so this method was not used for Adélies after hatching or for chinstraps. Instead, birds were collected from five nests where they were seen changing over. In this way, it was ensured that the bird had just returned from the sea and that it was breeding.

Techniques for non-destructive stomach sampling were not used because a) stomach contents are often not uniformly mixed (Croxall and Furse, 1980; Croxall and Prince, 1980), b) it was important to obtain an independent measure of the total mass of food available to chicks, c) stomach pumps (Emison, 1968) do not cope with large (> 30 mm) prey items (Croxall and Prince, 1980; Horne, in press), d) emetics have been unsuccessful (Horne, in press) and the proportion of stomach contents regurgitated is unkown, e) water off-loading (Wilson, in press) does not obtain complete contents (Horne, in press) and is less effective on tightly packed, full stomachs, the typical condition in pygoscelid penguins.

Data analysis

Birds were dissected almost immediately in 1981/82, but in 1980/81 they were frozen at -20C for analysis in the winter. Each bird was weighed and flipper length and culmen length and depth were measured. The stomach and oesophagus were removed and all contents were weighed. Much of the stomach material was in an advanced state of digestion, so only the top 10 - 15 % could usually be separated into individual food items. The remainder could usually be divided into obviously different sections and each was assumed to correspond to a separate food intake period during foraging. These periods were probably followed by a period of non-feeding activity since each section was at a different stage of digestion. Sections were divided into different food types and each was weighed. The weight of krill was expressed as the actual weight and as a percentage of the weight of the bird at the time of sampling.

The stomachs contained krill, fish, amphipods, and stones. The krill were counted in total or estimated by sub-sampling. Where digestion was in an advanced state, the number of pairs of eyes in the section was counted. Krill eyes resist digestion longer than other parts of the body and are therefore readily identifiable for longer. An exaggerated value of the number of krill per gram of stomach contents arises from counts of eyes in the digested sections since the krill bodies are digested and pass into the gut but the eyes accumulate at the bottom of the stomach. This could theoretically be corrected for by relating eye size to krill length and volume, but even the eyes became partially digested or broken up, so this could not be done reliably.

Fish were usually too digested to identify, and in many cases their presence was only indicated by eye lenses. Amphipods were always found in small numbers, and were distributed randomly amongst the krill. Stones were more common (up to five) in fasting birds. Counts of the number of each prey item gave the composition of the diet in terms of the relative number of each prey species present.

The relatively undigested krill in the top section of the stomachs were used to investigate variation in the length of krill consumed. Any complete krill were sorted into 5 mm length classes and the number in each class was used to construct a length - frequency distribution. These always showed a normal distribution, so the sample was assumed to be representative of the top section.

The krill length-frequency distribution refers only to the top section except where other sections were very obviously different. This occurred in birds which had fed on a lot of small krill of between 10 and 25 mm. By measuring an undigested sample of small krill from the top section of several stomachs, a standard length-frequency distribution for these small krill was obtained. This was then used to calculate the percentages of each size class of small krill in any stomach. These were combined with

the percentages of each size class from the top section to obtain an overall krill length-frequency distribution.

Individuals of each length class of krill were weighed in order to derive a relationship between length and weight (Figure 3.1). The relationship (Log Wt = 2.79 log L - 1.83, where Wt = weight in mg and L = length in mm) was similar to that calculated by Lockyer (in Mackintosh, 1973): Log Wt = 3.38 log L - 2.75. Differences between them could be due to two factors which might have affected the weight of the length classes of krill. First, krill measured and weighed for this study had been frozen and then thawed. According to Lockyer, this causes slight telescoping of the body segments. Second, exact measurement of partially digested krill from a penguin stomach is made difficult by their fragility. Using the relationship derived from the stomach samples, weight-frequency distributions were constructed. The mean length class taken by each species in each year was also calculated from the number and the weight of krill in each length class.

Each bird consumes krill to sustain itself during foraging. Assuming it feeds throughout a trip to sea and then stops before returning to the colony, its stomach will mainly contain krill caught during the last few feeds. The extent of digestion of this krill depends on the distance travelled between ingestion of the last feeds and reaching the colony. Thus, an index of digestion (weight of krill per number of krill in the stomach) can be constructed. This depends on the mean length of krill in the stomach and is therefore equivalent to the actual as opposed to theoretical mean weight of an individual krill of that length. A digestion index was calculated for the top section of each stomach by weighing and counting the number of krill. A higher digestion index of krill of a certain length coresponds to less digestion having taken place. A comparison of Adélie and chinstrap digestion indices might therefore indicate whether the last feeds were taken at different times before coming

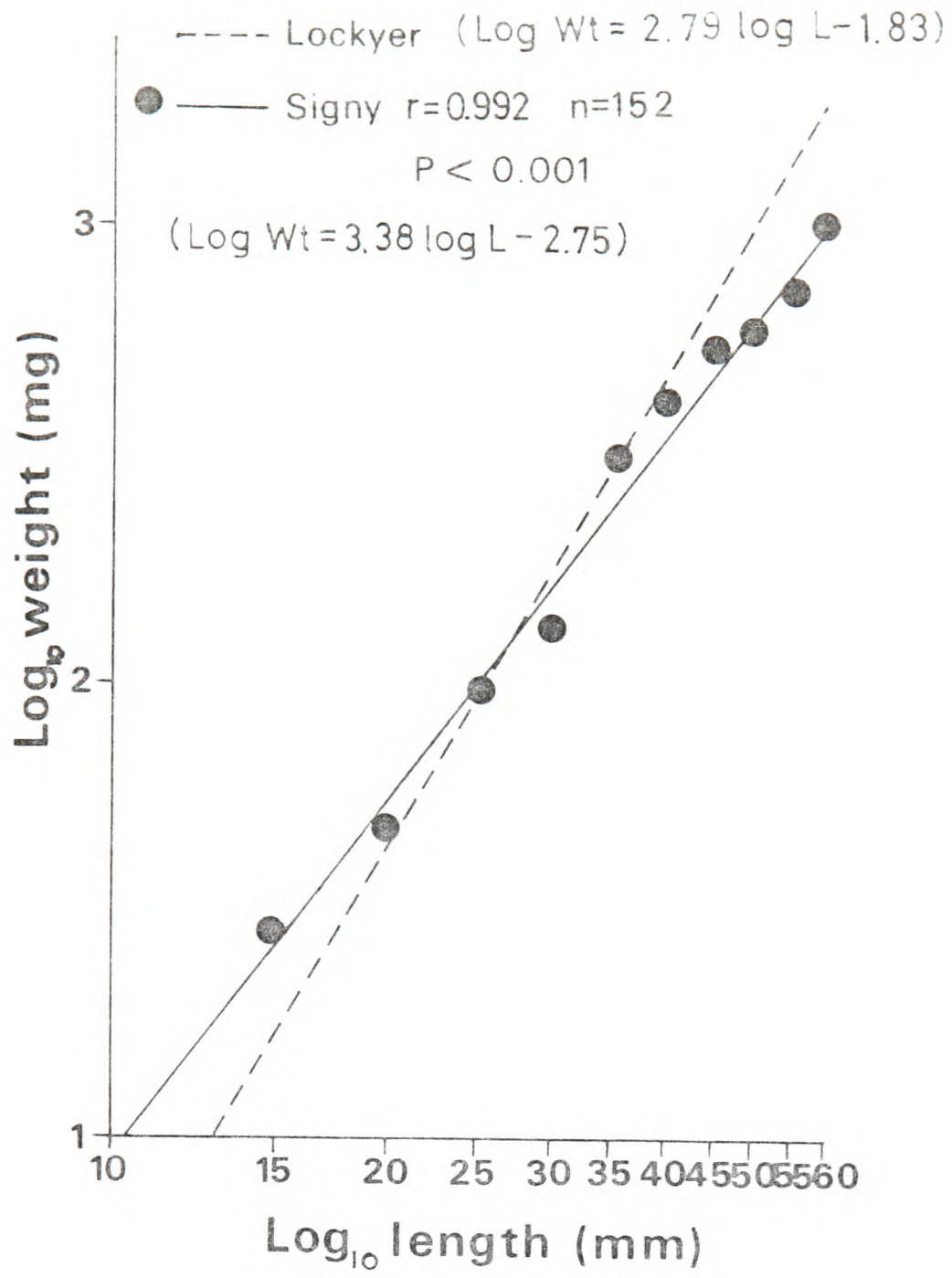



Figure 3.1. A comparison of the krill length/weight relationship (derived by Lockyer (in Mackintosh, 1973)) and that calculated from krill in the stomachs of penguins caught at Signy Island.

ashore. Assuming similar digestion rates and the same behaviour during return to the colony, this could suggest that the two species feed at different distances from the breeding site.

## RESULTS

### Diet composition

The mean number and mean weight of each prey type in each year, expressed as percentages, are shown in Table 3.1. Adélie stomachs contained more fish in 1980/81 than in 1981/82 ($P<0.05$) and chinstraps more krill in 1981/82 than in 1980/81 ($P<0.05$), but the importance of krill in the diet of both species remained the same. The percentage composition by weight was the same in both years, but the variances were different ($P<0.001$) except for amphipods in chinstrap stomachs. These different statistical results arise because fish and amphipods were concentrated in high percentages in a few stomachs - hence the high variances.

The stomach contents of both species consisted almost exclusively of krill Euphausia superba, but it appears that more fish and amphipods were taken in 1980/81. Table 3.2 shows the percentage of stomachs containing krill, fish and amphipods. Fish were present in 4 % more Adélie and 27 % more chinstrap stomachs in 1980/81 than in 1981/82 and there were amphipods in 20 % more Adélie and 17 % more chinstrap stomachs in 1980/81 than in 1981/82, although numbers were always low. There were no interspecific differences in the relative amounts of each prey type consumed.

#### 1. Fish

The only fish identified was the notothenid Trematomus eulepidotus or T. hansonii in a chinstrap stomach. In previous studies of the diet of Adélies and chinstraps breeding on the Antarctic Peninsula and

| Species/ Year | No of stomachs | Stomach composition | | | | | |
|---|---|---|---|---|---|---|---|
| | | By weight | | | By number | | |
| | | Euphausids | Fish | Amphipods | Euphausids | Fish | Amphipods |
| Adélie | 15 | 98.32 | 1.36 | 0.32 | 99.33 | 0.04 | 0.62 |
| 1980/81 | | ±3.05 | ±2.85 | ±0.51 | ±1.09 | ±0.05 | ±1.13 |
| Adélie | 13 | 99.14 | 0.42 | 0.44 | 99.76 | 0.003 | 0.27 |
| 1981/82 | | ±1.85 | ±0.99 | ±1.03 | ±0.69 | ±0.009 | ±0.68 |
| Chinstrap | 21 | 97.02 | 2.97 | 0.07 | 99.79 | 0.08 | 0.12 |
| 1980/81 | | ±1.85 | ±5.95 | ±0.21 | ±0.27 | ±0.14 | ±0.21 |
| Chinstrap | 14 | 99.76 | 0.15 | 0.05 | 99.96 | 0.01 | 0.02 |
| 1981/82 | | ±0.57 | ±0.38 | ±0.20 | ±0.08 | ±0.03 | ±0.09 |

Table 3.1. The percentage composition (± sd.) of stomach contents calculated from the number and weight of each prey type present.

| | Adélie | | Chinstrap | |
|---|---|---|---|---|
| | 1980/81 | 1981/82 | 1980/81 | 1981/82 |
| No. of stomachs examined | 15 | 13 | 21 | 14 |
| Krill (%) | 100 | 100 | 100 | 100 |
| Fish (%) | 35 | 31 | 33 | 6 |
| Amphipods (%) | 35 | 15 | 29 | 12 |

Table 3.2. The percentage of stomachs containing krill, fish and amphipods.

islands of the Scotia Arc, Croxall and Prince (1980 a) and Volkman and others (1980) identified fish from the Notothenidae and the Channichthyidae. It is probably reasonable to assume that fish found in the stomachs of penguins examined for this study were also from these families. In 1980/81, six of the seven Adélies with fish in their stomachs were killed in January (the other on 30/12/80). Amounts ranged from 0.4 to 9.9 % of the individual stomach weight. Similarly, fish were only found in stomachs of chinstraps killed in January, comprising 3.5 to 20.6 % of the stomach weight. In 1981/82, fish occurred in stomachs throughout the sampling period but only occasionally.

2. Amphipods

Of the 89 amphipods found, 17 % were relatively large specimens (25-30 mm long) from the Hyperiidae. In 1981/82, 64 amphipods were found in Adélie stomachs and only one in a chinstrap stomach. These and the remaining 1980/81 amphipods were Cyllopus batesi or C. lucasi and Parathemisto gaudichaudii, with a mean length of 16 mm. They were found either in ones or twos or in numbers of between 20 and 30, usually in stomachs which contained krill of similar small size, and may have been consumed when associated with this krill. The percentage contribution of amphipods to the stomach contents and the proportion of stomachs in which amphipods were found were very similar to that found in stomachs of Adélies and chinstraps from King George I (Jazdzewski, 1981).

3. Krill

a. Mean length

The krill in most samples of both species were larger in 1980/81. This was especially so in chinstrap samples taken in December and January (Table 3.3). However, Adélies took krill 28 % larger whereas chinstraps took krill only 11 % larger when compared with those taken in January 1982. There was

Adélie

| Overall | | | | | | | | | | Females | | | | | | | | | | Males | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1980/81 | | | | | 1981/82 | | | | | 1980/81 | | | | | 1981/82 | | | | | 1980/81 | | | | | 1981/82 | | | | |
| Date | Mean | sd. | No | No' | Date | mean | sd. | No | No' | Date | mean | sd. | No | No' | Date | mean | sd. | No | No' | Date | mean | sd. | No | No' | Date | Mean | sd. | No | No' |
| 20/11 | 35 | 6 | 164 | 2 | 17/11 | 33 | 7 | 36 | 2 | 20/11 | 35 | 6 | 164 | 2 | 17/11 | 33 | 7 | 36 | 2 | | | | | | | | | | |
| | | | | | 29/11 | 28 | 11 | 108 | 2 | | | | | | | | | | | | | | | | 29/11 | 28 | 11 | 108 | 2 |
| 30/12 | 40 | 6 | 84 | 2 | 19/12 | 27 | 9 | 734 | 4 | 30/12 | 42 | 4 | 33 | 1 | 19/12 | 23 | 6 | 241 | 2 | 30/12 | 39 | 6 | 51 | 1 | 19/12 | 29 | 11 | 493 | 2 |
| 06/01 | 41 | 5 | 908 | 5 | | | | | | 06/01 | 41 | 5 | 343 | 2 | | | | | | 06/01 | 42 | 5 | 564 | 3 | | | | | |
| 14/01 | 28 | 13 | 159 | 3 | 14/01 | 30 | 11 | 385 | 5 | 14/01 | 21 | 6 | 55 | 1 | 14/01 | 26 | 8 | 347 | 4 | 14/01 | 31 | 14 | 104 | 2 | 14/01 | 45 | 6 | 38 | 1 |
| 28/01 | 36 | 9 | 272 | 3 | | | | | | | | | | | | | | | | 28/01 | 36 | 9 | 272 | 3 | | | | | |

Chinstrap

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 28/12 | 35 | 9 | 60 | 3 | | | | | | 28/12 | 38 | 6 | 39 | 1 | | | | | | 28/12 | 34 | 10 | 21 | 2 |
| 17/01 | 41 | 6 | 153 | 2 | 05/01 | 39 | 8 | 195 | 3 | | | | | | 05/01 | 35 | 9 | 30 | 1 | 17/01 | 41 | 6 | 153 | 2 | 05/01 | 41 | 6 | 165 | 2 |
| 24/01 | 39 | 6 | 312 | 5 | 27/01 | 30 | 10 | 102 | 3 | 24/01 | 39 | 6 | 158 | 3 | 27/01 | 33 | 12 | 18 | 1 | 24/01 | 38 | 6 | 154 | 2 | 27/01 | 29 | 9 | 84 | 2 |
| 31/01 | 39 | 7 | 170 | 3 | | | | | | 31/01 | 38 | 5 | 16 | 1 | | | | | | 31/01 | 40 | 8 | 154 | 2 | | | | | |
| 07/02 | 45 | 6 | 406 | 5 | | | | | | | | | | | | | | | | 07/02 | 45 | 6 | 406 | 5 | | | | | |
| 14/02 | 40 | 8 | 335 | 4 | 17/02 | 40 | 7 | 308 | 5 | 14/02 | 40 | 8 | 239 | 3 | 17/02 | 42 | 5 | 52 | 1 | 14/02 | 40 | 8 | 96 | 1 | 17/02 | 40 | 6 | 256 | 4 |
| 06/03 | 44 | 8 | 253 | 2 | | | | | | 06/03 | 43 | 7 | 203 | 1 | | | | | | 06/03 | 46 | 8 | 50 | 1 | | | | | |

No = number of krill measured. No' = number of stomachs examined from which krill were measured.

Table 3.3. The mean length (mm) of krill taken by Adélies and Chinstraps.

no significant difference in the mean length of krill taken by each species as each season progressed, but both species appear to have taken larger krill during the 1980/81 sampling period than in 1981/82 and chinstraps seem to have taken larger krill than Adélies in both years (Figure 3.2). The sample sizes resulting from splitting the data into the two sexes were very small, but both sexes showed the same trends.

Chinstraps took larger krill than Adélies except in the early part of 1980/81 and late in 1981/82 when Adélies, and especially Adélie females, took larger krill. For part of both seasons, Adélie males took larger krill than females, but where females took larger krill this tended to be earlier in the year. Chinstraps were similar, with both males and females taking larger krill on different occasions.

Taking each season as a whole, the mean length taken by each sex and by both sexes combined was greatest in 1980/81 ($P<0.001$). Chinstraps took larger krill than Adélies in both years ($P<0.001$) and males of both species usually took signficantly larger krill than females (Table 3.4).

b. Length distribution

The overall frequency distributions of krill lengths (Figure 3.3) and the length of krill taken in each year (Table 3.5), calculated from the number and weight of krill in each length class summarise data presented in detail in Appendices 3.1-3.4. The most obvious differences are that, in 1981/82, Adélies took a greater proportion of smaller krill than in 1980/81 and than chinstraps.

J.L. Watkins (personal communication) calculates, from measurements of the eleven growth stages of krill, that those less than 31 mm in length are juveniles (100 % probability), but that juveniles can be up to 38 mm in length (12 % probability). If it is assumed that krill caught by Adélies and chinstraps in this study are juvenile if less than 31 mm long and either sub-adults or mature adults if greater than this length, the

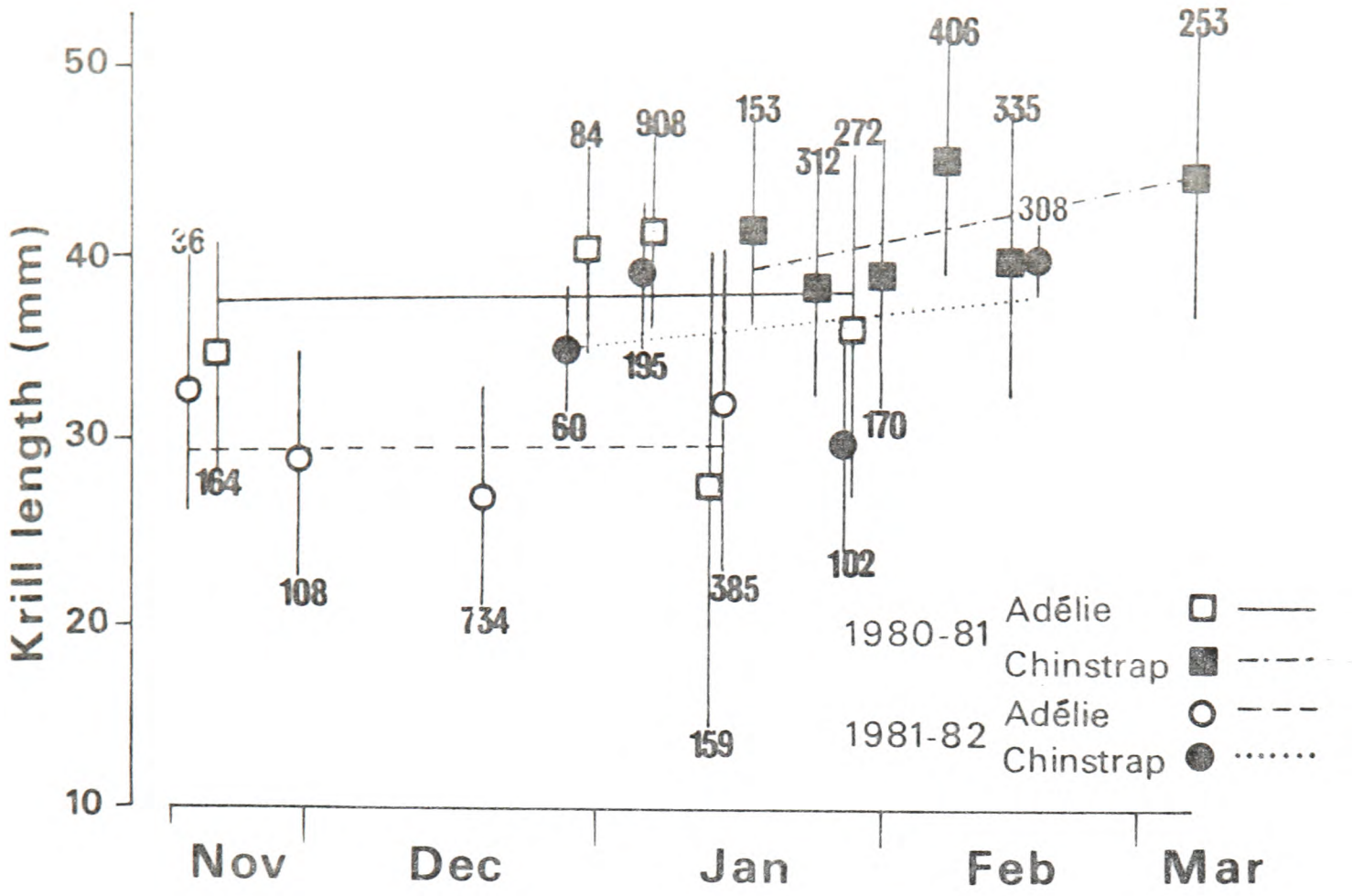



Figure 3.2. The mean length of krill taken in relation to time of year. (errors are 1 standard deviation, n = number of krill measured; although the correlation coefficients of the relationship between krill length taken and time of year were not significant at the 95% level, the regression lines have been drawn to indicate the trend in the variation of the mean krill length in the samples.)

| Year | | Overall | | Females | | Male | |
|---|---|---|---|---|---|---|---|
| | | Adélie | Chinstrap | Adélie | Chinstrap | Adélie | Chinstrap |
| 1980/81 | Mean | 36 | 42 | 35 | 40 | 37 | 42 |
| | sd. | 10 | 7 | 10 | 7 | 10 | 8 |
| | No | 1586 | 1629 | 595 | 616 | 991 | 1013 |
| | No' | 15 | 21 | 6 | 8 | 9 | 13 |
| 1981/82 | Mean | 29 | 36 | 28 | 37 | 34 | 36 |
| | sd. | 10 | 9 | 8 | 9 | 12 | 9 |
| | No | 1263 | 665 | 624 | 139 | 639 | 526 |
| | No' | 13 | 14 | 8 | 4 | 5 | 10 |

No = number of krill measured; No' = number of stomachs examined from which krill were measured.

Table 3.4. The mean length (mm) of krill taken by Adélies and chinstraps in each year.

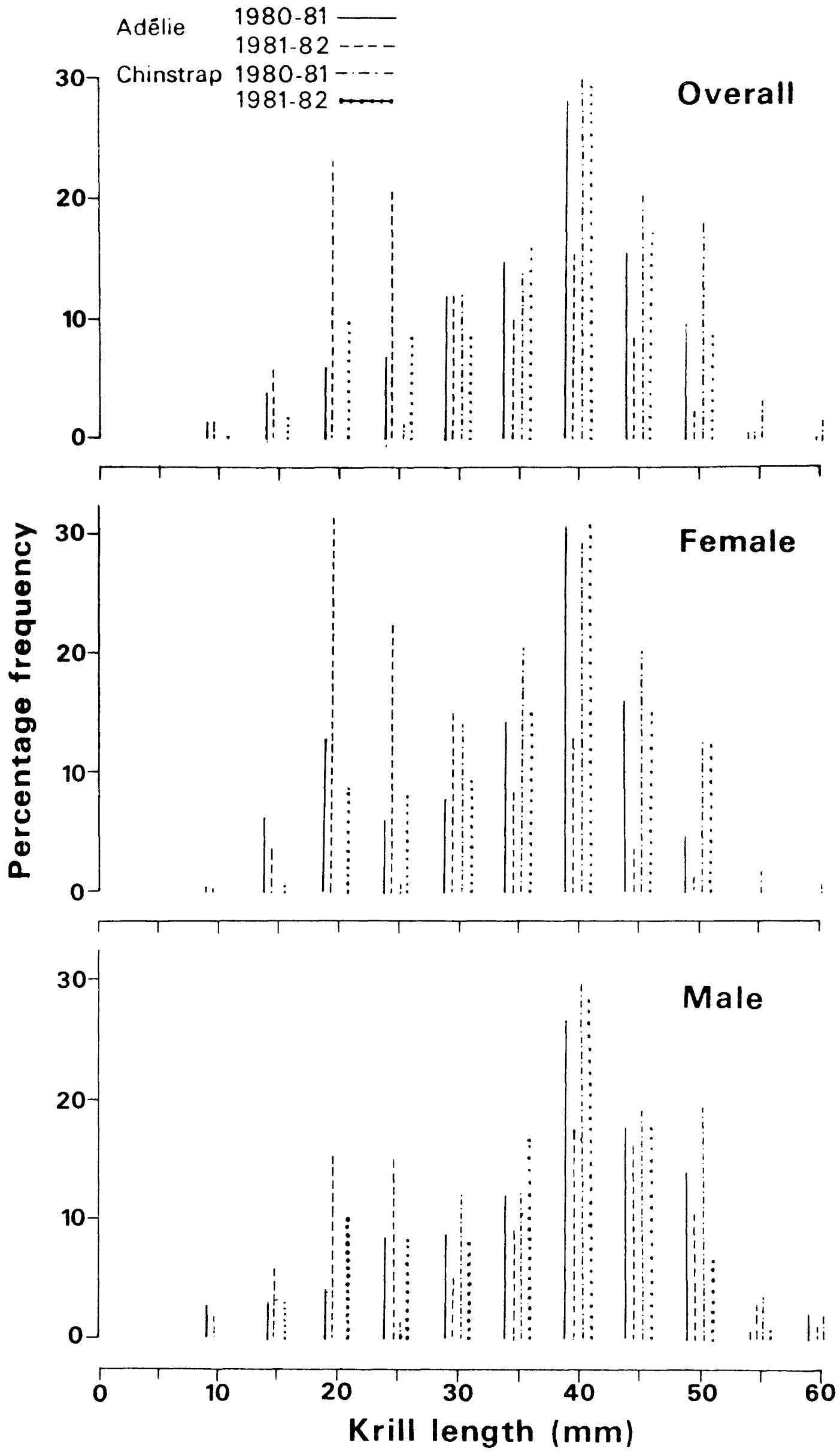



Figure 3.3. Length-frequency distribution of krill caught by penguins.

| Year | | Adélie length by no. | Adélie length by wt. | Chinstrap length by no. | Chinstrap length by wt. |
|---|---|---|---|---|---|
| 1980/81 | Mean | 36 | 37 | 42 | 42 |
| | sd. | 10 | 9 | 7 | 7 |
| 1981/82 | Mean | 29 | 34 | 36 | 40 |
| | sd. | 10 | 10 | 9 | 8 |

Table 3.5. A comparison of the mean length (mm) of krill taken by Adélies and chinstraps when calculated from the number and weight of krill in each length class.

proportion of juveniles caught by both species in 1981/82 was nearly twice that in 1980/81 and, in both years, Adélies caught twice the proportion of juvenile krill caught by chinstraps (Table 3.6). However, although still greater for Adélies than chinstraps, the weight of these krill comprised a much smaller proportion of the stomach contents and for Adélies the proportion in the two seasons was very similar. Mature krill are therefore a more important constituent of the stomach contents, particularly since fewer need be consumed to fill the stomach.

c. Total weight of krill in the stomachs

The mean actual weight and proportionate weight (in relation to adult weight) of all stomach contents are given in Appendix 3.5. The variation in the percentage of adult weight formed by the stomach contents is shown in Figure 3.4. There was a significant increase in the weight of stomach contents just after hatching. The proportion they formed of adult weight reached 11.5 % for Adélies in both years and 12.4 % for chinstraps in both years (attained on 5 January for Adélies and 14 February for chinstraps). Thus, although heavy chinstrap chick mortality was probably caused by a decrease in the weight of krill brought ashore in January 1981, those adults that successfully reared chicks until mid-February were still able to catch the same amount of krill relative to their body weight as in 1981/82.

There was no overall interspecific difference in the weight of krill brought ashore, but between years, and especially in January, the situation for the two species was quite different. There was no difference in the weight of krill brought ashore by Adélies but that by chinstraps was considerably lower in 1980/81 (Table 3.7). The same was true of the proportional krill weight. The mean weight of adults of both species killed in January was the same in both years, so it seems that Adélies caught the same amount of krill and had expended a similar amount of energy

| Krill length | Adélie | | Chinstrap | |
|---|---|---|---|---|
| class (mm) | 1980/81 | 1981/82 | 1980/81 | 1981/82 |
| **By number** | | | | |
| 10 | 0.46 | 0.91 | 0 | 0 |
| 15 | 5.60 | 5.50 | 0 | 2.15 |
| 20 | 11.40 | 23.50 | 0.03 | 9.75 |
| 25 | 6.80 | 20.60 | 1.18 | 8.00 |
| 30 | 11.00 | 12.20 | 12.02 | 8.60 |
| Total | 35.26 | 62.71 | 13.23 | 28.50 |
| **By weight** | | | | |
| 10 | 0.04 | 0.03 | 0 | 0 |
| 15 | 1.66 | 0.67 | 0 | 0.18 |
| 20 | 7.70 | 6.57 | <0.01 | 2.14 |
| 25 | 6.50 | 10.43 | 0.31 | 3.05 |
| 30 | 6.70 | 9.71 | 4.90 | 4.86 |
| Total | 22.60 | 27.41 | 5.22 | 10.23 |

Table 3.6. The mean percentage number and weight of krill in each juvenile length class (<31 mm length) found in Adélie and chinstrap stomachs.

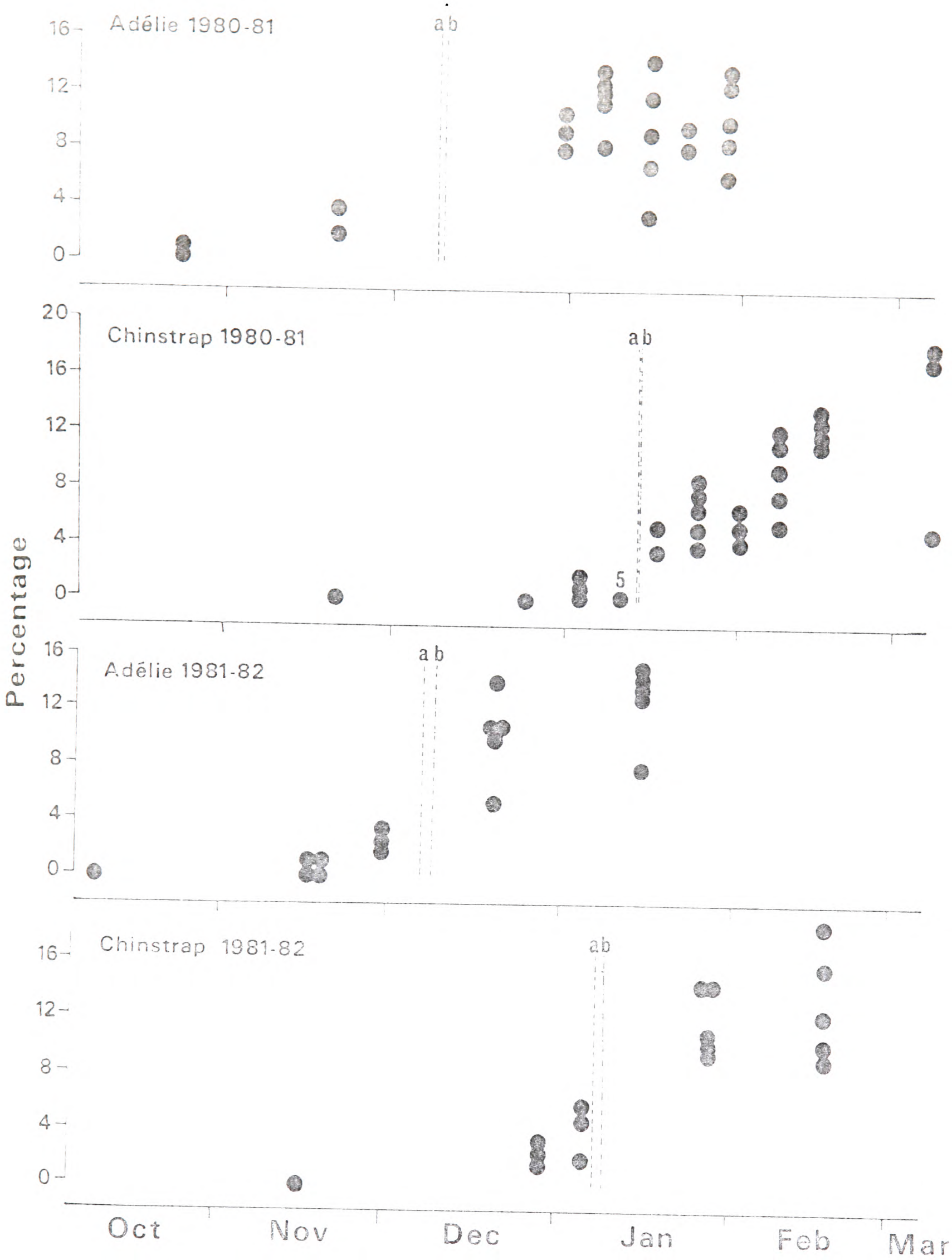



Figure 3.4. Variation with time in the weight of stomach contents as a percentage of adult weight. (a and b = first and second chick hatching dates)

| Year/date | | | Adélie | | | Year/date | | Chinstrap | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1980/81 | 1981/82 | | Overall | Female | Male | 1980/81 | 1981/82 | Overall | Female | Male |
| 20/11 | | Mean | 103.9 | 103.9 | | 03/01 | | 12.6 | 4.6 | 36.4 |
| | | sd. | 51.9 | 51.9 | | | | 16.0 | 2.4 | - |
| | | No | 2 | 2 | | | | 4 | 3 | 1 |
| | 17/11 | Mean | 27.1 | 27.1 | | | 05/01 | 166.3 | 65.0 | 207.0 |
| | | sd. | 26.2 | 26.2 | | | | 89.0 | - | 18.5 |
| | | No | 4 | 4 | | | | 3 | 1 | 2 |
| 30/12 | | Mean | 374.3 | 353.5 | 415.9 | 24/01 | | 227.4 | 206.1 | 259.5 |
| | | sd. | 71.7 | 87.7 | - | | | 65.5 | 77.6 | 41.3 |
| | | No | 3 | 2 | 1 | | | 5 | 3 | 2 |
| | 19/12 | Mean | 440.8 | 366.4 | 520.0 | | 27/01 | 456.6 | 510.0 | 380.0 |
| | | sd. | 160.9 | 176.6 | 87.5 | | | 66.9 | 9.0 | 1.7 |
| | | No | 5 | 3 | 2 | | | 5 | 2 | 3 |
| 14/01 | | Mean | 398.3 | 316.3 | 452.9 | 14/02 | | 491.9 | 471.3 | 553.6 |
| | | sd. | 189.8 | 17.2 | 228.8 | | | 51.1 | 37.2 | - |
| | | No | 5 | 2 | 3 | | | 4 | 3 | 1 |
| | 14/01 | Mean | 539.8 | 495.3 | 624.3 | | 17/02 | 563.0 | 336.7 | 601.0 |
| | | sd. | 150.7 | 162.0 | - | | | 203.0 | - | 194.0 |
| | | No | 5 | 4 | 1 | | | 5 | 1 | 4 |

Table 3.7. Comparison between years of the weight (g) of krill brought ashore during part of the chick rearing period of both species (complete data set in Appendix 3.5).

in January of both years, but chinstraps caught less krill, despite using a similar amount of energy, in January 1981 than in January 1982.

d. Krill number

In both years, the number of krill taken increased after hatching (Table 3.8), but in 1980/81, and especially in January 1981, most stomachs contained fewer krill than in 1981/82.

The smaller numbers in 1980/81 are partly a consequence of the larger krill caught in that year, but although chinstraps took only slightly larger krill in 1980/81, the number caught was always at least 40% and up to 80% less than the number caught in 1981/82. This is perhaps an indication that chinstraps were not feeding to capacity in 1980/81.

e. Relationship between amount of digestion and time since last feed.

The relationship between krill length and the logarithm of the digestion index is given in Figure 3.5. Although the difference is not significant, there is a suggestion that chinstraps may feed on large krill nearer to the time of coming ashore than Adélies.

f. Culmen dimensions.

Chinstrap culmen lengths were consistently larger than those of Adélies, with no Adélie culmen lengths greater than 41.5 mm and no chinstrap lengths less than 42.0 mm. There is no evidence, however, that these differences correlate with differences in the mean length of krill taken by the two species. Within each species, there was no relationship between mean krill length taken and culmen depth (Figure 3.6) or culmen length (Figure 3.7), although males did have greater depths than females (Table 3.9).

| Adélie | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1980/81 | | | | | 1981/82 | | | | |
| Date | Mean | sd. | range | No | Date | Mean | sd. | range | No |
| 20/11 | 400 | 201 | 199-602 | 2 | 17/11 | 224 | 14 | 210-239 | 2 |
| | | | | | 29/11 | 927 | 350 | 577-1278 | 2 |
| 30/12 | 1104 | 343 | 788-1581 | 3 | 19/12 | 3819 | 516 | 3132-4339 | 4 |
| 06/01 | 910 | 184 | 578-1125 | 5 | | | | | |
| 14/01 | 2664 | 856 | 1006-3350 | 5 | 14/01 | 4350 | 1653 | 2157-6346 | 5 |
| 21/01 | 1748 | - | - | 1 | | | | | |
| 28/01 | 1473 | 132 | 1295-1611 | 3 | | | | | |

| Chinstrap | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 1980/81 | | | | | 1981/82 | | | | |
| Date | Mean | sd. | range | No | Date | Mean | sd. | range | No |
| 03/01 | 62 | - | | 1 | 28/12 | 336 | 36 | 310-386 | 3 |
| 17/01 | 370 | 72 | 298-441 | 2 | 05/01 | 618 | 176 | 413-842 | 3 |
| 24/01 | 641 | 181 | 521-995 | 5 | 27/01 | 2927 | 554 | 2219-3749 | 5 |
| 31/01 | 588 | 46 | 552-653 | 3 | | | | | |
| 07/02 | 621 | 112 | 478-817 | 5 | | | | | |
| 14/02 | 1010 | 139 | 872-1224 | 4 | 17/02 | 1409 | 511 | 904-2212 | 5 |
| 06/03 | 739 | 318 | 290-989 | 3 | | | | | |

Table 3.8. Number of krill per sample.

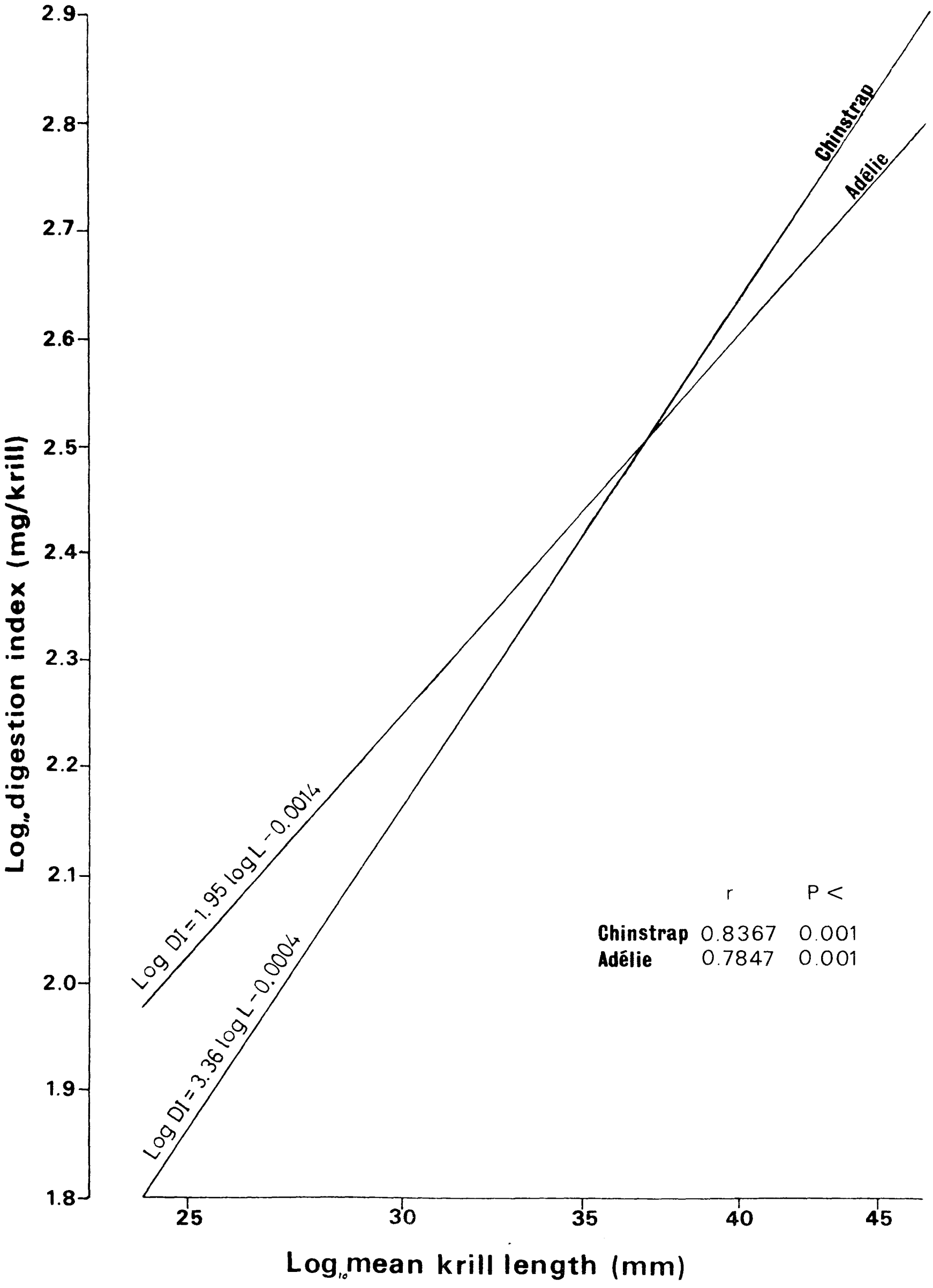



Figure 3.5. The relationship between the logarithm of the digestion index and logarithm of krill length for the top sections of 27 Adélie and 32

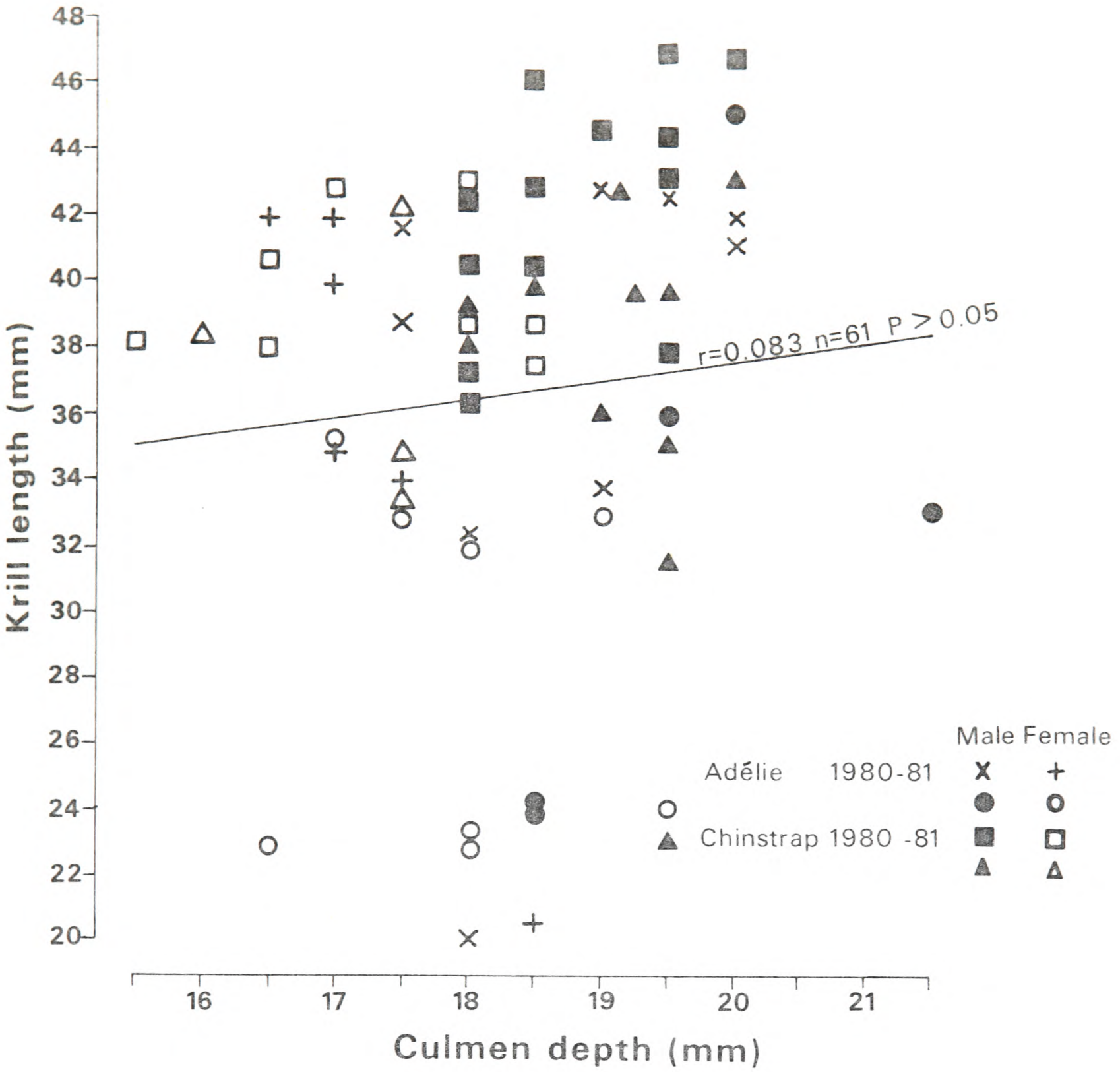



Figure 3.6. The relationship between culmen depth and mean krill length consumed. (Regression analysis carried out using pooled data for both sexes of both species produced no significant correlation.)

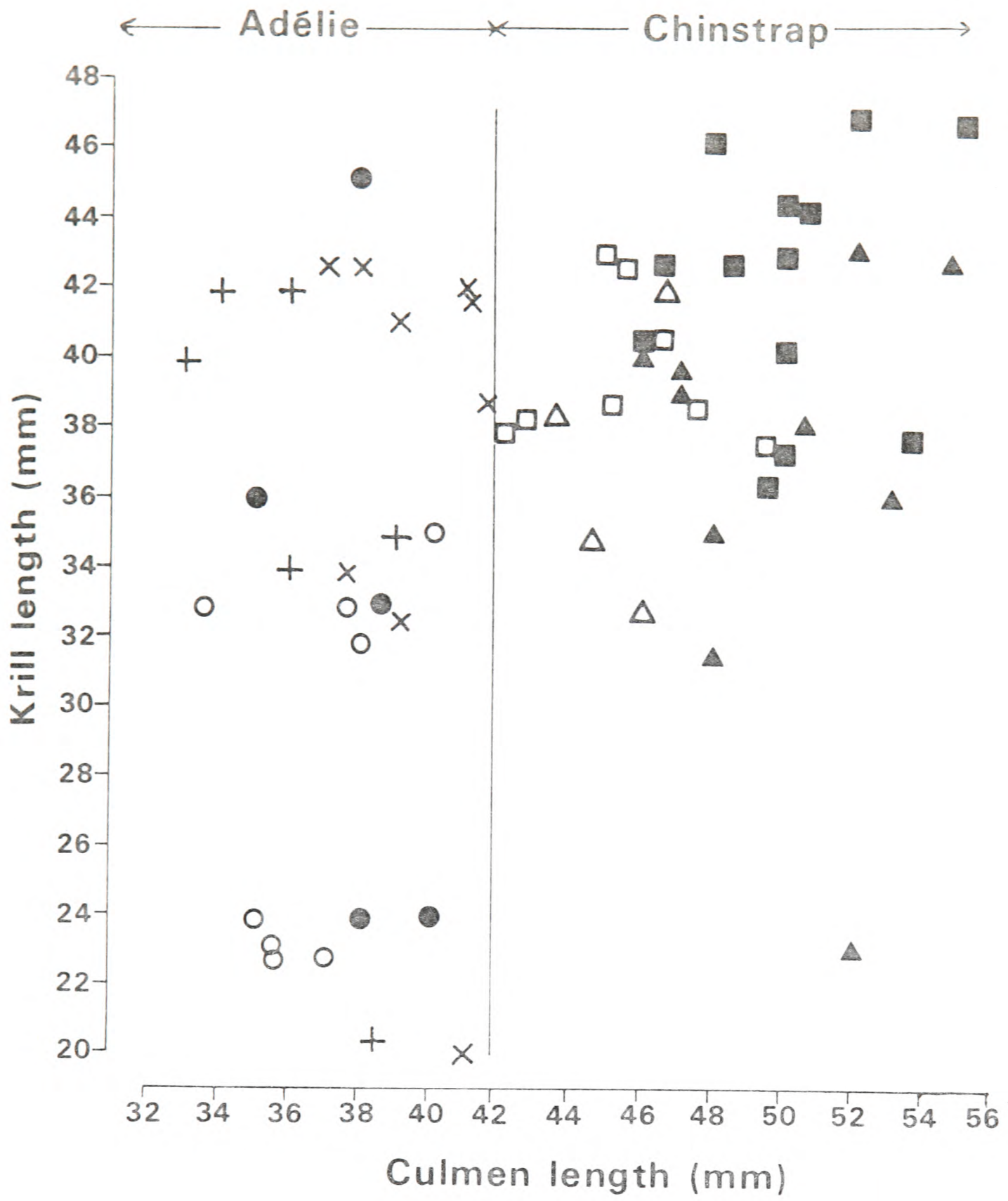



Figure 3.7. The relationship between culmen length and mean krill length consumed. (Key as for Figure 3.6)

Culmen depth (mm)

| | Mean | sd. | range | No |
|---|---|---|---|---|
| Adélie female | 17.5 | 1.0 | 15.5-19.5 | 22 |
| Adélie male | 19.1 | 1.0 | 17.0-21.5 | 32 |
| Chinstrap female | 17.3 | 0.8 | 16.0-19.0 | 24 |
| Chinstrap male | 18.8 | 0.7 | 17.5-20.0 | 39 |

Culmen length (mm)

| | Mean | sd. | range | No |
|---|---|---|---|---|
| Adélie female | 37.0 | 2.5 | 33.0-42.5 | 22 |
| Adélie male | 40.0 | 3.3 | 35.0-53-5 | 32 |
| Chinstrap female | 45.4 | 2.0 | 41.0-49.5 | 24 |
| Chinstrap male | 49.8 | 2.4 | 44.0-55.0 | 39 |

Depth :

Chinstrap females = Adélie females < chinstrap males = Adélie males

($P<0.001$)

Length :

Adélie females < Adélie males < chinstrap females < chinstrap males

(all $P<0.001$)

Table 3.9. Comparison of Adélie and chinstrap culmen depths and lengths.

# DISCUSSION

## 1. Diet composition

The different conditions of the two years did not change the importance of krill in the diet, although more fish were consumed in 1980/81, especially by Adélies. If the ice conditions were the cause of a change in diet, it was possibly because birds were forced to feed in different areas. This is indicated by the presence of Hyperiid amphipods in 1980/81 and their absence in 1981/82. Since the fish and amphipods were always integrated within the krill in the stomachs, it is likely that their ingestion was accidental rather than the result of selective feeding. Stones found in stomachs could have been ingested after reaching the colony, perhaps during a changeover at the nest (Emison, 1968) or brought from the sea (Bagshawe, 1938).

Previous dietary studies of Adélies and chinstraps (Emison, 1968; Croxall and Prince, 1980 b; Volkman and others, 1980) also emphasise the importance of krill in the diet, although Emison found that Adélies took only 91-95 % Euphausia crystallorophias by number, the remainder being fish and amphipods.

## 2. Krill

In both years, there was a significant increase in the weight and number of krill supplied by adults when chicks hatched. This is a logical response to the extra demand by chicks at this time.

There was no significant difference in the mean length of krill taken by each species as each season progressed. In most samples, and especially those from 1981/82, the majority of krill were juvenile (less than 31 mm in length) and there were proportionately more of these than in chinstrap stomachs. There are several possible explanations for the differences in the length of krill caught by the two species:

1. Adélies may be better adapted to feed on small krill,
2. sexual dimorphism in culmen and body size,
3. difference in the timing of breeding of Adélies and chinstraps,
4. the two species may forage in different areas at different times.

1. In the Ross Sea, where over 40 % of the total Adélie population breed (Ainley and O'Connor, in press), E. crystallorophias (c 20 mm average length) is the most important constituent of Adélie diet (Emison, 1968). If Adélies are well adapted to feed on these, it is not surprising that they are able to exploit efficiently juvenile E. superba of similar small size in the South Orkneys where E. crystallorophias are rarely found.

2. Ainley and Emison (1972) suggested that differences in krill size taken by Adélies in the Ross Sea were due to sexual dimorphism in culmen and body size. Thus, in the Ross Sea, where there is no interspecific penguin competition, perhaps reduction in intraspecific competition is particularly important. In the present study, no overall differences in the size of krill taken by either sex of Adélies or chinstraps were found, despite significant differences in culmen and body size. It is unlikely that culmen size differences are a cause of interspecific feeding differences at any stage in the breeding cycle, since although Adélies catch a large number of small krill they are also able to consume mature krill and fairly large fish. It is possible that the krill size differences noted by Ainley and Emison (1972) are indeed due to sexual dimorphism, but there is also the likelihood that they are due to differences in foraging area.

3. Adélies begin breeding at Signy about one month before chinstraps which results in a difference in the timing of peak energy demand by the two species. Energy demand reaches a peak at the beginning of the crêche period when the growth rate of the chicks is at its highest. The parents subsequently forage continuously in order to satisfy the energy demands of their chicks. For Adélies the peak is between the end of December, when

the crèche period begins, and the beginning of February, when the chicks fledge, and for chinstraps peak energy demand is between the beginning of February and the beginning of March. In the only study of monthly changes in the length-frequency distribution of krill (from Admiralty Bay, King George I, South Shetland Is), Stepnik (1982) showed that the highest proportions of sub-adult and adult krill (greater than an average of 33.4 mm in length) are present in February and March and perhaps January, and that there can be a high proportion of juveniles present in January, but not in February or March. There was appreciable variation between the two summers studied. It is not known whether the situation at the South Orkney Is is similar, and it may not be entirely realistic to compare the South Shetland Is data from 1979/80 with length-frequency distributions of krill from the stomachs of South Orkney Is penguins in 1980-82. However, no other relevant data exist. Stepnik's (1982) data suggest two explanations for differences in the length-frequency distribution of krill taken by Adélies and chinstraps at Signy:

a. Krill longer than 31 mm were available to chinstraps, but largely unavailable to Adélies, at the time of their peak energy demands.

b. Krill shorter than 31 mm were available to Adélies, but largely unavailable to chinstraps, at the time of their peak energy demands.

The proportion of juvenile and non-juvenile krill taken by each species is likely to be important in terms of maximising energy intake since different age-classes of krill contain different percentages of lipids at different times of year. Mature female krill contain a greater percentage of lipids just prior to spawning than juveniles which, in turn, contain a greater percentage of lipids than male krill (Clarke, in press). Female krill spawn from late January through to early March and their lipid content is at its highest just prior to spawning (Clarke, 1980; in press), which coincides with the time of highest energy demand by chinstraps. It is not known whether chinstraps actively select these krill but their presence in

large numbers may mean that they are frequently encountered. If this is so, then the timing of the chinstrap breeding season may even be adapted to the changes in the energy content of their main prey.

4. Adélies and chinstraps may forage for krill in different areas at different times. Marr (1962) and Mauchline and Fisher (1969) showed that swarms of krill can have greater homogeneity within than between swarms. This could account for differences in the size of krill caught by the two species and the reason why stomachs often contained a majority of krill with the same length. In addition, differences in foraging area, the location of swarms, growth rates or proportions of adult to juvenile krill in swarms might explain why krill caught by both species in 1980/81 were larger than those caught in 1981/82.

Adélies and chinstraps may encounter different swarms, and perhaps different sized krill in them, because they travel over different distances to feed. Adélies have long incubation shifts (Sladen, 1958; Penney, 1968; Conroy and others, 1975 b; Volkman and others, 1980; this study) and, while this may primarily be an adaptation to breeding further south, where ice is more likely to surround breeding sites at the start of the breeding season and more time is required for travel between the colony and a foraging area, a consequence of this is that they are also adapted to feeding further from the breeding site. Chinstraps breed later in the year (Sladen, 1955; Conroy and others, 1975 a; this study), and in areas where sea ice is less likely to obstruct travel, so shorter incubation shifts are typical (Conroy and others, 1975 a; Conroy and others, 1975 b; Volkman and others, 1980; this study) and they are correspondingly less likely to travel as far as Adélies on a foraging trip. Volkman and others (1980) found that stomachs of chinstraps from King George I contained more fresh krill than Adélie stomachs, as results from this study also indicated. At the South Orkneys, there is a confluence of the Antarctic circumpolar and Weddell Sea currents to the north of the island group (Bogdanov and others,

1969) and krill are reportedly associated with this and the continental shelf area (Elizarov, 1971). The confluence of the currents and the continental shelf area may constitute two separate feeding areas for Adēlies and chinstraps if juvenile and non-juvenile krill are each associated with one of them. Thus, chinstraps may feed mainly on larger krill nearer to the breeding site, over the continental shelf, and Adēlies may feed mainly on small krill to the north of the continental shelf in the ocean current confluence. Apart from any differences in length of krill caught, this could also account for any differences in the degree of digestion of krill in the stomachs.

Variation in the length-frequency distribution of krill in different swarms has been found between several areas of the Scotia and Weddell Seas (Shevtsov and Makarov, 1969). This variation may be reflected in the lengths taken by penguins from different areas at the same time of year since the percentage of the number of juvenile krill (less than 31 mm in length) taken by Adēlies and chinstraps, respectively, was only 5 % and 1.8 % at King George I in 1978/79 (Volkman and others, 1980) but 35 % and 13 % in 1980/81 and 63 % and 26 % in 1981/82 at Signy I. Similarly, Croxall and Furse (1980) found that over 80 % by number and 90 % by weight of chinstrap diet at Elephant I comprised adult and sub-adult krill. The degree with which the length-frequency distribution of krill caught by Adēlies and chinstraps reflects that of krill in the sea could ideally be determined by comparing krill from stomachs with those caught by net hauls in the same area in which the penguins were feeding. The available net haul data for the South Orkney Is were collected in 1980/81 outside the foraging range of Adēlies and chinstraps (estimated in chapter 4) and are compared with the length-frequency distributions of krill caught by Adēlies and chinstraps in the same year (Figure 3.8). There are broad similarities, but both penguins took more krill of all sizes from 10-40 mm than were present in net hauls and krill larger than 40 mm were under-represented in the penguin

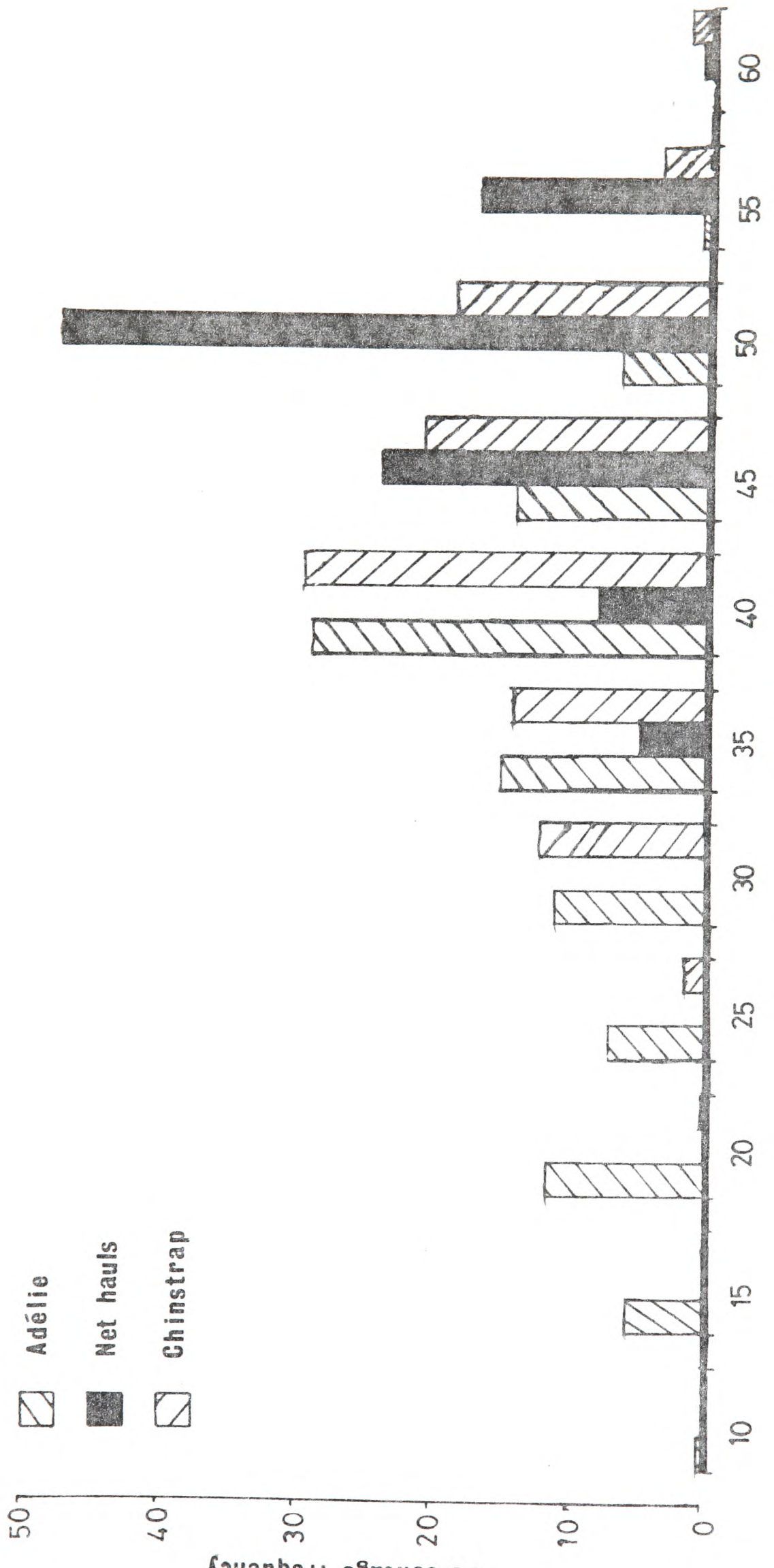



Figure 3.8. Length-frequency distributions of krill caught by Adélies and chinstraps at the South Orkneys in 1980/81 and by net hauls to the north-west of the South Orkneys in 1980/81 (net haul data from BIOMASS, 1982).

stomachs. Such discrepancies are not suprising, however, since the net hauls were made in an area well outside the maximum foraging range of chick-rearing penguins. Net haul data are also available for Admiralty Bay (Stepnik, 1982), in which it is believed that Adēlies and chinstraps from Volkman and Trivelpiece's study colony at Pt. Thomas, King George I were foraging. Length-frequency distributions of krill from these net hauls and Adēlie and chinstrap stomachs are compared in Figure 3.9. Stepnik's (1982) net haul data for November to March have been averaged for this comparison, since it must be presumed that the stomach data from Volkman and others (1980) are an average for the same period. The distributions are similar, although there are some differences. Thus, there is a tendency for Adēlies and chinstraps to catch more krill of 40-45 mm in length than are represented in the net hauls, Adēlies take more krill of all sizes from 10-45 mm than are present in net hauls and large krill, greater than 45 mm, are under-represented in the penguin stomachs. Differences in the frequency of 40-45 mm krill may be due to seasonal variation in the abundance of these particular lengths and the absence of small krill in net hauls, at Admiralty Bay and the South Orkneys, is probably because the mesh size of the nets allows most of these to escape. Large krill (reaching over 60 mm in length) have been recorded in net hauls from Admiralty Bay and the South Orkneys, with peaks in the length-frequency distributions as high as 53 mm (Nemoto and others, 1981; BIOMASS, 1982; Stepnik, 1982), yet there was a general absence of these krill in Adēlie and chinstrap stomachs examined by Volkman and others (1980) as well as those from this study. Croxall and others (in press c) suggest that this occurs because the birds do not usually forage where the large krill occur. This may perhaps be because larger krill swim at greater depths.

The only drawback to a comparison of these particular data is that the net haul and stomach data are not from the same year, so potential year to

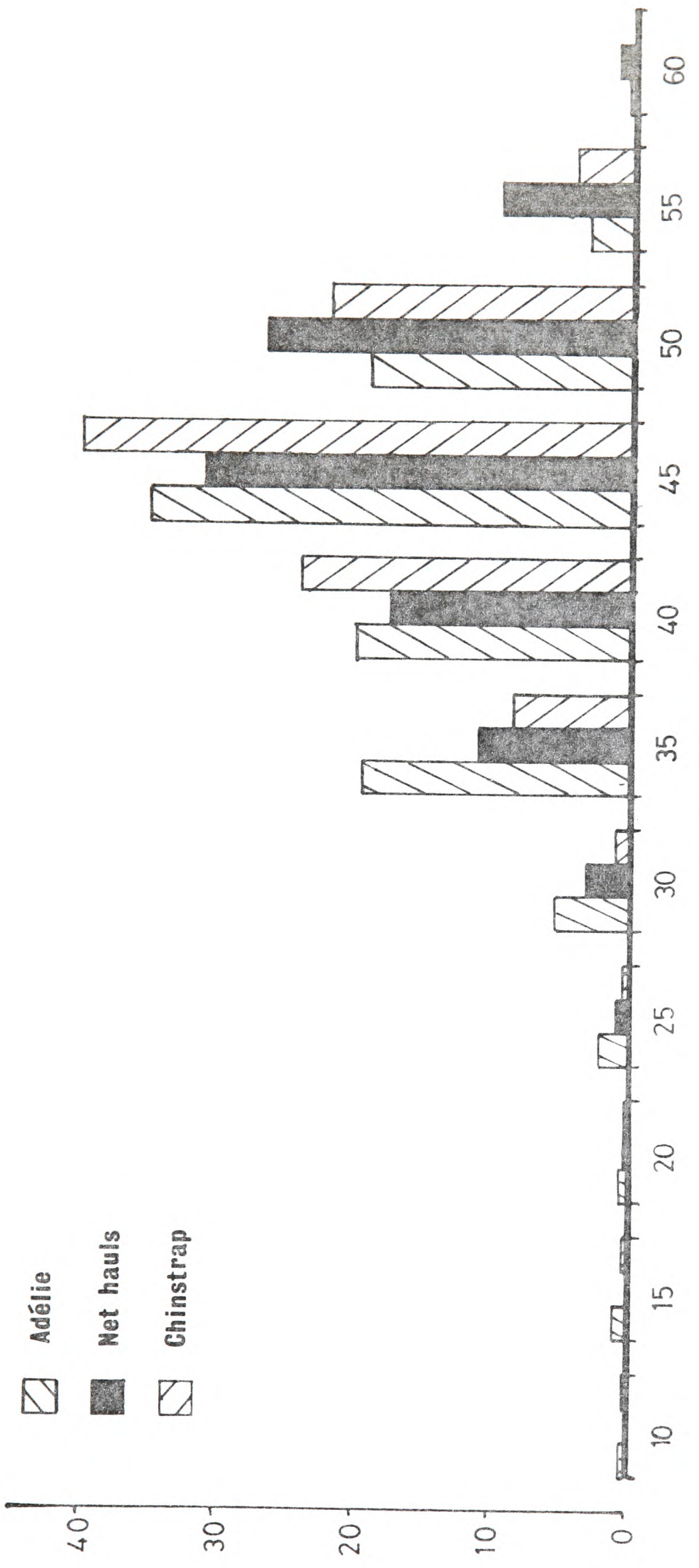



Figure 3.9. Length-frequency distributions of krill caught by Adélies and chinstraps in 1977/78 and by net hauls in 1979/80 in Admiralty Bay, South Shetland Is. (The cumulative length-frequency curve for krill from the stomachs of Adélies and chinstraps (Volkman and others, 1980 data) has been re-drawn as a length-frequency distribution and compared with the Admiralty Bay net haul data (from Stepnik, 1982).)

year variation in the length-frequency distribution of krill swarms in a particular area must be taken into account when drawing any conclusions.

We have seen that there are differences in the length-frequency distribution of krill caught by the two species. Although it could be expected that two species foraging at different times might catch different sizes of the same prey, it is interesting to note that, when Adélies and chinstraps are foraging at the same time, i.e., when their breeding seasons overlap there are still differences in the length-frequency distribution of krill caught. Thus, although the krill in penguin stomachs may indeed reflect what is available at the time of foraging, availability of krill may not necessarily determine the length-frequency distribution of krill when the Adélie breeding cycle overlaps with that of chinstraps. The major events of the Adélie and chinstrap breeding seasons are about one month apart at Signy, but during most of January and early February both species forage for food for their chicks. At this time, it is also likely that sub-adult and mature adult krill are abundantly available. These are exploited by chinstraps but Adélies continue to take a large proportion of juveniles, despite the obvious advantages of taking larger and perhaps more energy-rich krill. This can be illustrated by comparing the length-frequency distributions of krill taken by Adélies and chinstraps before chinstraps begin to forage for their chicks, when both species are foraging for their chicks and when only chinstraps are doing so (Figures 3.10 and 3.11). When foraging by both species does not overlap, differences in krill lengths taken could again be explained by differences in the availability of the various maturity stages, differences in foraging range or area or by an adaptation by Adélies to feeding on small krill. However, although the second and third of these explanations may also apply to the differences in length taken when both species are foraging at the same time, there are two other possible explanations:

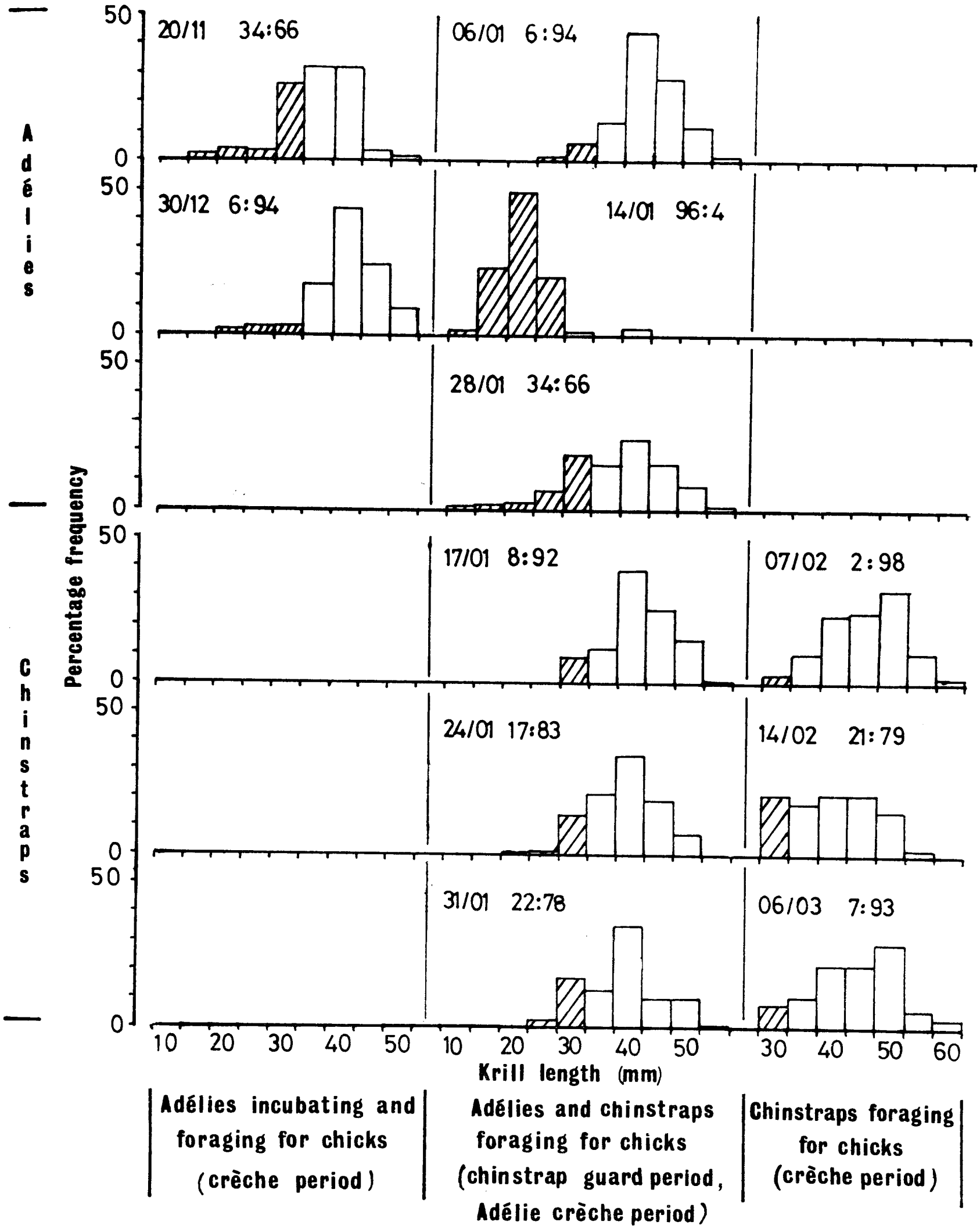



Figure 3.10. Length-frequency distributions of krill in Adélie and chinstrap stomachs during three stages of their breeding seasons in 1980/81. (Note: the ratio of juvenile to sub-adult and adult krill in each sample is given; shaded areas indicate juvenile krill.)

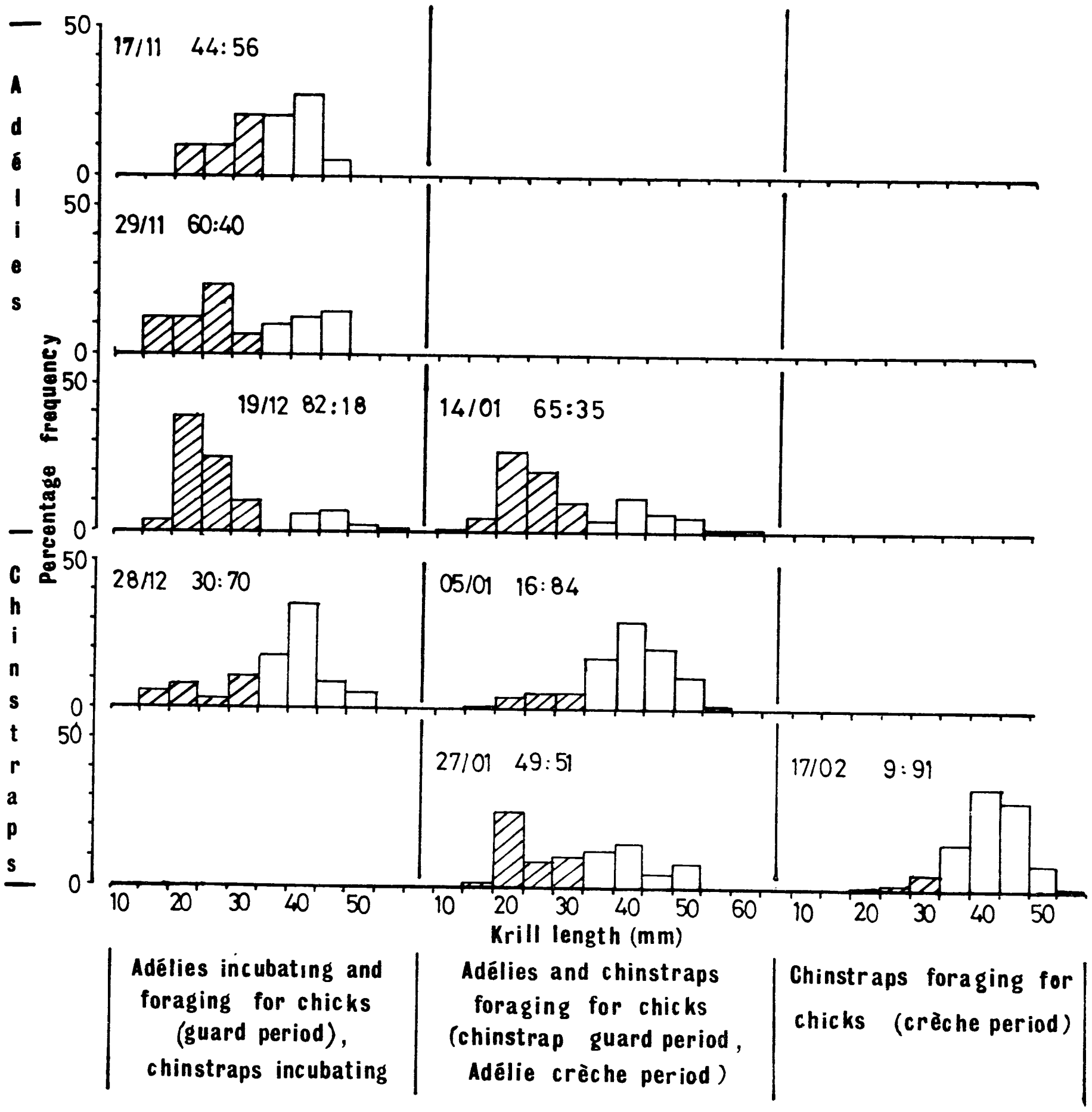



Figure 3.11. Length-frequency distributions of krill in Adélie and chinstrap stomachs during three stages of their breeding seasons in 1981/82. (Note: the ratio of juvenile to sub-adult and adult krill in each sample is given; shaded areas indicate juvenile krill.)

1. Adélies and chinstraps may be selectively feeding on different sized krill,

2. Adélies may be avoiding competition.

1. White and Conroy (1975) suggested that differences in krill size taken by Adélies and chinstraps are due to selective feeding on different sized krill. However, since the differences when Adélies and chinstraps are foraging at the same time are not consistent, it is more likely that they are due to differences in foraging location of the kind discussed earlier, rather than to any active selection of krill of a certain length.

2. When both species are foraging at the same time, Adélies are apparently feeding less economically on juvenile krill. It is possible that this is a consequence of avoiding competition for the same resource. However, by having longer foraging trips and perhaps travelling further to feed, Adélies are obviously still obtaining an adequate energy supply.

## CONCLUSIONS

Although both Adélies and chinstraps have a diet which consists almost entirely of krill, it is clear that, at Signy I at least, Adélies may take more juvenile krill than chinstraps. Spatial differences in feeding may be the main cause of this, especially when both are feeding at the same time, but it is also possible that earlier breeding by Adélies means that they catch more juvenile krill because mature krill are largely unavailable. Chinstrap breeding occurs later and coincides with the timing of peak availability of sub-adult or mature adult krill, which may be particularly energy rich. There is no clear evidence that Adélies and chinstraps have evolved specific dietary adaptations associated with avoiding competition where they are breeding sympatrically, other than those that may be a consequence of different foraging ranges and times.

# Chapter Four

## Feeding ecology

# INTRODUCTION

The examination of Adélie and chinstrap diet showed the amount and composition of food brought ashore by the adults. This chapter aims to examine further the ways in which feeding by Adélies and chinstraps might differ. This includes a study of the size and frequency of meals delivered to the chicks by the adults using data collected in the course of chick growth studies. Feeding frequency and meal size are compared intra- and interspecifically and between and within the two years studied. In addition, data are presented on the time of chick feeding and the foraging behaviour of the adults, including an estimate of the foraging range of the two species and some data on the diving depths and performance of chinstraps. These latter are the results of the first attempt to obtain detailed records of diving depths of one of the smaller penguins. It is an important aspect of their feeding ecology, as it may considerably influence the type of prey they encounter and can exploit efficiently.

# METHODS

## Data collection

Three methods were used to record meal size and feeding frequency:

1. Chicks at all study nests in A41 and C80 were weighed daily throughout most of the guard and crêche periods between 0900 and 1200 local time.
2. Chicks were weighed four times at three-hourly intervals between 0900 and 1800 local time during each day of several two or four day periods.
3. Chicks were weighed as soon as possible before and after an observed feed. During the guard period it was difficult to decide when the adult had finished feeding the chick, so four hours was allowed for the feed to take place before the chick was re-weighed.

The time of chick feeding was also assessed in three ways:

1. During the three-hourly weighing periods, the number of adults that had changed over at the study nests after each three hour interval and after the interval between 1800 and 0900 local time were recorded. Adélie chicks were weighed three-hourly over two days, starting at 0900 on the morning of the first day. Together with the weight at 0900 local time on the morning after the second day, feeds were therefore recorded over two 24 hour cycles. Chinstrap chick weights were similarly recorded over four consecutive 24 hour cycles. During the guard period, a feed between 1800 and 0900 local time was recorded if, on a visit to the nest at 0900, the adults were found to have changed over at the nest. It was assumed that they only changed once during this time.

2. The number of Adélies changing over at study nests or feeding a chick during each hour was recorded over several 24 hour periods.

3. The total number of birds entering the colony during each hour was recorded over several 24 hour periods. Feeding was not recorded and non-breeding and breeding birds were not distinguished, but the daily pattern of movement in the whole colony was obtained. This was carried out during the first two weeks of the crēche period in A41 in 1981/82.

The multiple maximum depth recorder (MDR) described by Kooyman and others (1983) was used to record diving depths. In brief, it is cylindrical (95.0 mm long by 23.0 mm diameter) and weighs 95 g (approximately 2.4 % of adult chinstrap penguin body weight). The MDR contains eight electronic counters which respond to different pressure thresholds, each of which is equivalent to a different depth. The counters record the number of dives which exceed each pressure threshold. The intervals between the thresholds depend on the maximum pressure threshold of each MDR.

The MDR was attached to feathers in the middle of the back with two worm-drive hose clips. MDR's were deployed on four breeding chinstraps captured during the chick crēche period in January and Feburuary 1981.

When the birds returned to sea to feed and dived below the surface of the water, the increase in pressure with depth was converted to a voltage shift by a pressure transducer in the MDR. If the voltage exceeded the threshold of one or more of the electronic counters, this was recorded in each of them. On returning to the colony after a single foraging trip, the duration of which was recorded, the bird was re-captured and the MDR removed. On two occasions the weight of food given to the chick after the foraging trip was recorded by weighing the chick before and after a feed.

Data analysis

1. Meal size

Meal sizes were calculated from the positive weight increments between two consecutive daily weighings of chicks . Weight differences less than 10 g were considered to have been caused by weighing error, so were not used. If the time of feed was unknown, the amount of weight lost between a feed and a weighing would also be unknown. Therefore, all the feed sizes obtained in this way, except for those calculated from weights taken before and after an observed feed, contain an error. It was assumed that all daily weighings were taken the same amount of time after a feed and therefore that this error was constant.

The data on meal sizes were separated into four categories: chicks single from hatching (singles), first and second chicks in a brood of two (firsts and seconds) and surviving chicks which had lost a sibling since hatching (survivors). The data from each of these categories were subdivided into meal sizes given during the guard period and the creche period. The meal sizes indicated by daily weighings were used in most comparisons since they comprised the largest data set. As a test of the accuracy of meal sizes calculated from daily weighings, two relationships between chick age and meal size given to Adélie chicks were calculated from

daily weighings and weights taken before and after observed feeds, and these were compared.

The variation of meal size with chick age for all four categories and for the total food given to broods of two (twins) was analysed by linear regression and the slopes of the regressions were compared between singles and broods of two for each year and each species.

2. Feeding frequency

Estimates of feeding frequency were obtained from the frequency of positive weight increase recorded by daily and three-hourly weighings. Frequencies were calculated from three-hourly weighings which are accurate to within ± 1.5 h. There was no significant difference between feeding frequencies calculated from daily or three-hourly weighings, so it was assumed that those calculated from daily weighings were a good estimate of feeding frequency.

3. Feeding behaviour

a. Time of return from foraging trips by adults

The number of birds recorded entering A41 in each hour was compared with a count of nests from a photograph of the colony taken during the late stages of incubation. Although many nests had failed since the photograph was taken, non-breeders and failed breeders remain in or near the colony for some time and often enter or leave it. At the time of the crèche period there is a large influx of these birds during what is called the re-occupation period. It has been well documented for the Adélie penguin (Sladen, 1958; Sapin-Jaloustre, 1960; Taylor, 1962; Penney, 1968; Spurr, 1977; Ainley and others, 1978; Davis, 1980) but not for chinstraps. To obtain an estimate of the percentage of breeding birds entering the colony in each hour, it had to be assumed that the number of nests that failed between taking the photograph and recording the movement pattern was

equaled by the number of failed breeders and non-breeders entering the colony during the re-occupation period.

b. Foraging distance

An estimate of the distance from the breeding site to the foraging area of Adélies and chinstraps at Signy was calculated from estimates of penguin swimming speed and the time spent absent from the colony between feeds to chicks. The swimming speed of Adélies was measured at 7.13 km $h^{-1}$ in a zoo tank (Clark and Bemis, 1978) and 7.2 km $h^{-1}$ between two ice holes 120 m apart (Kooyman, 1975). A maximum and minimum possible foraging distance was calculated using swimming speed, the highest and lowest estimates of feeding frequency obtained from daily and three-hourly weighings and an estimate of the amount of time during a foraging trip which was spent diving for food and resting between dives. The amount of time spent diving was calculated from the mean number of dives made by chinstraps during a foraging trip (recorded by MDR's) and the estimated duration of each dive. For these purposes, the duration of each dive was assumed to be 1.6 min. This is based on reasoning that if 90% of dives take place at night, and are all of the same duration, then with an average of 5 h of darkness at the South Orkneys in January - February, the duration of each dive would be 1.6 min. (see discussion of diving depths). To obtain an indication of the amount of time spent resting during a foraging trip, diving time was then compared with an assumption that 40 % of a foraging trip is spent resting and diving for food. This is based on estimates for foraging Antarctic fur seals Arctocephalus gazella, which have similar diet, dive times and diving depths (Croxall and others, in press a; Kooyman and others, in press). It is probably a better estimate to use than that for the inshore feeding jackass penguin Spheniscus demersus which spends nearly 70 % of an average 9 h foraging trip resting and diving and only 30 % travelling (Nagy and others, in press). Of each

foraging trip, only 14 % of a foraging trip was spent diving, compared with about 38 % for chinstraps (this study) and 35% for Antarctic fur seals (Kooyman and others, in press). It was assumed that Adélies and chinstraps swim at the same speed and in a straight line to and from the foraging area and the colony, and that birds went to sea immediately after leaving the colony. In reality, birds often remained near the colony for several hours after leaving the nest, but it was not possible to quantify this. The estimated foraging ranges were compared with the depth of water around the South Orkneys.

c. Diving depth

The number of dives logged in each counter of the MDR's was read from a decoding processor which was attached to the MDR in the laboratory. The frequency of dives within the depth ranges corresponding to the eight counters was then calculated.

## RESULTS

1. Meal size

The mean and standard deviation of meal size given to chicks of the four categories each day, calculated from daily weight increments, are given in Appendices 4.1-4.4. The estimates of the mean meal size during the guard and crēche periods, calculated from daily weight increments, three-hourly weighings and weights taken before and after a meal, are summarised in Appendix 4.5. The regression analyses of the data from Appendices 4.1-4.4, and the meal sizes recorded by weighing before and after a meal, are given in Figures 4.1-4.4.

Where meal sizes to chicks of a certain category were recorded by daily weight increment and by weighing before and after a meal, there were

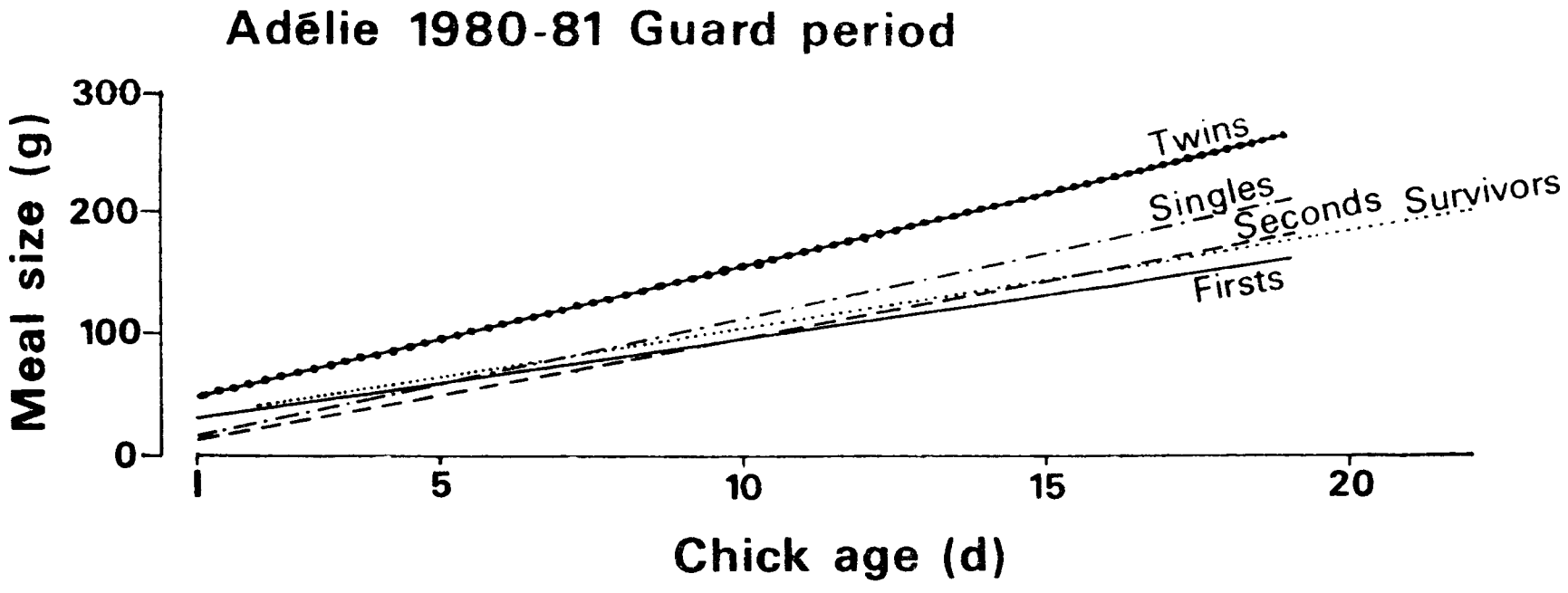



Figure 4.1. The relationship between chick age and meal size given to Adélie chicks in 1980/81. (Firsts: s = 7.14; r = 0.7498, P < 0.001; seconds: s = 9.37; r = 0.6362, P < 0.001; singles: s = 10.79; r = 0.6299, P < 0.001; twins: s = 11.76; r = 0.8078, P < 0.001; survivors: s = 8.49; r = 0.4395, P < 0.01; s = rate of increase in meal size ($gd^{-1}$).)

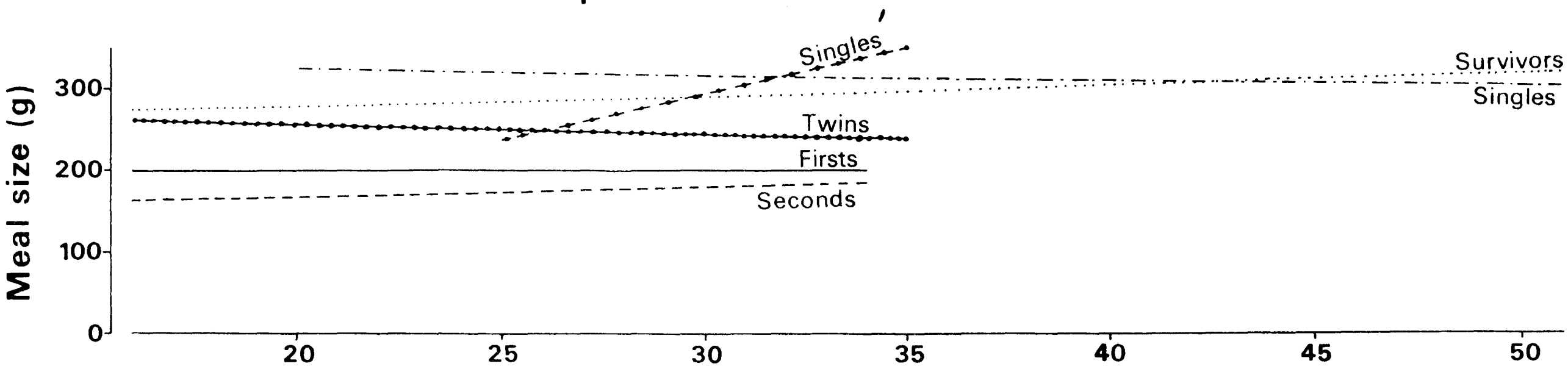



Figure 4.1. (continued).

(Firsts: s = 0.014; r = 0.0189, P > 0.05; seconds: s = 1.32; r = 0.0386, P > 0.05; singles: s = -1.43; r = -0.0207, P > 0.05; singles (from before and after weighings): s = 11.11; r = 0.5502, P > 0.05; survivors: s = 1.43; r = 0.0410, P > 0.05; twins: s = -1.11; r = -0.0374, P > 0.05).

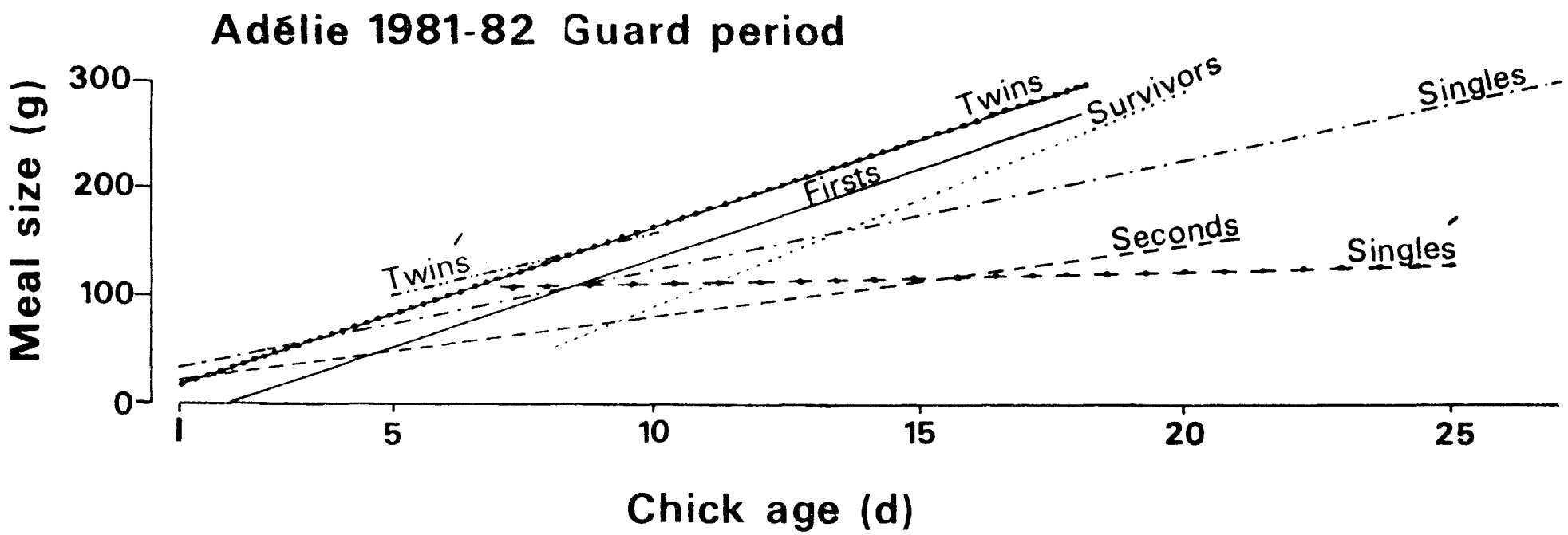



Figure 4.2. The relationship between chick age and meal size given to Adélie chicks in 1981/82. (Firsts: $s = 16.66$; $r = 0.6134$, $P < 0.001$; seconds: $s = 6.66$; $r = 0.4947$, $P < 0.001$; singles: $s = 10.07$; $r = 0.9129$, $P < 0.001$; survivors: $s = 19.78$; $r = 0.6305$, $P < 0.01$; twins: $s = 16.66$; $r = 0.6432$, $P < 0.001$; singles[1] (from before and after weighings): $s = 1.43$; $r = 0.0784$, $P > 0.05$; twins[1] (from before and after weighings): $s = 11.51$; $r = 0.3665$, $P > 0.05$).

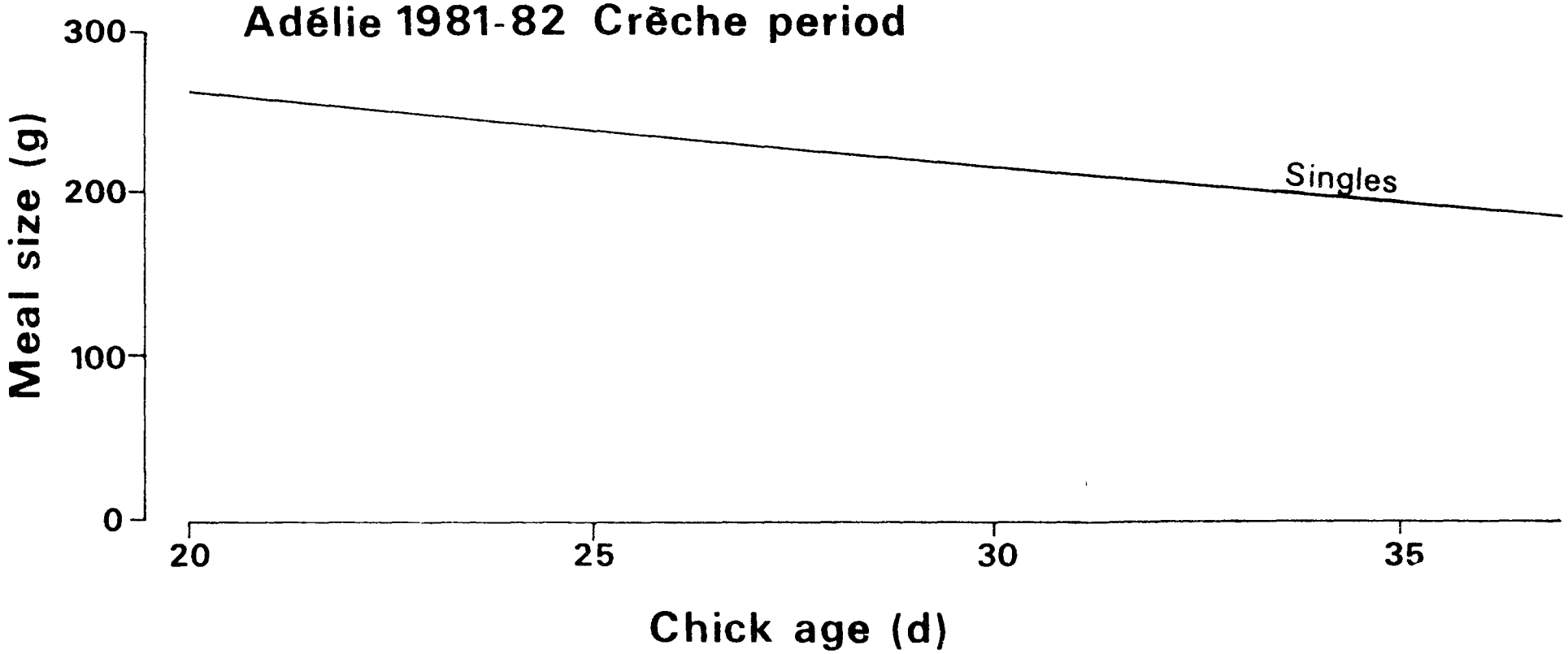



Figure 4.2. (continued)

(Singles[1] (from before and after weighings): s = -4.16; r = -0.2689,

P > 0.05).

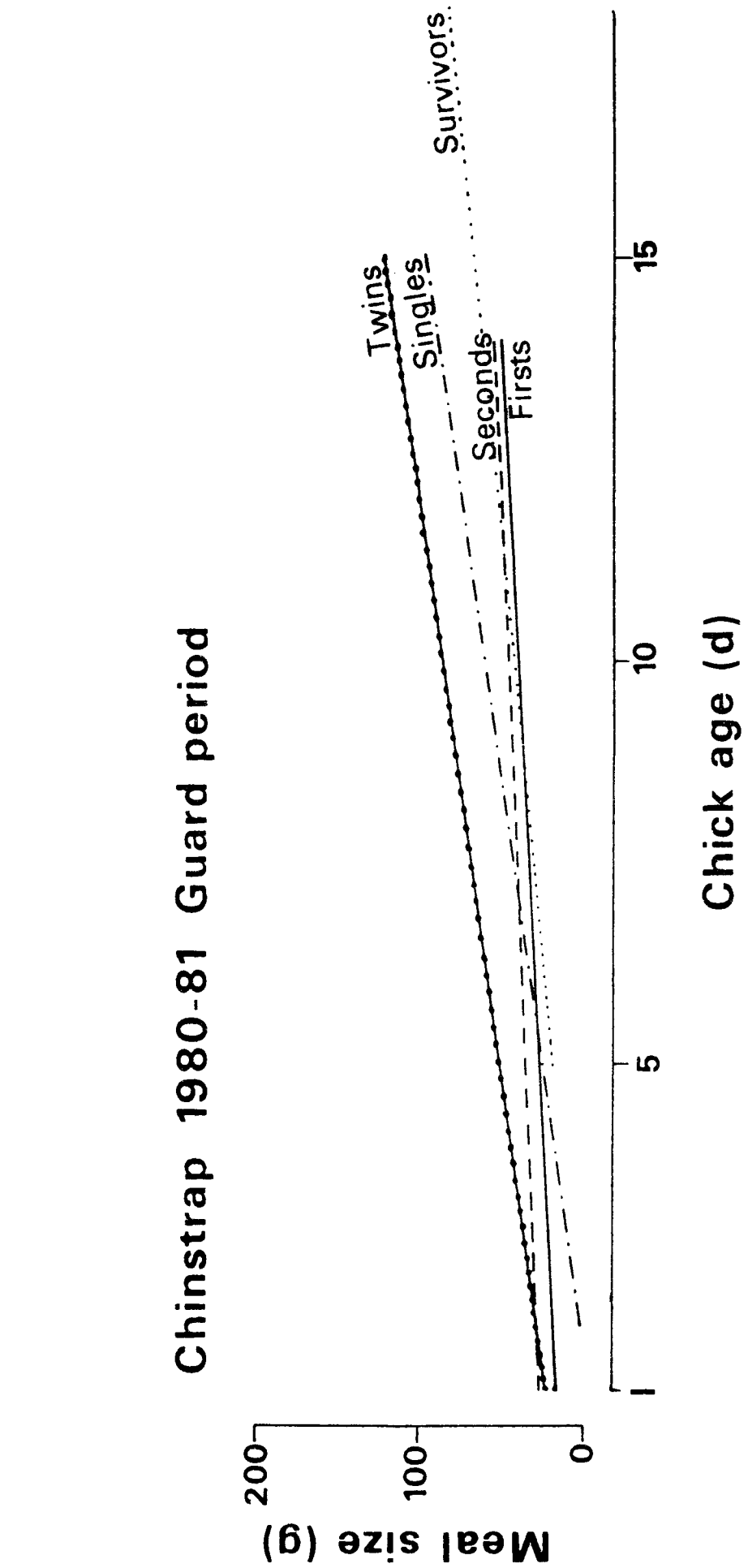



Figure 4.3. The relationship between chick age and meal size given to chinstrap chicks in 1980/81. (Firsts: s = 2.77; r = 0.5852, P < 0.001; seconds: s = 1.82; r = 0.3700, P < 0.01; survivors: s = 5.03; r = 0.5417, P < 0.001; singles: s = 7.55; r = 0.6585, P < 0.001; twins: s = 6.66; r = 0.7587, P < 0.001).

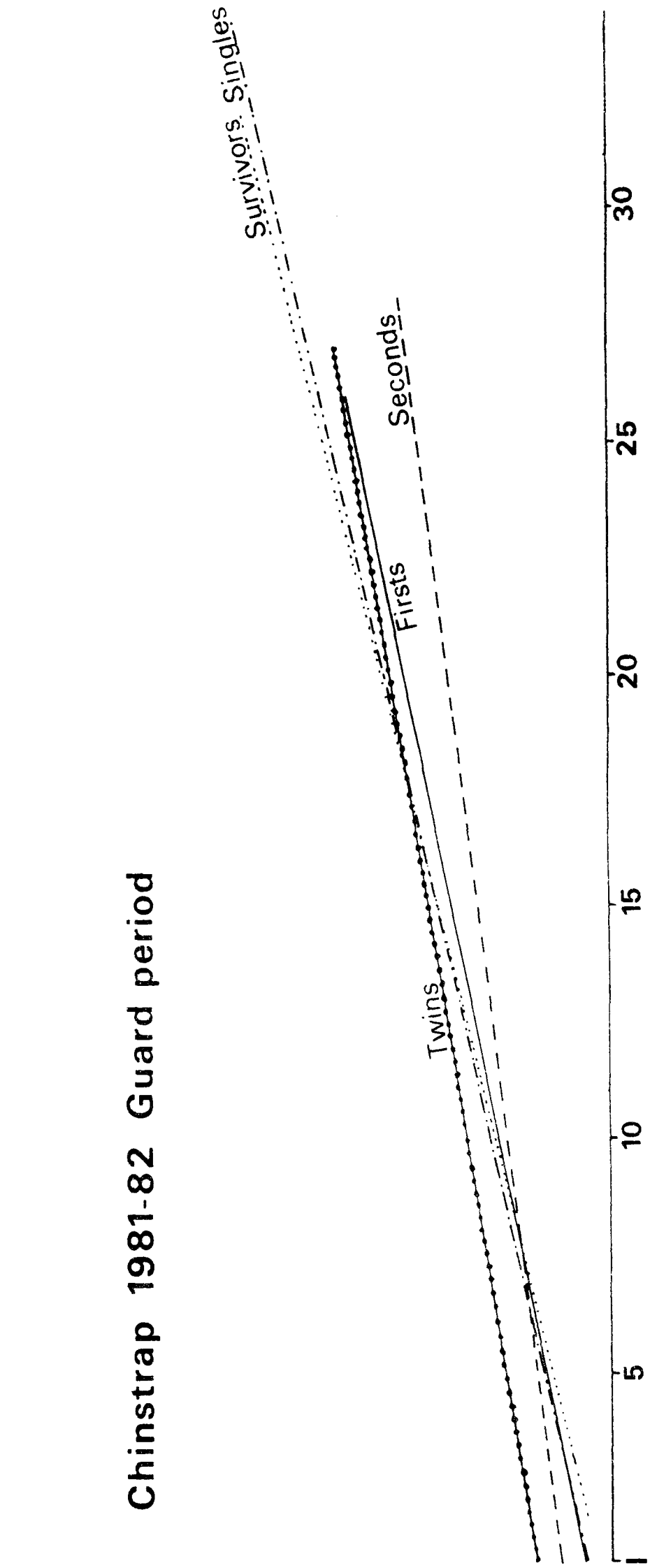



Figure 4.4. The relationship between chick age and meal size given to chinstrap chicks in 1981/82. (Firsts: s = 10.0; r = 0.6822, P < 0.001; seconds: s = 6.25; r = 0.5060, P < 0.001; twins: s = 8.33; r = 0.5208, P < 0.001; singles: s = 10.79; r = 0.6549, P < 0.001; survivors: s = 12.58; r = 0.6305, P < 0.001).

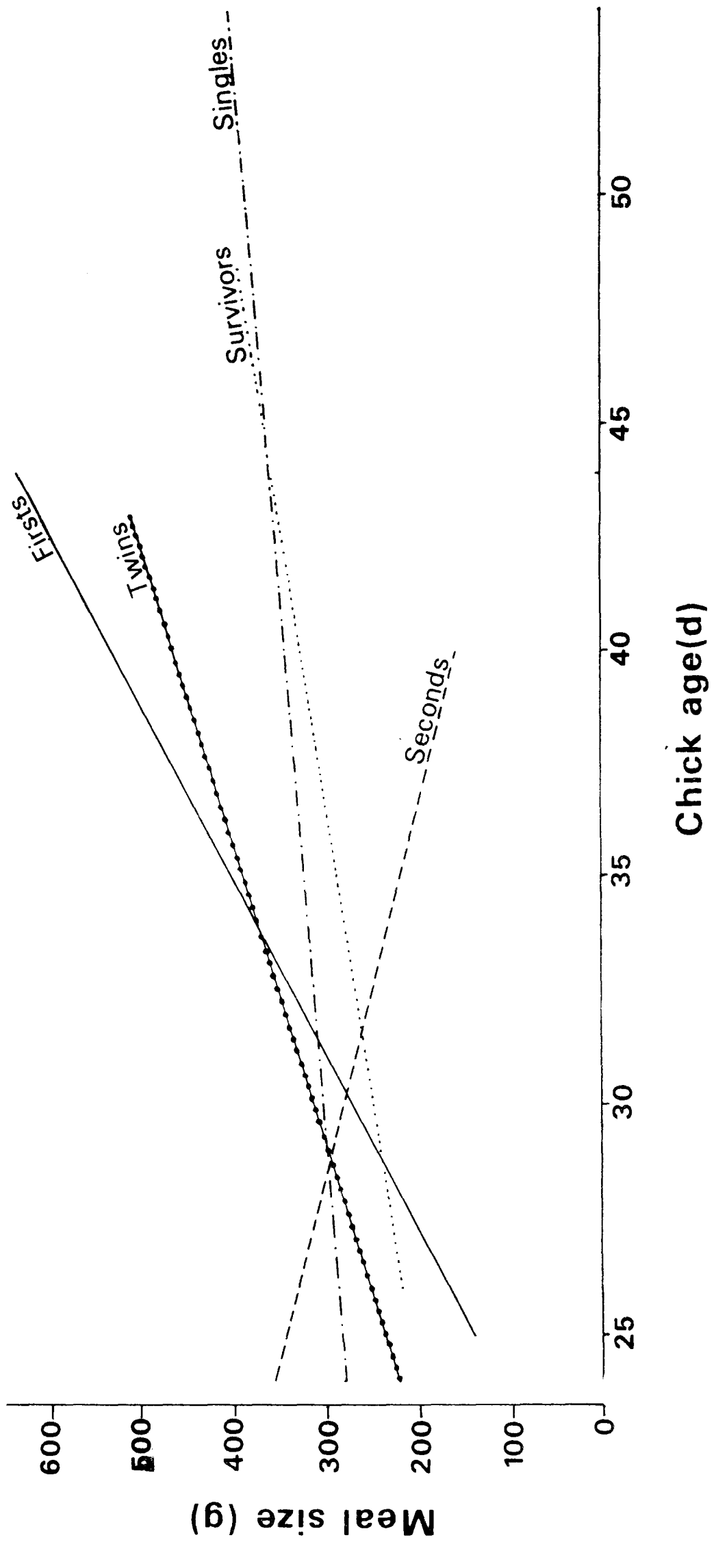



Figure 4.4 (continued)

(Firsts: s = 26.25; r = 0.7691, P > 0.05; seconds: s = −12.50; r = −0.5278, P > 0.05; singles: s = 4.32; r = 0.1290, P > 0.05; survivors: s = 7.62; r = 0.2330, P > 0.05; twins: s = 16.5; r = 0.5149, P > 0.05).

no overall differences in the slopes of the regressions (Figures 4.1 and 4.2). However, Appendix 4.5 shows that the mean meal sizes calculated from daily weight increments tend to be lower than the mean meal sizes calculated from three-hourly weighings and weights taken before and after a meal. There will be some weight loss after a feed and before a weighing which will underestimate meal size calculated from daily and three-hourly weighings. Only weighing immediately before and after a meal will remove this error completely. An estimate of the rate of weight loss was calculated from the three-hourly weighings of chicks that were unfed for at least 24 h. This was 8.2 g $h^{-1}$ (n=32). From estimates of the time of chick feeding obtained from three-hourly weighings (see Figure 4.6), it was found that the modal time of chick feeding by Adélies was 0900-1200 local time and that of chinstraps was usually 1200-1500 local time. Daily weighings were made between 0900 and 1200 local time so, from these figures, the maximum underestimate of meal size obtained from daily weighings could have been as high as 196 g for Adélies and 172 g for chinstraps. However, the differences between meal sizes calculated from daily and three-hourly weighings for the two species are not as big as this, probably because many chicks were fed outside the modal chick feeding period. As chicks were weighed daily throughout the rearing period, meal sizes calculated from these weights were perfectly suitable for comparative purposes.

Irrespective of category, meal sizes increased steadily during the guard period. In 1980/81, they increased to about 175 g for Adélies and about 75 g for chinstraps. In 1981/82, meal sizes reached about 250 g at the end of the guard period. Thus, meal sizes were larger in 1981/82 and, in 1980/81, were larger for Adélies than chinstraps. They varied greatly during the crèche period, but averaged about 300 g in both years for both species. There was no significant increase or decrease in meal size during this time, except for those given to chinstrap first chicks in 1981/82, which was based on a sample of only four meals.

During the guard period, there was no difference between meal sizes given to singles and survivors except that, toward the end of the guard period in 1981/82, Adélie survivors received larger meals than singles. The sample was of only 18 meals, compared with 290 meals given to singles, so this difference is ignored in further comparisons. In 1981/82, meal sizes given to firsts were larger than those given to seconds ($P<0.001$) but in 1980/81 there was no difference.

Meal sizes given to singles and the total given to both twins during the guard period are compared in Figure 4.5. Between them, twins of both species received larger meals than singles in 1980/81 and the difference increased with chick age ($P<0.001$). In 1981/82, twins again received larger meals than singles but the difference remained constant with increase in chick age (Adélies : $P<0.01$; chinstraps : $P<0.001$). Meal sizes given to singles were larger in 1981/82 than in 1980/81 (Adélies : $P<0.01$; chinstraps : $P<0.001$) and meals given to chinstrap twins were larger in 1980/81 than in 1981/82 ($P<0.05$). For each category in both years during the guard period, meal sizes given to Adélies were greater than those given to chinstraps ($P<0.001$).

If the total meal to both twins is halved and compared with singles, the amount of food fed to each chick is larger for singles ($P<0.001$). The difference is constant for Adélies but increases with chick age for chinstraps. Despite this, meal sizes given to chicks in broods of one and two in 1980/81 were still very similar but, in 1981/82, single chicks received considerably more food than chicks from broods of two.

## 2. Feeding frequency

All feeding frequencies calculated from daily and three-hourly weighings are shown in Appendix 4.5. To see whether daily weighings gave a reasonable assessment of feeding frequency, feeding frequencies calculated from daily weighings throughout the guard period and from one weight taken

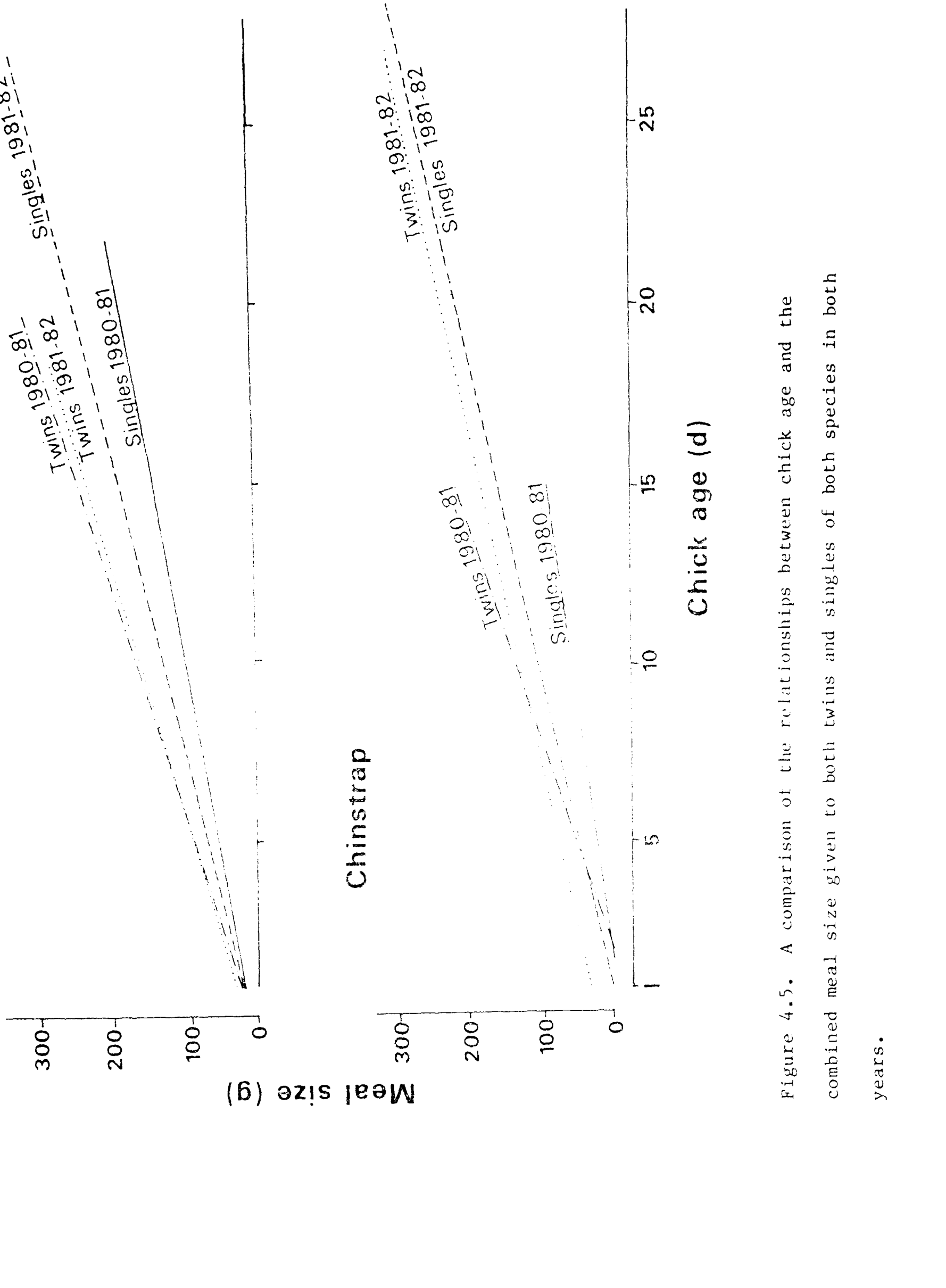



Figure 4.5. A comparison of the relationships between chick age and the combined meal size given to both twins and singles of both species in both years.

on each day of the three-hourly weighing periods were compared with those calculated from the three-hourly weighing periods. There were no significant differences in both cases (Table 4.1). Unlike the feeding frequencies calculated from three-hourly weighings, which are likely to be a good assessment of feeding frequency, those from daily weighings apply to the whole of either the guard or the crēche period, so these were used in any comparison between chick categories.

The mean feeding frequencies during the guard and crēche periods, calculated from daily weighings, are given in Table 4.2. Most chicks of both species in both years were fed between 0.5 and 0.7 times per day, i.e.once every 1.4-2.0 days. During the guard period in 1980/81, Adélie chicks received feeds more frequently than chinstrap chicks ($P<0.001$). In 1981/82, there were no differences, except that chinstrap singles were fed more frequently than Adélie singles ($P<0.001$). Between years, chinstrap chicks were fed more frequently in 1981/82 than in 1980/81 ($P<0.001$) and Adélie singles were fed more frequently in 1980/81 than in 1981/82 ($P<0.02$). In comparisons between feeding frequencies during the guard and crēche periods, there were no consistent differences, although chinstrap singles were fed more frequently during the crēche period in 1981/82. Within species, there was no difference in feeding frequency except that Adélie twins were fed more frequently than singles during the crēche period in 1980/81 ($P<0.001$) and chinstrap singles were fed more frequently than twins in 1981/82 ($P<0.001$).

3. Feeding behaviour

a. Time of return from foraging trips by adults

Feeding times obtained from the three-hourly weighings are given in Figure 4.6. These are assumed to correspond to the time of return to the colony from foraging trips. Most arrivals at the nest during the crēche period by adults of both species took place between 0900 and 1800 local time. During

| | | | Feeding frequency (feeds/day) | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Twins | | | Singles | | |
| | | | Daily weights | | 3-hourly | Daily weights | | 3-hourly |
| Species | Year | | 1 | 2 | weights | 1 | 2 | weights |
| Adélie | 1980/81 | Mean | 0.47 | 0.61 | 0.58 | 0.39 | 0.62 | 0.52 |
| | | sd. | 0.17 | 0.39 | 0.41 | 0.16 | 0.40 | 0.36 |
| | | No | 55 | 316 | 77 | 29 | 187 | 49 |
| Chinstrap | 1981/82 | Mean | 0.58 | 0.56 | 0.66 | 0.61 | 0.68 | 0.66 |
| | | sd. | 0.18 | 0.39 | 0.34 | 0.23 | 0.39 | 0.46 |
| | | No | 30 | 149 | 33 | 58 | 255 | 69 |

Notes : 1. calculated from one weight taken on each day during the three-hourly weighing period.

2. calculated over the whole of the guard period from daily weights.

Table 4.1. A comparison of feeding frequencies during the guard period calculated from daily and three-hourly weighings.

| | | Guard period | | | |
|---|---|---|---|---|---|
| | | Twins | | Singles | |
| Year | | Adélie | Chinstrap | Adélie | Chinstrap |
| 1980/81 | Mean | 0.61 | 0.39 | 0.62 | 0.46 |
| | sd. | 0.39 | 0.23 | 0.40 | 0.29 |
| | No | 316 | 113 | 187 | 98 |
| 1981/82 | Mean | 0.59 | 0.56 | 0.55 | 0.68 |
| | sd. | 0.32 | 0.39 | 0.32 | 0.39 |
| | No | 111 | 149 | 528 | 255 |

| | | Crèche period | | | |
|---|---|---|---|---|---|
| Year | | Adélie | Chinstrap | Adélie | Chinstrap |
| 1980/81 | Mean | 0.58 | no | 0.44 | no |
| | sd. | 0.34 | data | 0.25 | data |
| | No | 24 | | 215 | |
| 1981/82 | Mean | no | no | no | 0.79 |
| | sd. | data | data | data | 0.43 |
| | No | | | | 53 |

Table 4.2. Feeding frequencies calculated from daily weighings.

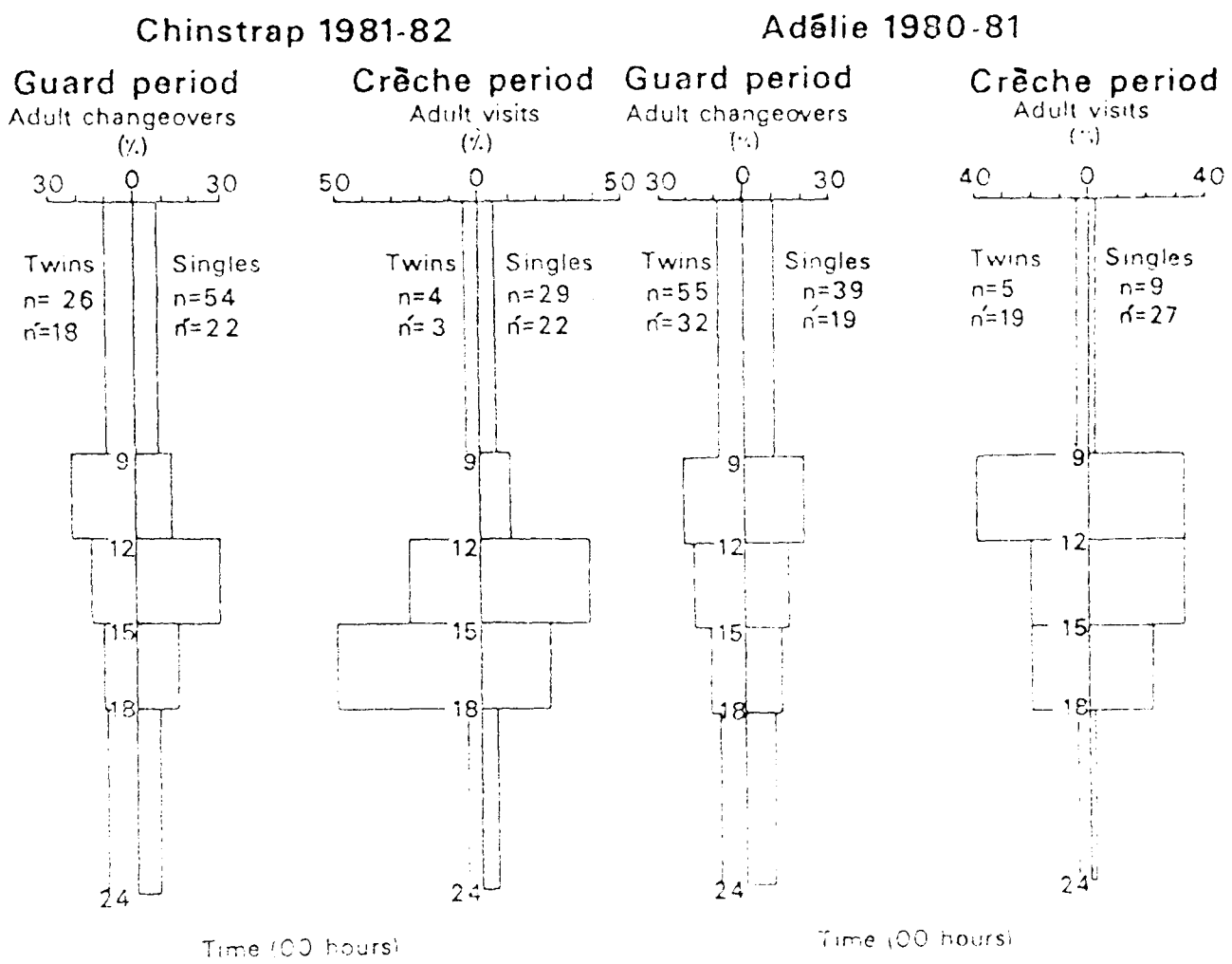



Figure 4.6. Timing of feeds, as indicated by the frequency of adults visiting or changing over at the nests. (Calculated from three-hourly weighings recorded during two (Adélie) or four (chinstrap) 24 h periods.)

the guard period, there was a more even spread over the 24 hour period, but in most cases the modal changeover period was 0900-1200 local time. Feeding times obtained from actual observations of Adélie study nests over the 24 hour period are given in Figure 4.7. Again, most returns from foraging during the crêche period occured in daylight (c. 0400 - 2000 local time, December - February), but the modal period was 1500-1900 local time. There was also a distinct decrease in activity between 2300 and 0700 local time, except for the 0300 to 0400 period. The numbers of birds entering A41 over the 24 hour period are given in Figure 4.8. The most active period was again 1500-1900 local time and the period of lowest activity was 2100-0700 local time. Thus, the three methods used to determine colony activity patterns produced results which broadly agree.

b. Foraging distance

Estimates of travelling times between the colony and the foraging area and the total distance travelled during a foraging trip are given in Table 4.3. The maximum foraging distances calculated for each species are related to the sea-bottom topography around the South Orkneys in Figure 4.9. Those for chinstraps in 1980/81 are not included since the low feeding frequencies are more likely to have been caused by ice slowing the progress of the penguins rather than long foraging distances. The estimate of the maximum foraging ranges of both species coincide with the limits of the South Orkney continental shelf and with the confluence of two major ocean currents. Although there is considerable overlap of the estimated foraging ranges of Adélies and chinstraps, part of the foraging range of Adélies is outside that of chinstraps. This is particularly so when the two species were foraging during their respective guard periods in 1981/82. Thus, in December 1981, Adélies may have foraged further than chinstraps in January 1982.

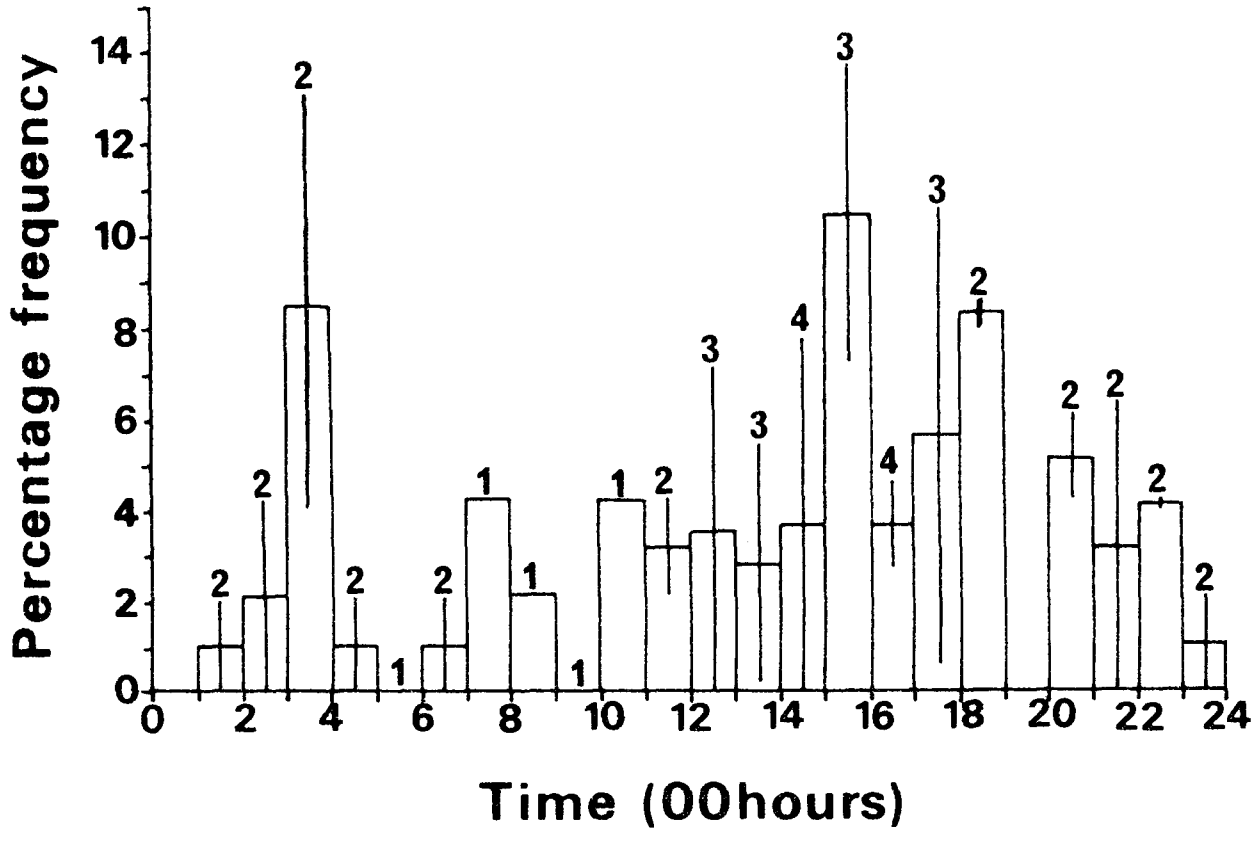



Figure 4.7. The percentage frequency of feeds delivered to Adēlie study nests with chicks over several 24 h periods during the crēche period. (Errors are 1 standard deviation; numbers are number of times the colony was observed during each hour.)

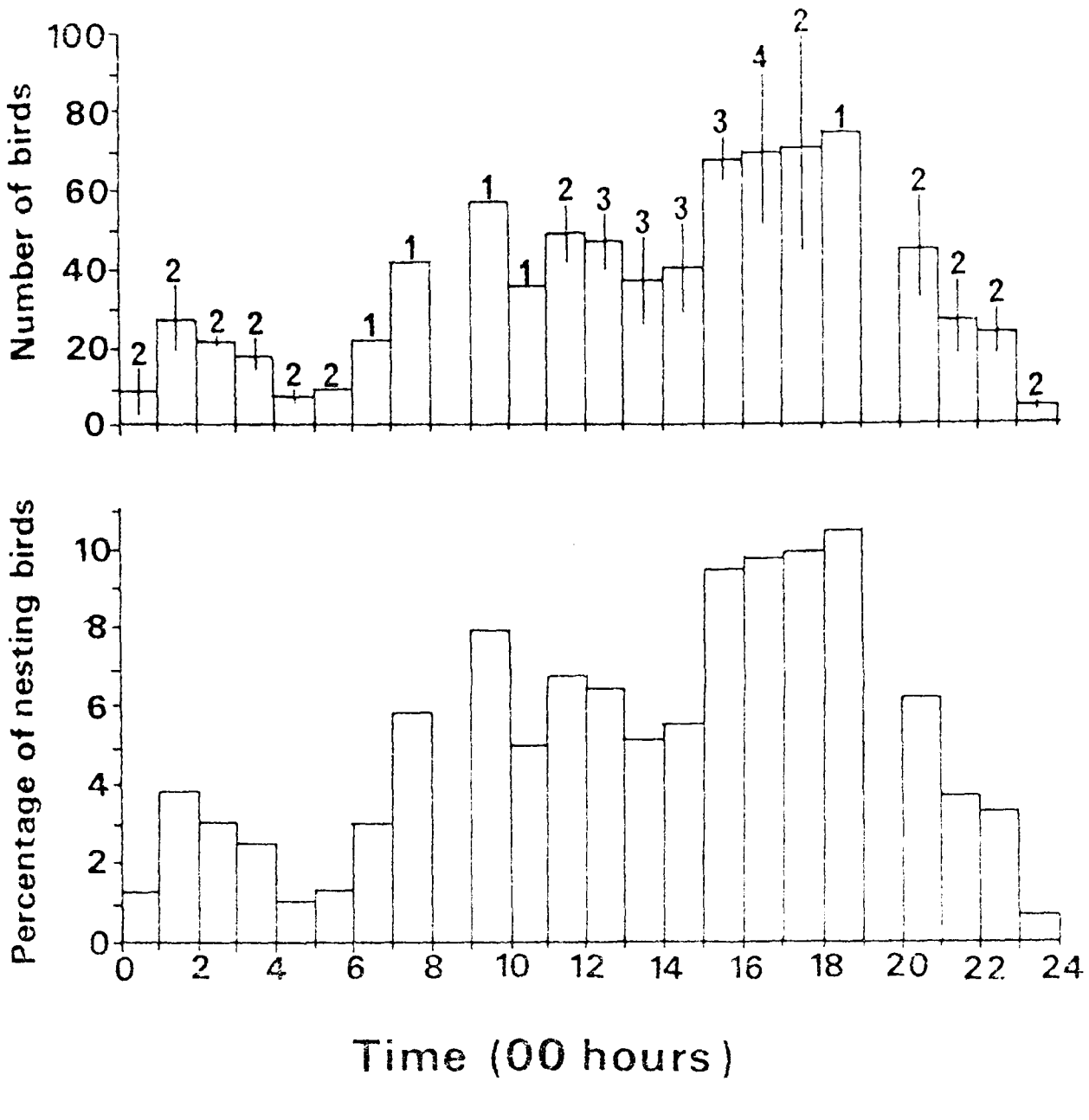



Figure 4.8. The number of adult Adélies recorded entering colony A41 during a 24 hour period, expressed as absolute numbers and as a percentage of the 712 birds nesting in the colony (counted toward the end of incubation). (n= number of times the colony was observed during each hour; errors are 1 standard deviation.)

| | Adélie | | | Chinstrap | | |
|---|---|---|---|---|---|---|
| | 1980/81 | | 1981/82 | 1980/81 | 1981/82 | |
| | Guard period | Crèche period | Guard period | Guard period | Guard period | Crèche period |
| Feeding frequency (feedsd$^{-1}$)[1] | 0.61-0.62 | 0.44-0.58 | 0.55-0.59 | 0.39-0.46 | 0.56-0.68 | 0.79 |
| Interval between feeds (h)[2] | 38.6-39.4 | 41.5-55.0 | 40.8-43.9 | 52.6-61.2 | 35.3-42.5 | 30.5 |
| Maximum foraging distance (km)[3] | 278-284 | 299-396 | 294-316 | 379-441 | 254-306 | 220 |
| Travelling time (h)[4] | 23.2-23.6 | 24.9-33.0 | 24.5-26.3 | 31.6-36.7 | 21.2-25.5 | 18.3 |
| Assumed distance travelled (km)[5] | 167-170 | 179-238 | 176-189 | 228-264 | 153-184 | 132 |
| Foraging distance (km)[6] | 83.5-85 | 89.5-119 | 88-94.5 | 114-132 | 76.5-92 | 66 |

Notes :

[1] feeds given by a parent to its brood per day (calculated from daily weighings).

[2] obtained from feeding frequency, e.g. 0.61 feeds $d^{-1}$ = 38.6 h feeding interval.

[3] assumes bird spends the whole of a foraging trip travelling in a straight line directly to and from the feeding ground at 7.2 km $h^{-1}$.

[4] assumes 40 % of feeding interval is spent resting and diving for food.

[5] distance to and from the feeding grounds, calculated from new travelling times.

[6] distance to feeding ground from colony, i.e. half the distance to and from the feeding grounds.

Table 4.3. Estimates of travelling times between the colony and the foraging area and the total distance foraged.

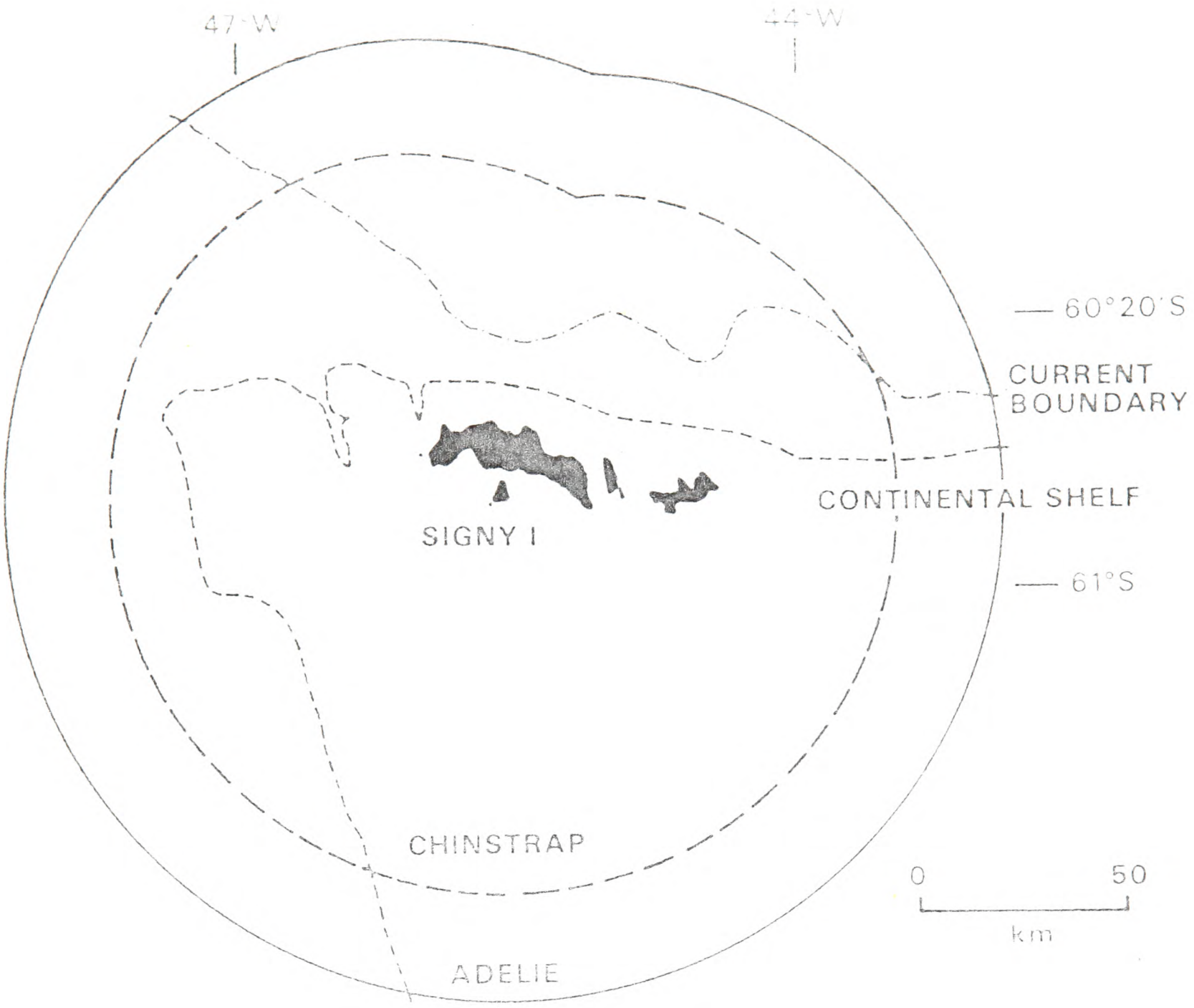



Figure 4.9. The estimated foraging ranges of Adélies and chinstraps from Signy and their relationship with the sea-bottom topography around the South Orkney Is.

(---- region of rapid increase in water depth from 80 to 350 fathoms;

-·- approximate boundary between Antarctic circumpolar current and Weddell sea waters.)

c. Diving depths

The number of dives to each depth range made by each bird is shown in Figure 4.10. Taking all four birds together, 90 % of the dives were shallower than 45 m, and 40 % were to less than 10 m. Details of the foraging trips for which the diving depths were recorded (Table 4.4) show that the number of dives per hour during foraging trips of equivalent duration by two females (birds 2 and 3) were similar. A third female (bird 1) and the only male (bird 4) were at sea for similar lengths of time and delivered similar amounts of food to their chicks, but the male made twice the number of dives per hour. A feed size of approximately 480 g is within the range of other estimates determined by weighing chicks of the same age before and after a feed.

## DISCUSSION

1. Meal size

Chicks of both species received smaller meals in 1980/81 than in 1981/82, probably because ice conditions increased the time taken to return to the colony after foraging. A considerable proportion of the stomach contents would have been digested, resulting in smaller meals available to chicks. Since the amount of food brought ashore by chinstraps was less in January 1980/81 than in January 1981/82 (Chapter 3) and chinstrap chicks received smaller meals than Adēlies in 1980/81, it is possible that, as well as being hindered by ice, chinstraps also caught less food during foraging in 1980/81 and were forced to return to the colony without full stomachs. Chinstraps may have taken even longer than Adēlies over some foraging trips in 1980/81, since they fed their chicks less frequently than Adēlies during the guard period.

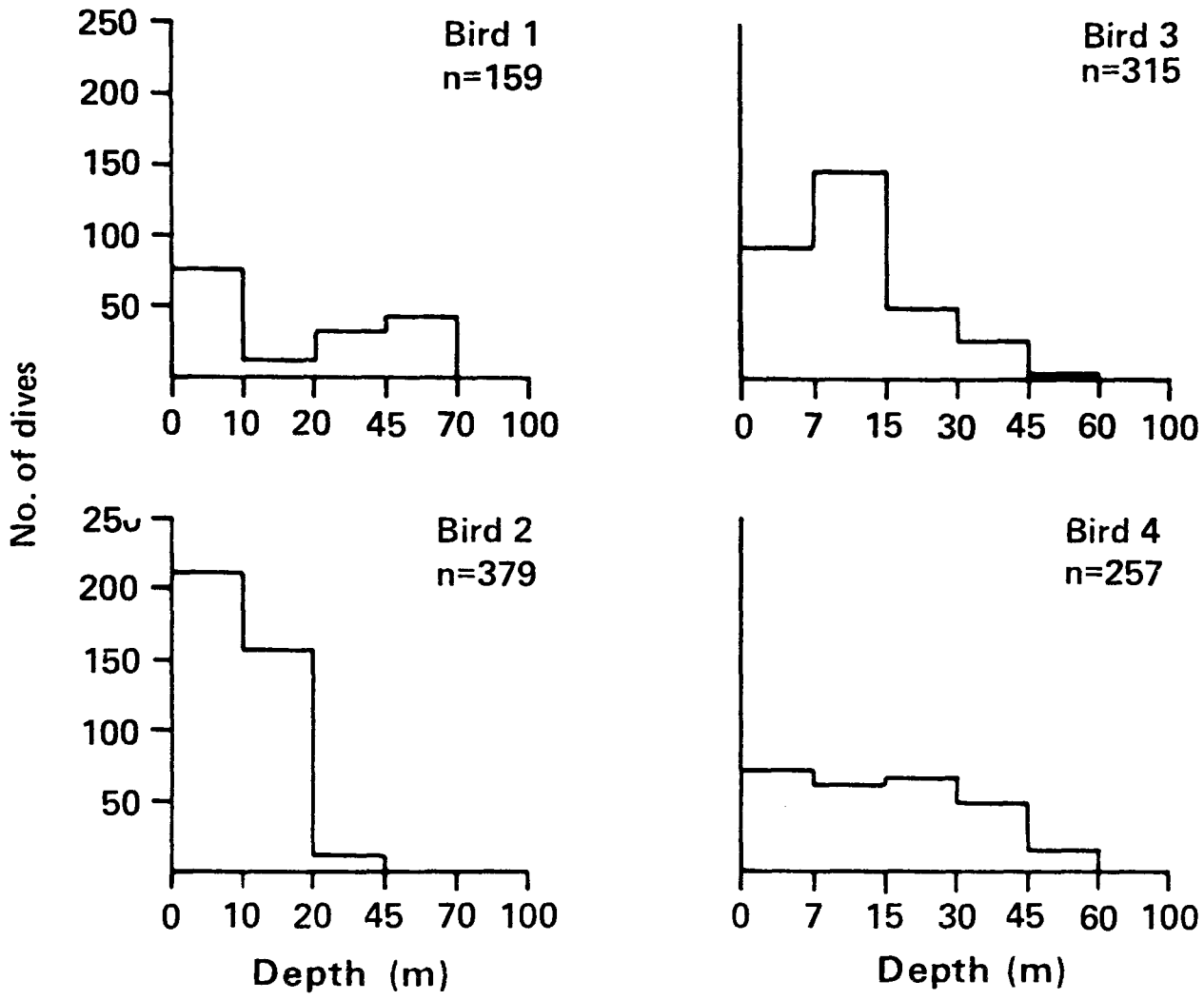



Figure 4.10. Diving depths of the chinstrap penguin.

| Bird | Sex | Number of chicks | Number of dives | Maximum time absent (h) | Dives per hour | Feed size (g) |
|---|---|---|---|---|---|---|
| 1 | Female | 1 | 159 | 22 | 7.2 | 495 |
| 2 | Female | 1 | 379 | 44 | 8.6 | no data |
| 3 | Female | 1 | 315 | 48 | 6.6 | no data |
| 4 | Male | 1 | 257 | 18 | 14.3 | 470 |

Table 4.4. Details of the foraging trips of the chinstrap penguins studied.

Meal sizes to chicks of both species increased steadily during the guard period in both years and remained at a fairly constant level during the crēche period. An increase during the guard period was probably due to increased chick stomach capacity (and therefore chick weight) with age, although the rate of increase ultimately depends on meal size and feeding frequency. Croxall and Furse (1980) also recorded chinstrap meal sizes increasing with chick weight during the guard period and Williams (1982) states that food intake of macaroni and rockhopper penguin chicks is limited by stomach capacity. During the guard period, the increase in meal size was slower for chinstraps than for Adélies, i.e. chinstrap chicks received smaller meal sizes than Adélies. While this may have been due to ice conditions in 1980/81, it is uncertain what might have been the cause in 1981/82. If, as seems possible (see section 3), chinstraps feed closer to the colony than Adélies, this may mean that travelling often to a foraging area a shorter distance from the colony removes the need for adults to bring ashore the maximum possible amount of food after each trip. Alternatively, a smaller foraging range than Adélies may mean that chinstraps sometimes have problems in finding enough food.

No other meal size data similar to those given here are available for Adélies or chinstraps. However, Croxall and Furse (1980) use stomach contents weights as an indication of feed size and suggest that about 500 g is representative of the feed size given to chinstrap chicks at Elephant I during the crēche period. This figure is considerably greater than the mean meal size (calculated from daily weighings) given to chinstrap chicks during the crēche period at Signy. However, if the estimate of the maximum possible discrepancy in the meal sizes calculated by daily weight increase (172 g for chinstraps) is taken into account, the meal sizes given at Signy would have a range of 434-485 g, which agree more closely with the estimate from Elephant I and are also similar to many of the meal sizes recorded by weighing a chick before and after it had been fed.

Parents provided twins with more food than single chicks, but meals given to single chicks were larger than those given to each chick in broods of two. Consequently, singles grew faster (see chapter 5), and were always heavier and therefore presumably had larger stomach capacities than twins of the same age. However, since the meal size given to singles and the total meal size given to twins were similar, it is likely that the amount of food available to both brood sizes at any one time was the same, so adults probably fed all of their stomach contents to twins in approximately half the time it would have taken to feed all of the food brought ashore to just one chick. A shorter time taken for a parent to provide twins with all the food it has available is unlikely to allow an increase in feeding frequency since the difference in feeding duration between broods of one and two was always small (personal observation). In 1980/81, meal sizes given to singles were very similar to meal sizes given to individual chicks in broods of two. Thus, the smaller meal sizes in that year meant that parents of single chicks were only providing sufficient food to sustain one chick at the same level of growth as an individual chick from broods of two.

2. Feeding frequency

Chinstrap chicks were fed less frequently than Adélies during the guard period in 1980/81, and it is likely that this was due to the ice conditions in that year. The only other significantly different feeding frequencies were during the guard period in 1981/82, when chinstrap singles were fed more frequently than Adélie singles. In addition, although not strictly comparable with any of the other figures, because they were not from the same year or the same stage in the breeding cycle, the feeding frequency to single chinstrap chicks during the crēche period in 1981/82 was significantly higher than any of the others recorded. It is possible, therefore, that chinstrap chicks were, in 1981/82, fed more frequently than Adélie

chicks. Previous estimates of Adélie and chinstrap feeding frequency are compared with those from this study in Table 4.5. Although many of the data may have been obtained from the direct observations of nests, it is difficult to assess their accuracy from the methods described in each case. Nevertheless, it is apparent that Adélie feeding frequencies during the guard period were similar in all studies. Adélie chicks at Signy were perhaps fed less frequently during the crèche period, but the only other information on crèche feeding frequency (Thompson, 1981) is rather anecdotal, so this difference may not be real. Signy chinstrap feeding frequencies were, however, much lower throughout the chick rearing period than those recorded at the South Shetland Is. The continental shelf is only about 15-35 km from Elephant and Clarence Is, compared with about 60 km from Signy. If chinstraps feed in the shelf area of both these locations, the different distances could account for the different feeding frequencies. A similar situation may occur at South Georgia, where it has been shown that part of the macaroni penguin diet comprises immature krill. These may be associated with the continental shelf edge and it is suggested that this is within the foraging range of the macaroni penguin which has a lower frequency than the inshore feeding gentoo penguin, whose krill diet comprises only mature individuals (Croxall and Prince, 1980 a).

3. Feeding behaviour

a. Time of feeding and foraging distance

The calculations and estimates of the time at which chicks are fed indicate that perhaps as many as 90 % of feeds are during daylight hours and that 50 % are between about 1500 and 2100 h. Estimates of the travelling time to and from the colony and the foraging area (Table 4.3) show that an inward or outward journey by either species, unhindered by ice and assuming no time was spent foraging during travelling, lasted 9-13 h. Using the median estimated travelling time, modal chick feeding time and estimates of

| Guard period | | Crèche period | Derivation | Location | Reference |
|---|---|---|---|---|---|
| Mean | range | Mean | | | |
| **Adélie** | | | | | |
| 0.5 | 0.2-1.0 | | Nest observations[1] | Signy I | Sladen (1958) |
| | 0.7-1.0 | | " | Cape Royds | Taylor (1962) |
| | 0.6-0.7 | | " | Cape Crozier | Emison (1968) |
| | | c 1.00 | " | Cape Hallett | Thompson (1981) |
| 0.55-0.62 | | 0.44-0.58 | Daily weighings | Signy I | This study |
| **Chinstrap** | | | | | |
| c 2.3 | | | Traffic counts[2] and nest observations | Elephant I | Conroy and others (1975 b) |
| | | c 1.40 | Traffic counts | Clarence I | Croxall and Furse (1980) |
| 0.56-0.68 | | 0.79 | Daily weighings | Signy I | This study |

Notes

[1] observations made of the frequency of parental visits to a sample of nests.

[2] derived from a 24 h count of birds arriving and departing at a colony.

Table 4.5. Feeding frequencies (adult visits per day) recorded during Adélie and chinstrap studies.

the time spent resting and diving during a foraging trip, an indication of the division into different activities of the time spent at sea by adults can be obtained (Figure 4.11). The arrangement of the time spent resting and diving between 1600 and 0700 h is purely speculative, but it certainly seems likely that, for those adults returning to the colony at 1800 h, feeding takes place, at least partly, during darkness or semi-darkness. This is by no means applicable to all feeding since those birds returning twelve hours earlier, at 0600 h, would have been feeding entirely in daylight. The proportion of birds returning at this time is, however, small in relation to those returning in the 1500-2100 h time period.

Acoustic echo-integration surveys of krill around South Georgia have shown that swarms of krill may migrate vertically toward the surface at night but that krill may either be dispersed throughout the water column or aggregated at depths up to about 200 m during daylight (Everson, 1982; 1983). A broadly similar pattern of vertical migration prevails around the South Orkney Is (Kalinowski and Witek, 1980) so, even without any indication that Adélies and chinstraps feed at night, the presence of krill at the surface at night would make them obvious feeding grounds.

It has been suggested that juvenile krill rise nearer to the surface at night than adult krill (Shevtsov and Makarov, 1969; Nemoto and Nasu, 1975), and that adults are deeper than juveniles during the day (Everson, 1977; Jazdzewski and others, 1978). This is surprising since chinstraps mainly take large krill and the majority of their dives are shallow though it may be that adult krill are still at depths within the range of most chinstrap dives.

Pursuit divers such as penguins should theoretically be much less restricted to nocturnal feeding than surface feeders such as the grey-headed albatross Diomedea chrysostoma, which spends an average of 50 % of the night on the sea during foraging trips (Prince and Francis, in press). The relative ease with which penguins are presumably able to catch

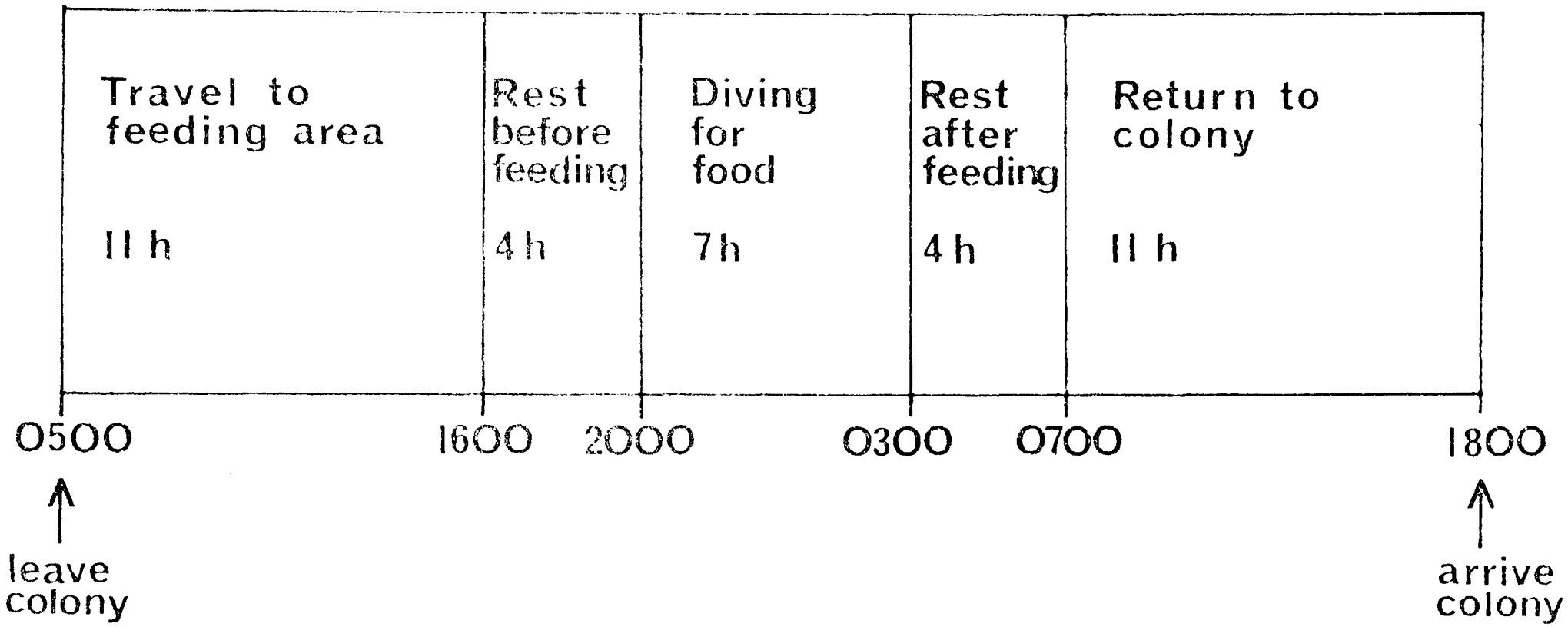



Figure 4.11. Suggested activity pattern during a foraging trip by a penguin which has arrived at the colony at 1800 h.

krill at the surface as opposed to those at depth would be the most likely reason for Adélies and chinstraps to feed at night.

At Elephant I, there was a much less developed diurnal pattern of movement into and out of the colonies than at Signy. Since feeding frequency was as high as 2.3 feeds per day (Conroy and others, 1975 b), i.e.just over one feed by each parent per day, it is possible that one parent foraged during the day and the other at night.

There are insufficient data to properly compare time of feeding of Adélies and chinstraps or relate the size of krill caught by each species to their position in the water column at the time when they might have been caught. However, it is possible to compare where the two species might have been feeding since differences in feeding frequency have been found and these may be an indication of foraging in different areas. Bogdanov and others (1969) and Elizarov (1971) suggest that krill are associated with the confluence of two major currents and with the continental shelf to the north of the South Orkneys, which are within the estimated foraging range of both species. Evidence that these may nevertheless comprise separate feeding areas for Adélies and chinstraps is provided by Mackintosh (1973) who found that juvenile krill are associated with the confluence of the two ocean currents. Since Adélies caught large numbers of juvenile krill, and these were mainly absent from chinstrap stomachs, it is possible that the greater maximum foraging distance estimated for Adélies is an indication that they swim further north than chinstraps in order to feed.

b. Diving depths and performance

There has been only one previous study of the diving depth profiles of penguins. Kooyman and others (1982) found that 50 % of dives by king penguins were deeper than 50 m and two dives exceeded 240 m. This contrasts markedly with the chinstrap penguin pattern. Although king penguins, being approximately three times the size of chinstraps, will have

a greater diving capacity (Butler and Jones, 1982), the difference in diving depths probably also reflects their different diets. Thus, king penguins feed mainly on squid and some fish (Croxall and Prince, 1982) and the former are particularly characteristic of deeper waters. Gentoo penguins are about twice the size of chinstraps, so will also have a greater diving capacity, and yet, of 19 maximum dive depths recorded, 16 (84 %) were to less than 20 m (Adams and Brown, in press). This pattern probably reflects their diet of fish and krill, which may occur in shallow waters, and inshore feeding habits (Croxall and Prince, 1980 a). Chinstrap penguins almost exclusively eat krill (Croxall and Furse, 1980; Volkman and others, 1980; this study), which is often abundant near the surface. It is also, however, widespread at least as deep as 200 m (Everson, 1982), but the study birds did not dive below 70 m to feed and mainly made shallow dives to around 10 m. There are two possible reasons for this. Firstly, chinstraps may be physiologically incapable of diving to greater depths. Chinstraps are of similar size to Adélies, whose maximum enforced submergence time is 6 min (Kooyman, 1975). Emperor penguins reach depths of 250 m and can remain submerged for 18 min (Kooyman and others, 1971). If dive depths are proportional to dive duration then chinstrap penguins submerging for 6 min might only be able to reach c80 m.

Secondly, if chinstraps can catch all the food they require above 70 m, there is no reason for them to exceed this depth. This was concluded to be the reason for only 3 % of 4273 dives by Antarctic fur seals Arctocephalus gazella, which feed almost exclusively on krill during their breeding season (Bonner, 1968), being to below 75 m, despite the fact that over 40 % of the krill in the water column was below this depth (Croxall and others, in press a). Seventy six percent of seal dives were to less than 40 m and 26 % shallower than 20 m, a pattern very similar to that of chinstrap penguins. Furthermore, 75 % of these dives were at night when they were consistently shallower than 30 m, in contrast to most daytime

dives being to between 40 and 75 m. This diving pattern can be interpreted as reflecting the diurnal differences in the vertical distribution of krill around South Georgia (Everson, 1982). Thus, nearly all krill in the water column was below 75 m between 0600 and 1500 GMT and 23 - 38 % of krill was above 40 m between 2100 and 0600 GMT.

A similar pattern of vertical migration prevails around the South Orkney Is (Kalinowski and Witek, 1980) so krill are likely to be abundantly available at night above 45 m (a depth above which 90 % of chinstrap dives terminate) and chinstraps may indeed feed mainly on krill at night.

If it is assumed that all chinstrap dives shallower than 45 m were at night, then with an average of 5 h of darkness at this latitude in January - February, the frequency of dives would be 38.2 ± 9.3 dives per hour. If all dives are of the same duration, this would be equivalent to one every 1.6 min, which is well within a maximum submergence time of 6 min.

The number of krill caught per dive can be estimated if the mean length and weight of krill taken is known and if the energy and food requirements of the adult and its chick can be calculated.

The mean length of krill caught by chinstraps at Signy I in 1981/82 was 36 ± 9 mm (n = 665) (see chapter 3). Using Lockyer's (1973) relationship, individual krill of this length weigh 0.331 g. About 480 g of krill was delivered to the chicks after the foraging trips in this study (Table 4.4), which represents 1450 krill.

The average daily metabolic rate (ADMR) at sea of the macaroni penguin, which is a krill-eating penguin of similar mass to the chinstrap penguin, is 2.9 times the standard metabolic rate (SMR) (Davis and others, 1983). In 1981, the average SMR of 215 fasting chinstrap penguins, with a mean weight of 3.5 Kg, was 2.9 $W.Kg^{-1}$ (see chapter 5). If the weight of the diving penguins is assumed to be the same, the ADMR at sea of chinstrap penguins would have been 8.4 $W.Kg^{-1}$.

The energy consumption for each of the study birds on its foraging trip is calculated in Table 4.6, together with the estimated weight and number of krill caught. Adults consume 949 ± 436 (range 518 - 1380) g of krill per feeding trip, which represents 2867 ± 1318 (range 1565 - 4169) krill of 36.3 mm length. Combining this with the food delivered to the chick means that on average 16.2 ± 4.3 (range 11.6 - 21.4) krill are caught in each dive, i.e. one krill is caught every 6 s.

While this may not be unrealistic, especially considering the potential ability of krill to avoid capture, it is as likely that on finding a krill swarm, chinstrap penguins will dive for longer periods and catch as many krill as possible in each dive. Many dives, including the deeper ones, may be exploratory and not necessarily successful in terms of foraging.

## CONCLUSIONS

The feeding strategies of Adélies and chinstraps at Signy I may differ in several ways. In particular, Adélies appear to have a lower feeding frequency, which may be indicative of longer distances to travel to foraging areas, and larger meal sizes brought to chicks than chinstraps. This may be largely due to the effects of ice, but it is conceivable that a higher chinstrap feeding frequency either reduces the need to catch as much food or creates a short-term food shortage and makes it impossible to catch as much food.

Estimates of the time at which chicks are fed in the colony indicate that at least some diving for food may take place at night. Since dives by chinstraps are mainly shallow, and large numbers of krill are near the surface at night, it seems probable that these krill are being caught at night, at least by chinstraps.

| | Foraging trip | | Krill consumption | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Energy | Adult | | Chick | Total | Per dive | |
| | Duration | consumption[1] | Weight[2] | No.[3] | No. | No. | Weight | No. |
| Bird | (h) | (Kj) | (g) | | | | (g) | |
| 1 | 22 | 2328 | 633 | 1912 | 1495 | 3407 | 7.1 | 21.4 |
| 2 | 44 | 4657 | 1265 | 3822 | c1450 | 5272 | 4.6 | 13.9 |
| 3 | 48 | 5080 | 1380 | 4169 | c1450 | 5619 | 5.9 | 17.8 |
| 4 | 18 | 1905 | 518 | 1565 | 1420 | 2985 | 3.8 | 11.6 |

Notes: [1] At 8.4 $W.Kg^{-1}$ (see text).

[2] With average calorific value of krill = 4.6 kJ $g^{-1}$ (Clarke and Prince, 1980) and 80 % conversion efficiency (Costa in Kooyman and others, 1982).

[3] Average weight 0.331 g (see text).

Table 4.6. Energy consumption and weight and number of krill caught during foraging trips.

Adēlies and chinstraps differ in the amount of juvenile krill they consume. It has been suggested that juvenile krill occur in an area which is within the range of both species, but which may constitute a separate feeding area for Adēlies.

# Chapter Five

## Chick growth

# INTRODUCTION

Growth patterns of chicks vary in the rate of growth, the maximum size reached during growth (the asymptote*) and the ratio of the asymptote to the adult weight. Although chicks have some flexibility in their growth patterns, this is limited by inherited constraints, so this variability reflects selective forces producing adaptations for breeding (Ricklefs, 1968 a; 1973). Variation of growth rates within bird populations is related to environmental conditions, brood size, the position of the chick in the hatching order, habitat and geographical locality (Lack, 1966; Ricklefs, 1968 a). Growth patterns are interpreted as an index of ecological conditions, especially local food supply or the distance adults travel to feeding areas (Ashmole and Ashmole, 1967; Lack, 1968; Nelson, 1970; Ashmole, 1971) and it has been shown that the rate of supply of nutrients to the chick is a major factor affecting the evolution of growth rates (Prince and Ricketts, 1981).

There are two main arguments concerning the evolution of growth parameters. Lack (1968) stated that parents work to capacity and adjust their brood size and growth rate accordingly, i.e. the number of offspring is limited by the amount of energy the parents can supply as food, so clutch size is adjusted to the maximum number of young which can be supported by this income (Lack, 1947; 1954) or, in the case of year-to-year fluctuations in food supply, brood reduction can occur (Lack, 1954; Ricklefs, 1965). If the brood size has reached a minimum of one and energy is still in short supply, then there will be a decrease in growth rate,

* The true asymptotic weight is reached when chicks reach adult weight at maturity. For the purposes of growth pattern analysis in this study, the peak weight reached during the chick rearing period is referred to as the asymptote.

even to the extent that breeding may occur less than once per year (Stonehouse, 1960; Ashmole, 1962; Harris, 1966; 1969 a; Boersma, 1976; Prince, 1980 b). Although this reduces energy requirements where food is a limiting factor (Lack, 1968; Nelson, 1977) and, where it is not limiting, allows the bird to raise more offspring, this must be balanced against the greater protection from predation which is associated with fast growth. An optimum growth pattern is therefore determined by selection upon growth rate and this, and brood size, are, in turn, determined by the predictability and stability of the food supply (O'Connor, 1977). Any decrease in growth rate reduces the daily commitment of parents, but the consequent increase in the length of the chick rearing period will increase total maintenance costs, so the total cost of raising a chick will increase (Drent and Daan, 1980).

Ricklefs (1968 a; 1969; 1973; 1979 a and b) found that chick asymptotes are related to rate of chick development and to adult body weight so that, within groups of similar avian species, precocial young and chicks of larger species have slower rates of growth and a high ratio of asymptote to adult weight. Thus, aerial feeding birds, which need to be fully developed for flight at the time of fledging, have high asymptotes. The same should also be true of penguins since they need to be able to swim at the time of fledging. He also found, as Lack did, that variations in growth rate correlate with differences in breeding success caused by predation and the level of food supply, and suggested that growth rate determines brood size. Thus, Lack thought that growth rates were largely regulated by the provisioning rate of adults and Ricklefs thought that growth rates were determined by the processing of capacity of chicks, i.e. by physiological factors. In more recent work, Case (1978) suggests that physiological factors may not be critical in ultimately determining growth rates because environmental factors intervene. Similarly, Ricklefs (in press) suggests that, within the physiological limits, chick growth rates might be

optimised at intermediate levels determined by brood size and environmental factors which affect predation, growth and maintenance energy requirements.

Seabirds are characterized by particularly slow growth and therefore reduced daily energy requirements, which is presumably an adapatation to an irregular or poor food supply. In many cases, there is differential growth of some body components, such as legs or wings towards the end of the chick growing period when maintenance and energy requirements are higher (Ricklefs, 1968 a). For most pelagic seabirds an irregular or poor food supply has resulted in the evolution of a slower growth rate to reduce the daily energy requirements of the growing young. However, in optimal conditions, some seabirds can raise larger broods (Lack, 1966).

By studying the pattern, rate and duration of chick growth it is possible to demonstrate some of the effects that adult breeding and feeding strategies can have on chicks. Intra- and interspecific growth differences should indicate the strategy used by each species. This chapter aims to demonstrate and account for these differences, determine any evolutionary and ecological growth adaptations and make comparisons with previous studies.

## METHODS

### Data collection

Growth rates of chicks from the two main study colonies (A41 and C80) were recorded in both years. Each chick was weighed with an appropriate 'Pesola' spring balance on most days from the day it hatched until the end of the guard period, and as often as possible during the crēche period. It was not always possible to find every bird on each day during the crēche period because paint marks and flipper bands were often obliterated by moulting down or mud.

In addition to weight, flipper length and culmen length and depth were recorded with vernier calipers on up to four occasions during the development of each chick.

Data analysis

When the variation of chick weight with time was plotted, it was apparent that growth followed a sigmoid curve. Such growth curves can be mathematically described which permits the parameters of growth (rate, shape and magnitude) to be easily and objectively compared between and within species. Before subjecting the data to growth curve analysis, several criteria were used to eliminate unsuitable material.

Since Adélie chicks surviving to crēche age at 15-19 days old can thermoregulate efficiently and recognise their parents and the nest-site (see chapter 2), it was assumed that chinstrap chicks also attained these abilities and so could potentially crēche at this age. The weights of any chicks of both species that reached 'crēche age' were therefore used in chick growth analysis. The actual crēche ages used are those recorded for Adélies in 1981/82 (Table 2.11). It was assumed that chicks that died before reaching 'crēche age' had not been able to develop normally, so the growth data of these chicks were not used.

If the siblings of dead chicks survived beyond 'crēche age', they were treated as 'survivors'. Single chicks (from hatching) that survived beyond crēche age were grouped as 'singles'. If twins both survived beyond crēche age they were treated as either 'first' or 'second' chicks. The weights of chicks in each of the categories were used to produce separate relationships between mean weight and age. In 1980/81, none of the chinstrap chicks in the sample reached 'crēche age' so they were all classified according to their status when hatched. Because the growth of the chicks that died before reaching 'crēche age' was so abnormal, growth curves could not be fitted, so no analysis was attempted.

If there were fewer than five chicks in any weight sample, the sample was eliminated. The remaining data were analysed by attempting to fit a growth curve. The slopes and asymptotes of the fitted growth curves were then compared statistically. Data sets containing few weights from the latter part of the crêche period did not give realistic asymptotic weights when analysed in this way, but when growth curves were fitted to pooled data sets for each species or year, the asymptotes obtained were realistic since they appeared close to those which could be fitted by eye.

The fitted growth curves apply to the data that were accepted for use in analysis and some curves were very good fits of these data. However, it is not possible to state with absolute certainty that the pattern of growth beyond the last data point is a continuation of the growth curve. Thus, the fitted asymptotes which are projections beyond the data, must be considered assumptions. A change in the growth pattern, which can occur during the last few days before fledging, but which was not observed in this study, is a decrease in mean weight after peak chick weight had been reached.

The method of growth curve analysis was similar to that described by Ricketts and Prince (1981). Two types of sigmoid growth curve were used to describe Adélie and chinstrap growth statistically. These were the logistic and Gompertz curves. The form of each curve depends on the value, $\lambda$, which indicates the proportion of the asymptotic weight at which the inflection point in the sigmoid curve, or the maximum growth rate, occurs. The Gompertz curve describes the case where $\lambda$ converges toward zero and the inflection point is at 1/e of the asymptotic weight. The equation of the Gompertz curve is $W = A \exp(-\exp^{-k(t-ti)})$, where W is weight in kg, A is the asymptotic or maximum weight in kg, k is the growth rate per day and ti is the chick age in days at which inflection or maximum growth rate occurs. In contrast to the logistic growth curve, it describes an asymmetric sigmoid growth pattern, such that 37 % of the asymptote is

attained when the inflection point in the curve is reached, i.e. maximum growth rate occurs at an earlier stage than in the logistic curve (Ricklefs, 1968 a). The Gompertz curve proved to be the best description of Adélie and chinstrap growth. It was fitted to the data by using a weighted least squares technique from the MLP program (Ross and others, 1980). For each data point, the square of the difference between the observed and fitted values (the residual) was multiplied by $\sqrt{n}/W$, where n was the number of chicks used to calculate the mean weight, W, of each sample. Multiplication by $\sqrt{n}/W$ ensured that the squares of the residuals were normally distributed about zero and that there was a constant coefficient of variation along the curve.

There was a paucity of data from the later stages of chick growth, so growth curve analysis only resulted in three growth curves for individual chick categories to which the data were a reasonable fit. In this study, a curve was considered a reasonable fit if the standard error of the asymptote was less than 10 % of the asymptote. Pooling the data sometimes gave a more acceptable growth curve, but in many cases, intra- and interspecific comparisons could only be made by comparing the actual weight of chicks of various ages or by fitting a curve to the smooth exponential growth that occurred between hatching and the age of between 14 and 17 days. The equation of this curve is $W = A + B \exp^{-kt}$, where W is weight in kg, A is the asymptote and k and B are growth constants. The curve was fitted to the data using a weighted least squares technique from the MLP program, and each data point was weighted by n/W which gave the most normal distribution about zero of the squares of the residuals. This method analysed growth before crèche so 'survivors' were classed in their original category and only three categories of exponential growth were compared.

The shapes of curves were compared by fitting common non-linear parameters, k and ti, and performing an analysis of variance. The asymptotes of curves were compared by fitting a common value of A and again performing an analysis of variance.

The increase in culmen and flipper dimensions was analysed by linear regression rather than by fitting a growth curve to the data. This was mainly because the sample sizes were small but also because the period over which the data were recorded approximately spanned a period of linear growth.

To determine whether disturbance had affected the growth of the study birds, control weights of chicks from an undisturbed colony were recorded and compared with the weights of the study birds. There was no reason to believe that the mean hatching dates of the study and control colony chicks were different, especially since the study nest chick hatching dates had a normal distribution, so the age of the control colony chicks was assumed to be equal to the mean age of the study nest chicks on the same day.

## RESULTS

The relationship between mean chick weight and age is shown in Figures 5.1-5.4. The sample size of first and second chicks was small in comparison with that of single chicks, but the growth pattern of all categories was very similar. The weight of second chicks tended to be less than the weight of first or single chicks, but these differences were not consistent.

Gompertz growth curves were fitted to several data sets. The parameters of these curves are given in Table 5.1. Good fits were obtained for growth of Adélie first, single and surviving chicks recorded in 1980/81 (Figures 5.5 and 5.6). A comparison of these three Adélie curves showed that the shapes and asymptotes of the first and surviving chick growth curves were the same ($F=1.26$, $P>0.05$). The data from these were combined and compared with single chicks (Figure 5.7). Their shape was the same

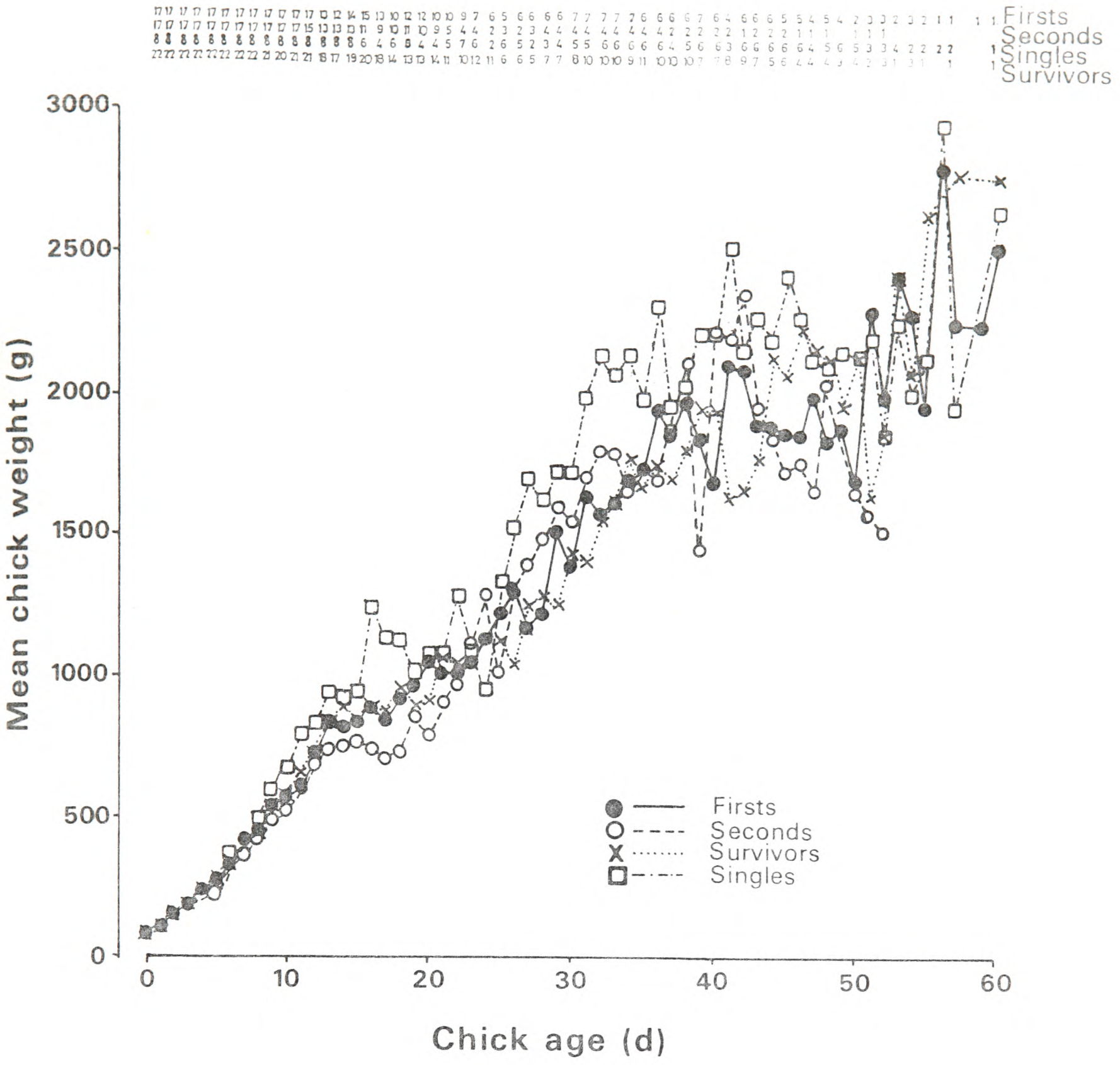



Figure 5.1. The relationship between mean weight and age of Adēlie chicks in 1980/81.

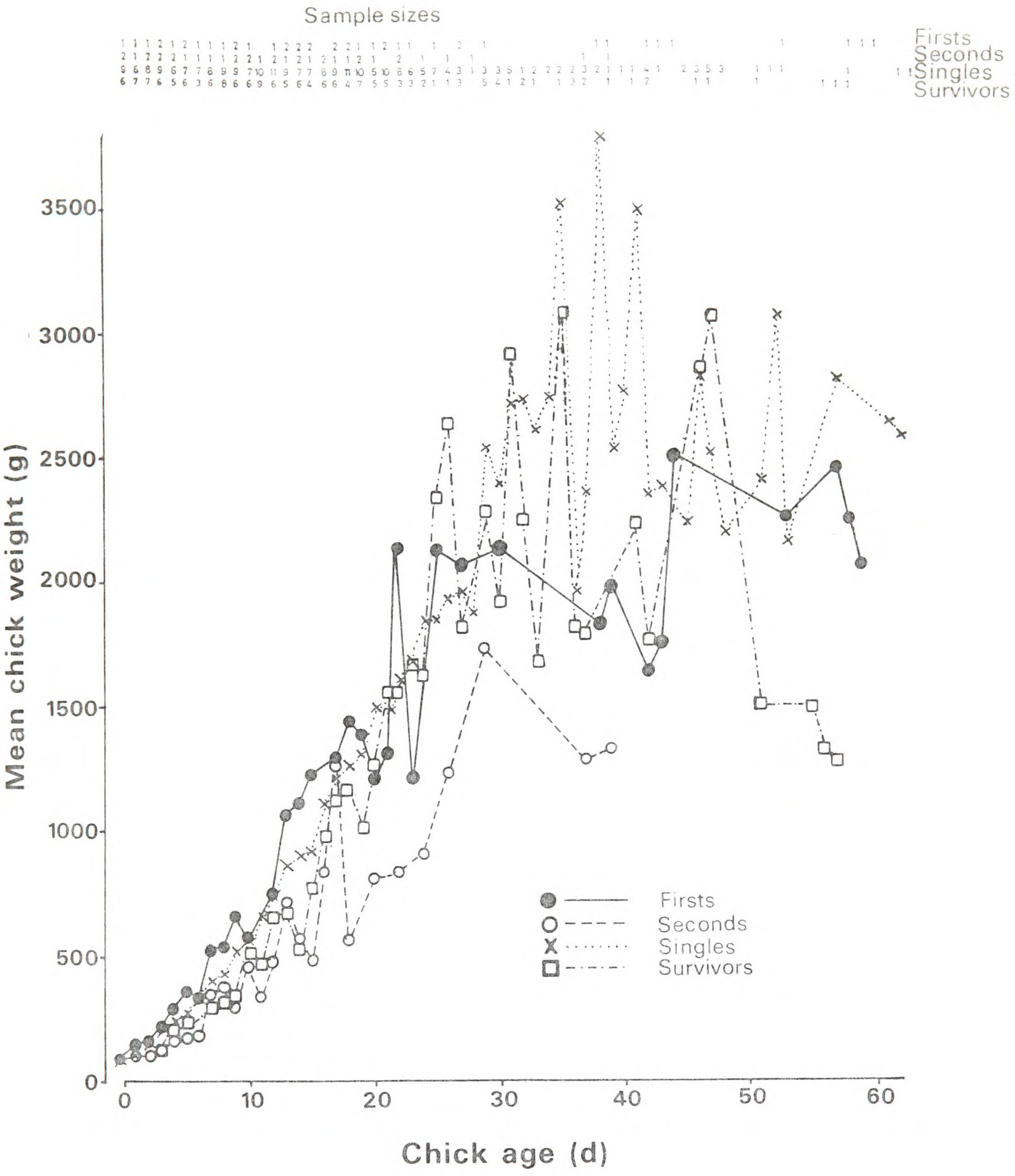



Figure 5.2. The relationship between mean weight and age of Adélie chicks in 1981/82.

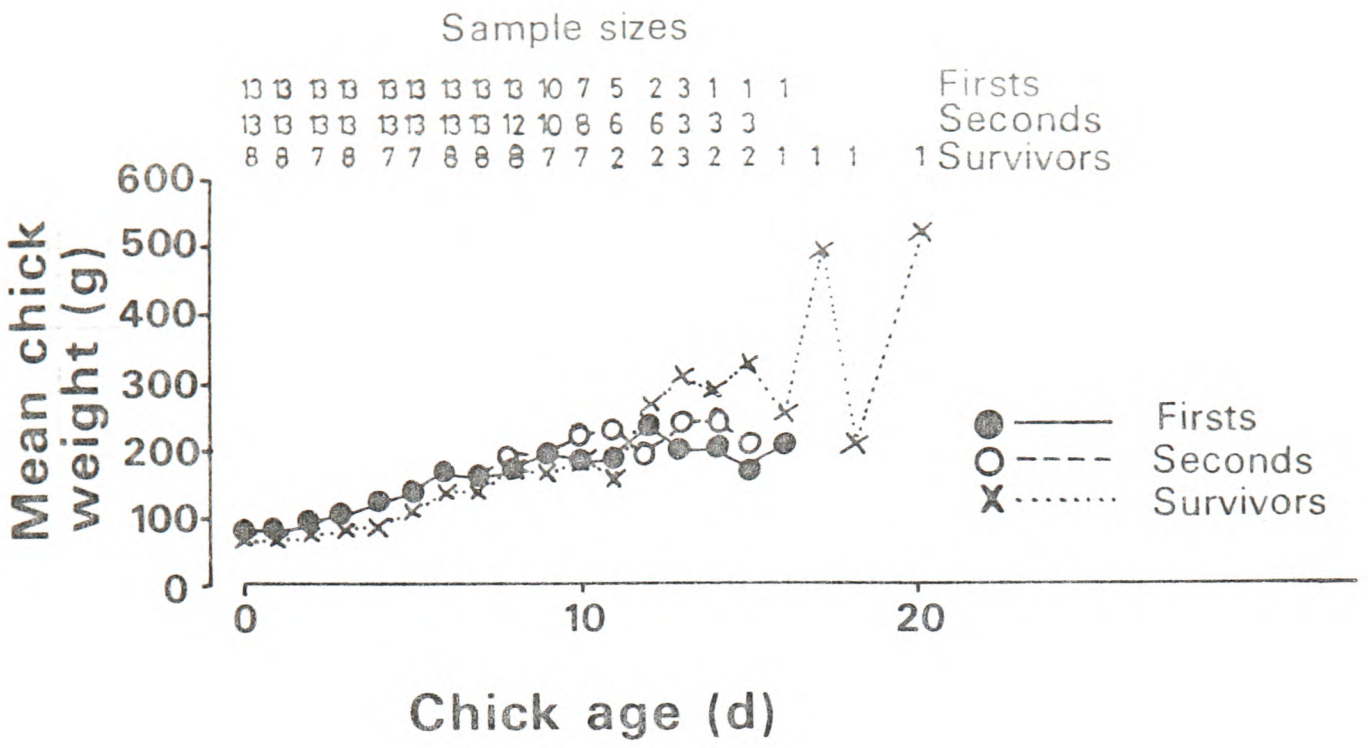



Figure 5.3. The relationship between mean weight and age of chinstrap chicks in 1980/81.

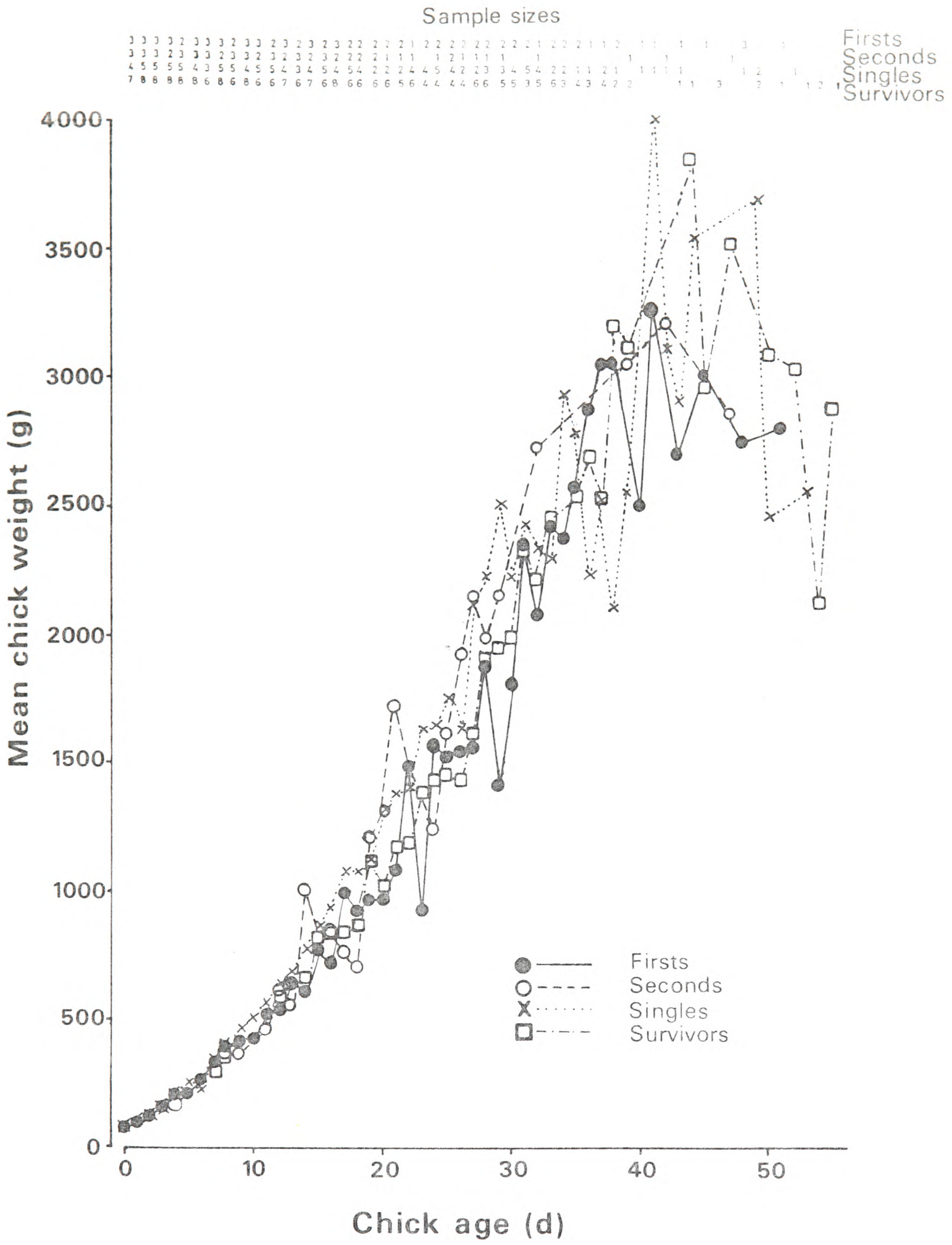



Figure 5.4. The relationship between mean weight and age of chinstrap chicks in 1981/82.

| Species | Year | Chick status | ti | K | A | |
|---|---|---|---|---|---|---|
| Adélie | 1980/81 | First | 14.13 | 0.076 | 2.05 | Figure 5.5 |
| | | Single | 14.10 | 0.083 | 2.38 | |
| | | Survivor | 13.40 | 0.080 | 1.92 | |
| Adélie | 1981/82 | Single | 16.58 | 0.080 | 2.87 | Figure 5.6 |
| Chinstrap | 1981/82 | Single | 26.85 | 0.051 | 4.90 | |
| Adélie | 1980/81 | Single | 14.10 | 0.083 | 2.38 | Figure 5.7 |
| | | First & Survivors | 13.75 | 0.078 | 1.98 | |
| Adélie | 1980/81 | All | 15.39 | 0.072 | 2.23 | Figure 5.9 |
| | 1981/82 | All | 16.30 | 0.080 | 2.78 | |
| Chinstrap | 1981/82 | All | 27.81 | 0.050 | 5.11 | |

Table 5.1. Parameters of chick growth from hatching to fledging (illustrated in Figures 5.5-5.7 and Figure 5.9).

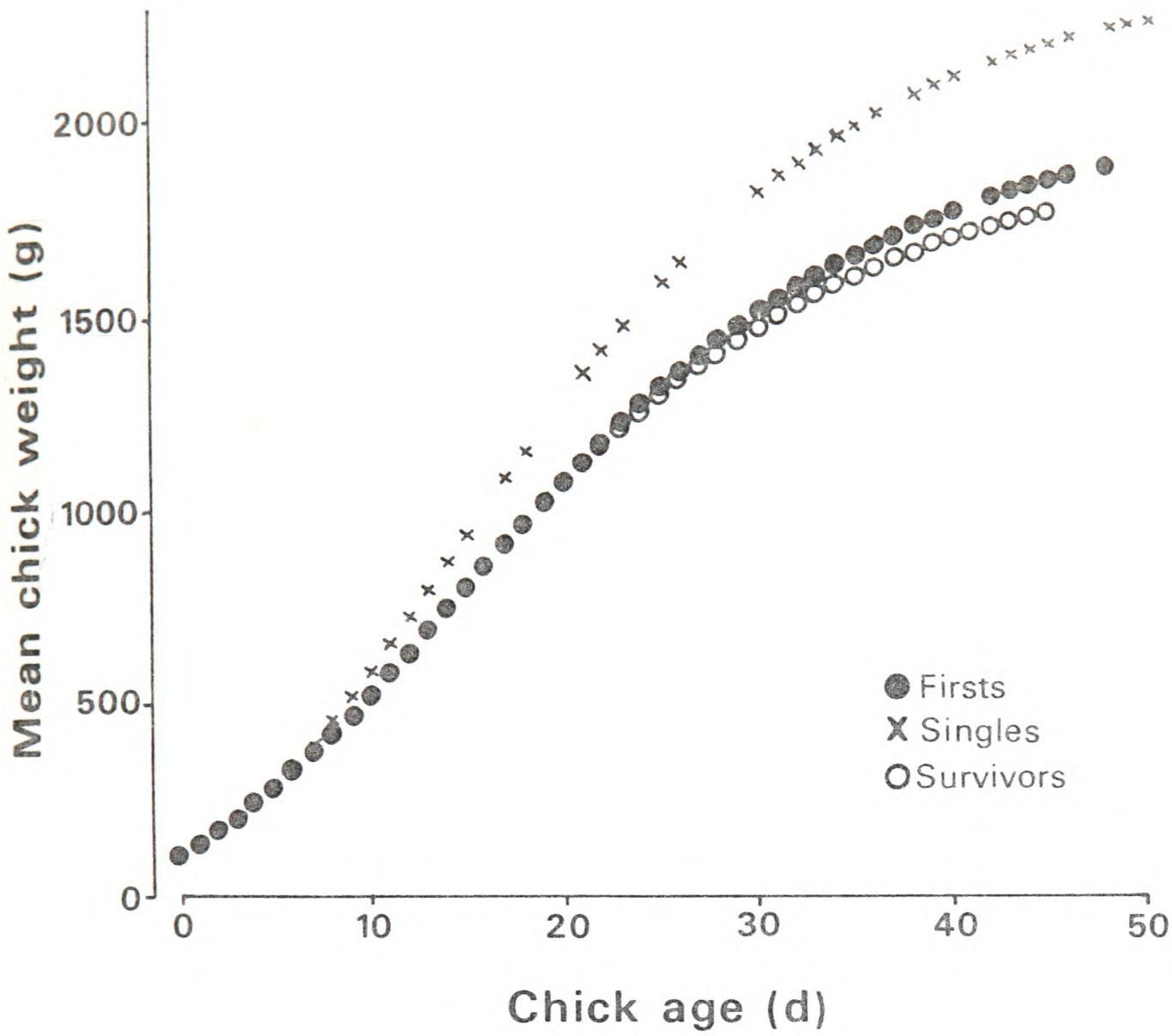



Figure 5.5. The fitted growth curves of Adélie first, single and surviving chicks in 1980/81.

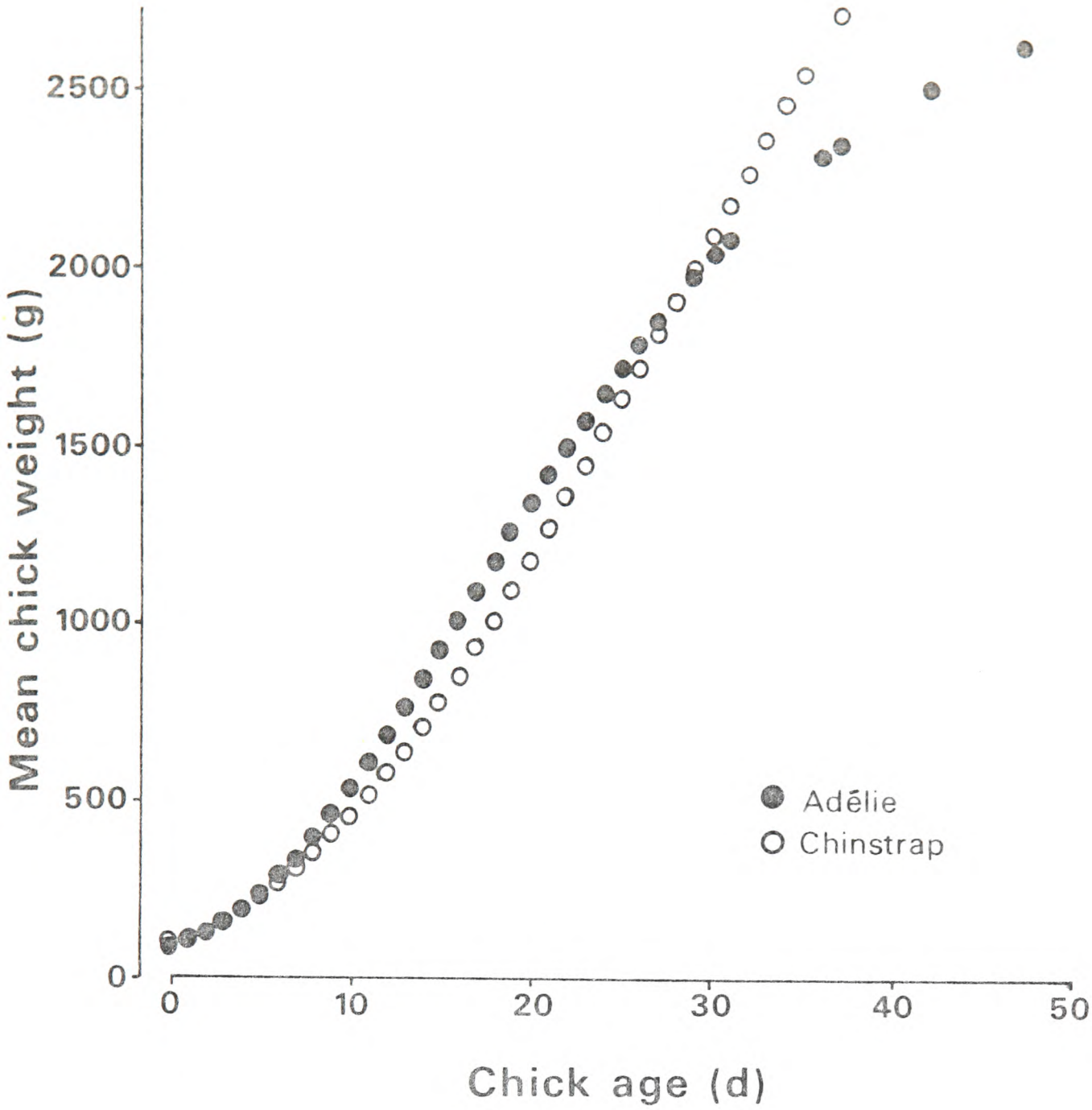



Figure 5.6. The fitted growth curves of Adélie and chinstrap single chicks in 1981/82.

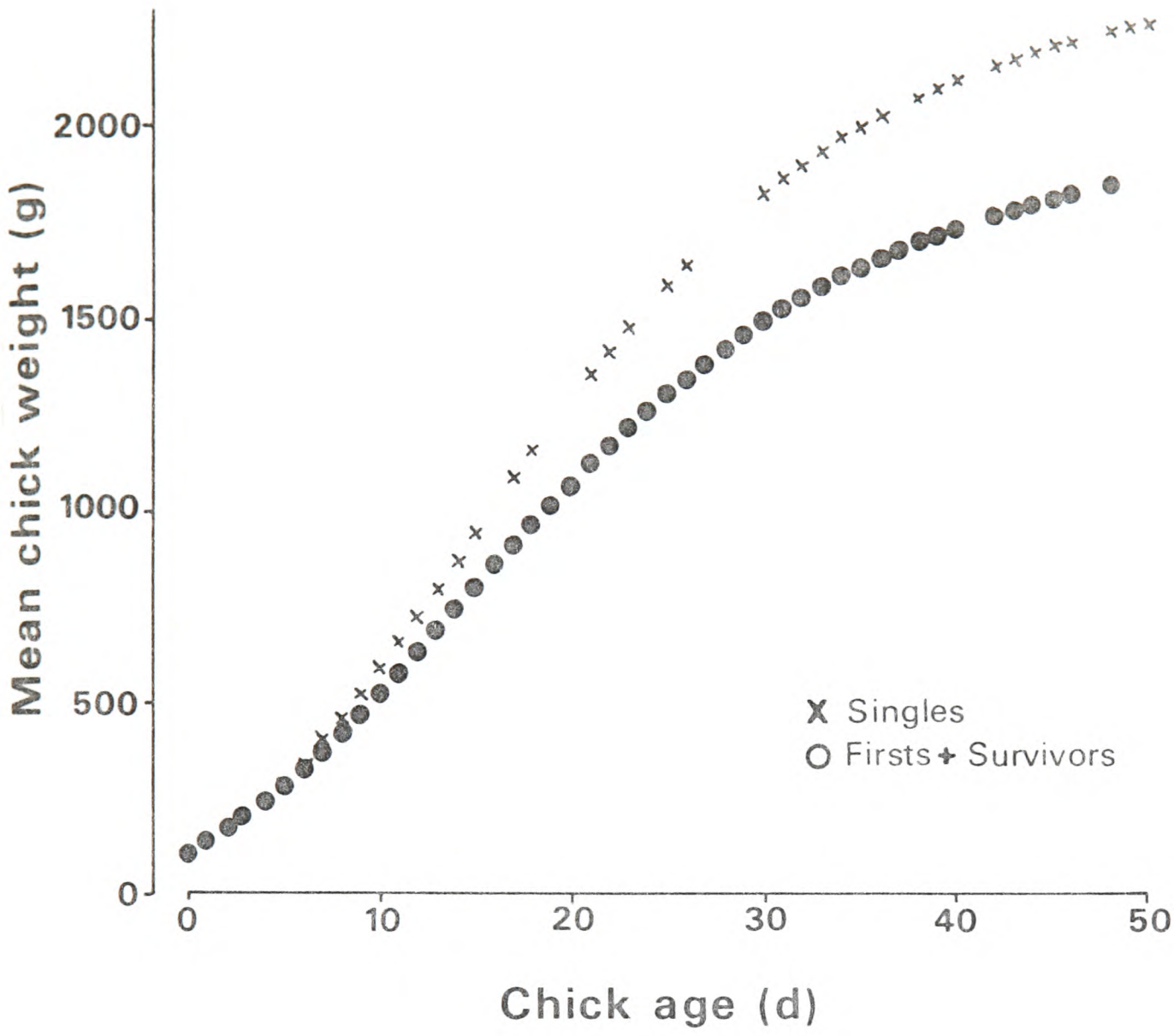



Figure 5.7. The fitted growth curves of Adélie single and first plus surviving chicks in 1980/81.

($F=2.85$, $P>0.05$) but the asymptote of singles was significantly greater than that of first and surviving chicks ($F=62.9$, $P<0.001$).

The mean weights of all the chick categories from Adélies in 1980/81 and 1981/82 and chinstraps in 1981/82 were combined (Figure 5.8) and growth curves were fitted to the three sets of data (Figure 5.9). The asymptotes were 2.23, 2.78 and 5.11 kg, respectively. The asymptote for Adélies in 1980/81 was the only one of these that was considered an acceptable value from the fitted growth curve. A visual comparison of the growth curves shows that the growth of Adélies and chinstraps in 1981/82 was similar, but the growth rate of Adélies was lower in 1980/81 than in 1981/82. To test these differences and similarities, the mean weight of chicks was compared at 5-10 day intervals as far as possible throughout the chick rearing period (Table 5.2). Only samples of five or more chick weights were compared, so in order to compare older chicks, weight samples from up to three consecutive days were combined. Adélie and chinstrap growth was similar in 1981/82, but chinstrap chicks older than 35 days were heavier than Adélies of the same age. Adélie chicks were lighter in 1980/81 than in 1981/82, but only those 20-30 days and 47-48 days old.

The exponential growth of chicks is shown in Figures 5.10-5.12 and the growth parameters given in Table 5.3. Comparisons showed that for Adélies in both years, first chicks grew at a faster rate than second chicks (1980/81 : $F=10.7$, $P<0.001$; 1981/82 : $F=3.96$, $P<0.03$), but chinstrap first and second chicks grew at the same rate ($F=0.21$, $P<0.05$). In addition, single chicks grew faster than first chicks in 1981/82 (Adélie : $F=7.77$, $P<0.001$); chinstrap : $F=4.03$, $P<0.025$).

The weights of control and study chicks assumed to be of the same age are shown in Table 5.4. There are no major differences between the two so it can be concluded that handling of chicks had very little effect on their growth in 1980/81. Any chick mortality caused by disturbance can therefore be attributed to losses due to sudden starvation through nest desertion

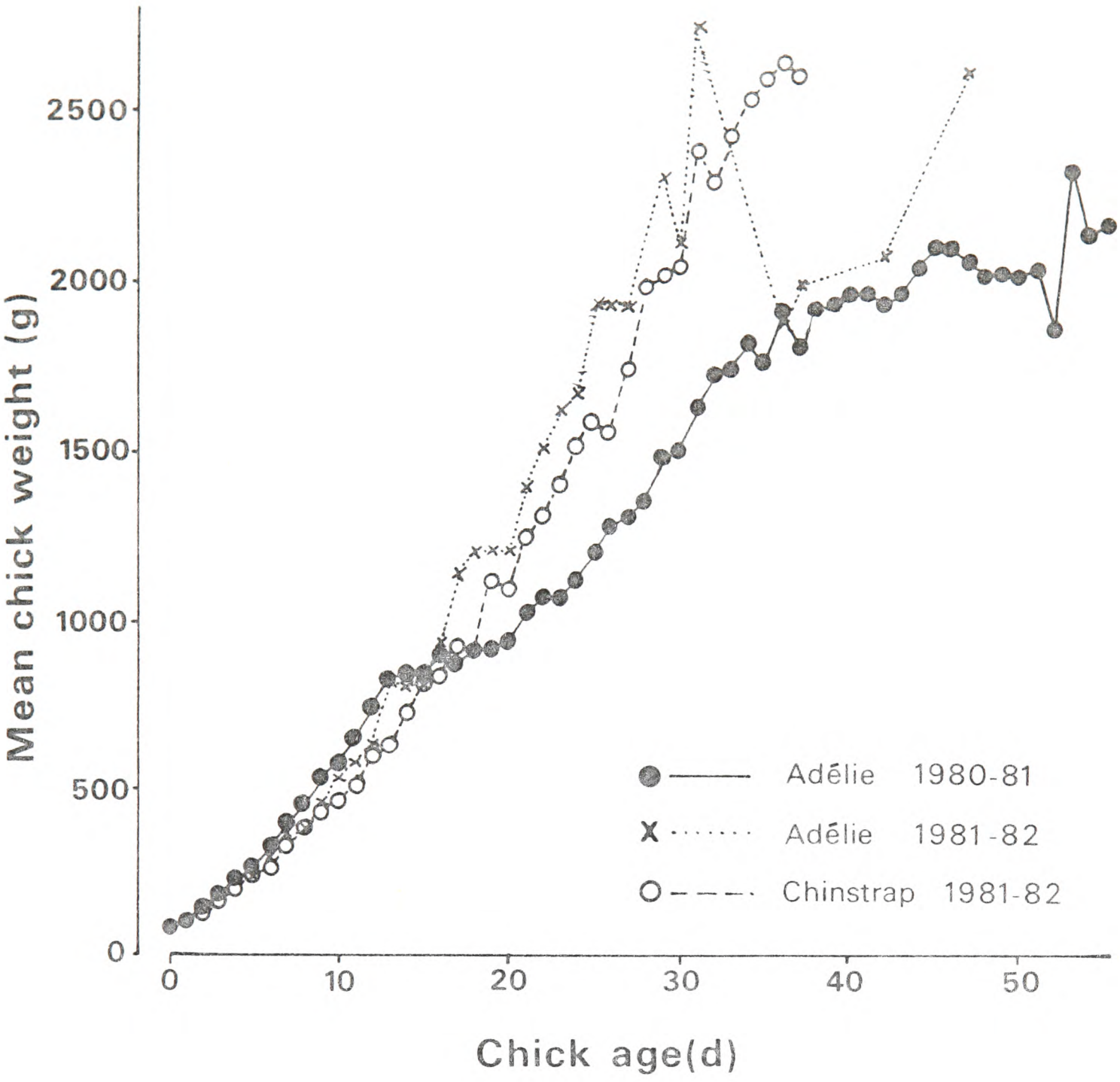



Figure 5.8. The variation of mean weight with age of Adélie and chinstrap chicks of all categories.

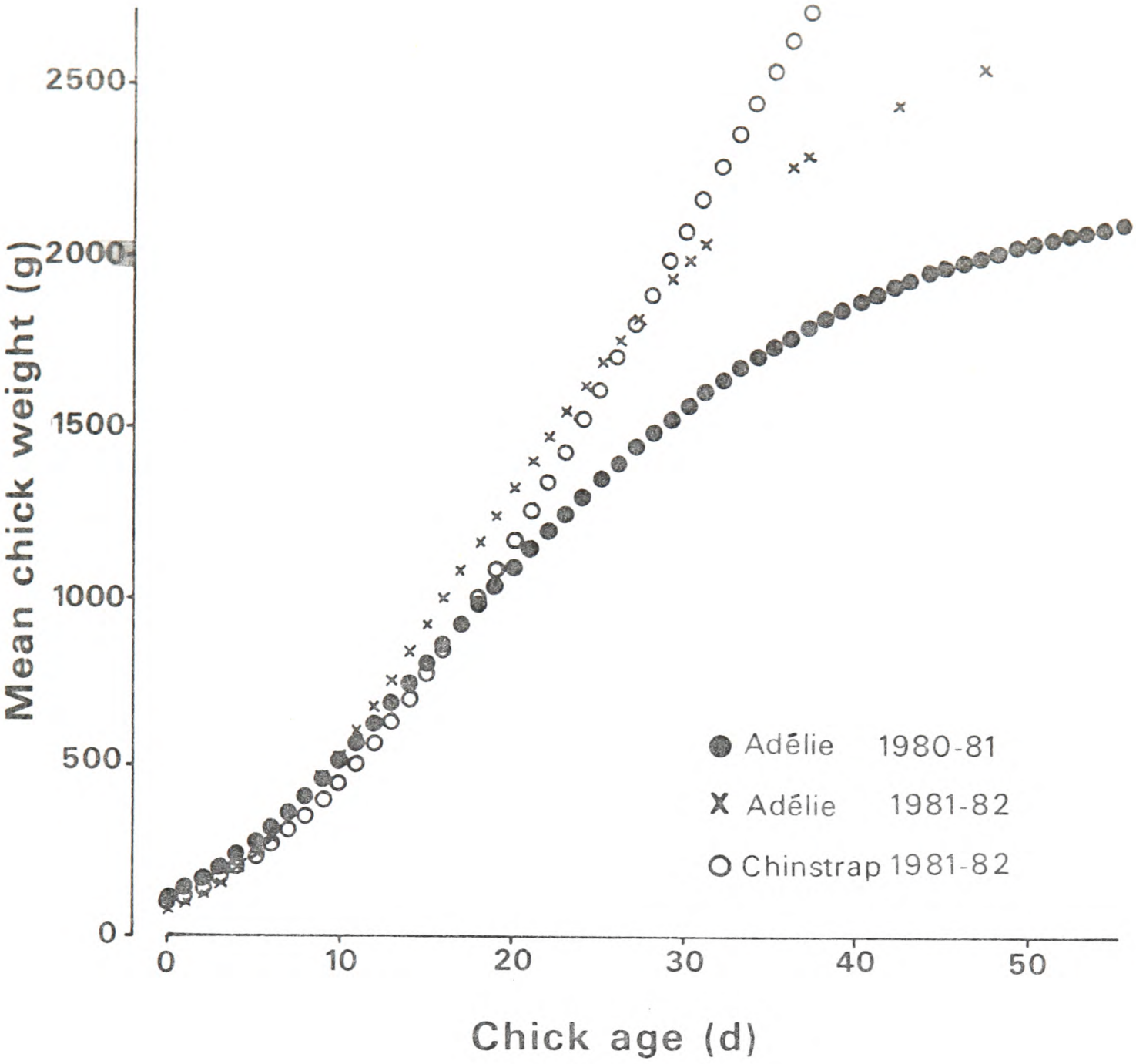



Figure 5.9. The fitted growth curves of Adélie and chintrap chicks of all categories, using the pooled weights for each species in each year.

| Chick age | 1981/82 Adélie Mean | sd | range | n | Chinstrap Mean | sd | range | n | Probability Chinstrap>Adélie |
|---|---|---|---|---|---|---|---|---|---|
| 0 | 82.8 | 9.5 | 66-100 | 18 | 79.9 | 10.0 | 63-98 | 17 | >0.05 |
| 5 | 258.6 | 65.6 | 175-395 | 16 | 234.1 | 32.9 | 175-318 | 18 | >0.05 |
| 10 | 522.8 | 156.2 | 290-780 | 16 | 455.7 | 88.9 | 361-621 | 16 | >0.05 |
| 15 | 806.4 | 311.1 | 320-1350 | 14 | 804.6 | 140.5 | 610-1020 | 16 | >0.05 |
| 20 | 1206.7 | 343.1 | 720-1900 | 12 | 1088.6 | 316.6 | 645-1570 | 11 | >0.05 |
| 25 | 1923.3 | 311.9 | 1435-2325 | 9 | 1582.9 | 419.8 | 795-2215 | 12 | >0.05 |
| 30 | 2118.1 | 346.9 | 1725-2625 | 7 | 2035.9 | 488.9 | 1185-2650 | 11 | >0.05 |
| 36 | 1870.0 | 295.1 | 1475-2275 | 5 | 2634.0 | 327.1 | 2220-2950 | 5 | <0.02 |
| 41-43 | 2211.4 | 528.9 | 1625-3475 | 11 | 3191.7 | 406.6 | 2700-4000 | 6 | <0.01 |
| 47-48 | 2463.9 | 381.5 | 2050-3050 | 9 | 3085.7 | 499.3 | 2325-3650 | 7 | <0.05 |

| | Adélie 1980/81 | | | | 1981/82 | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 0 | 85.6 | 13.4 | 65-128 | 62 | 82.8 | 9.5 | 66-100 | 18 | >0.05 |
| 5 | 257.3 | 62.5 | 114-407 | 64 | 258.6 | 65.6 | 175-395 | 16 | >0.05 |
| 10 | 572.5 | 116.3 | 327-857 | 63 | 522.8 | 156.2 | 290-780 | 16 | >0.05 |
| 15 | 836.0 | 185.8 | 415-1190 | 54 | 806.4 | 311.1 | 320-1350 | 14 | >0.05 |
| 20 | 932.7 | 293.6 | 430-1650 | 39 | 1206.7 | 343.1 | 720-1900 | 12 | <0.02 |
| 25 | 1194.0 | 376.5 | 665-2135 | 21 | 1923.3 | 311.9 | 1435-2325 | 9 | <0.001 |
| 30 | 1495.6 | 520.9 | 800-2700 | 21 | 2118.1 | 346.9 | 1725-2625 | 8 | <0.001 |
| 36 | 1910.4 | 451.0 | 1020-3100 | 27 | 1870.0 | 295.1 | 1475-2275 | 5 | >0.05 |
| 41-43 | 1964.8 | 408.6 | 1060-3050 | 62 | 2211.4 | 528.9 | 1625-3475 | 11 | >0.05 |
| 47-48 | 2031.8 | 354.8 | 1400-2975 | 28 | 2463.9 | 381.5 | 2050-3050 | 9 | <0.005 |
| 57-59 | 2230.0 | 579.8 | 1165-2765 | 5 | 2167.0 | 510.1 | 1270-2800 | 5 | >0.05 |

Table 5.2. Comparison between Adélies and chinstraps in 1981/82 and between Adélies in 1980/81 and 1981/82 of mean chick weight at 5-10 day intervals throughout most of the chick rearing period.

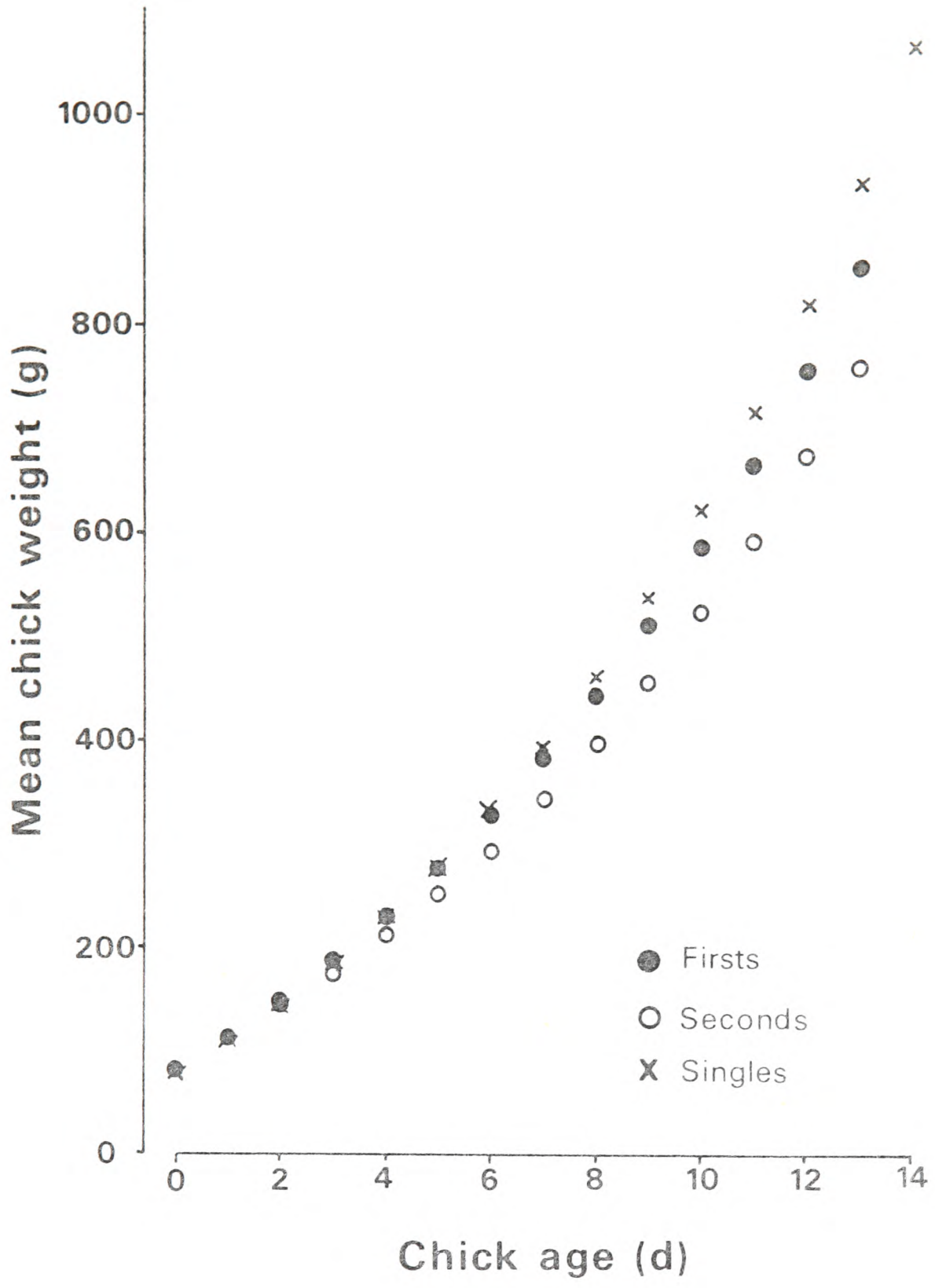



Figure 5.10. Growth curves fitted to the exponential growth phase of Adélie chicks in 1980/81.

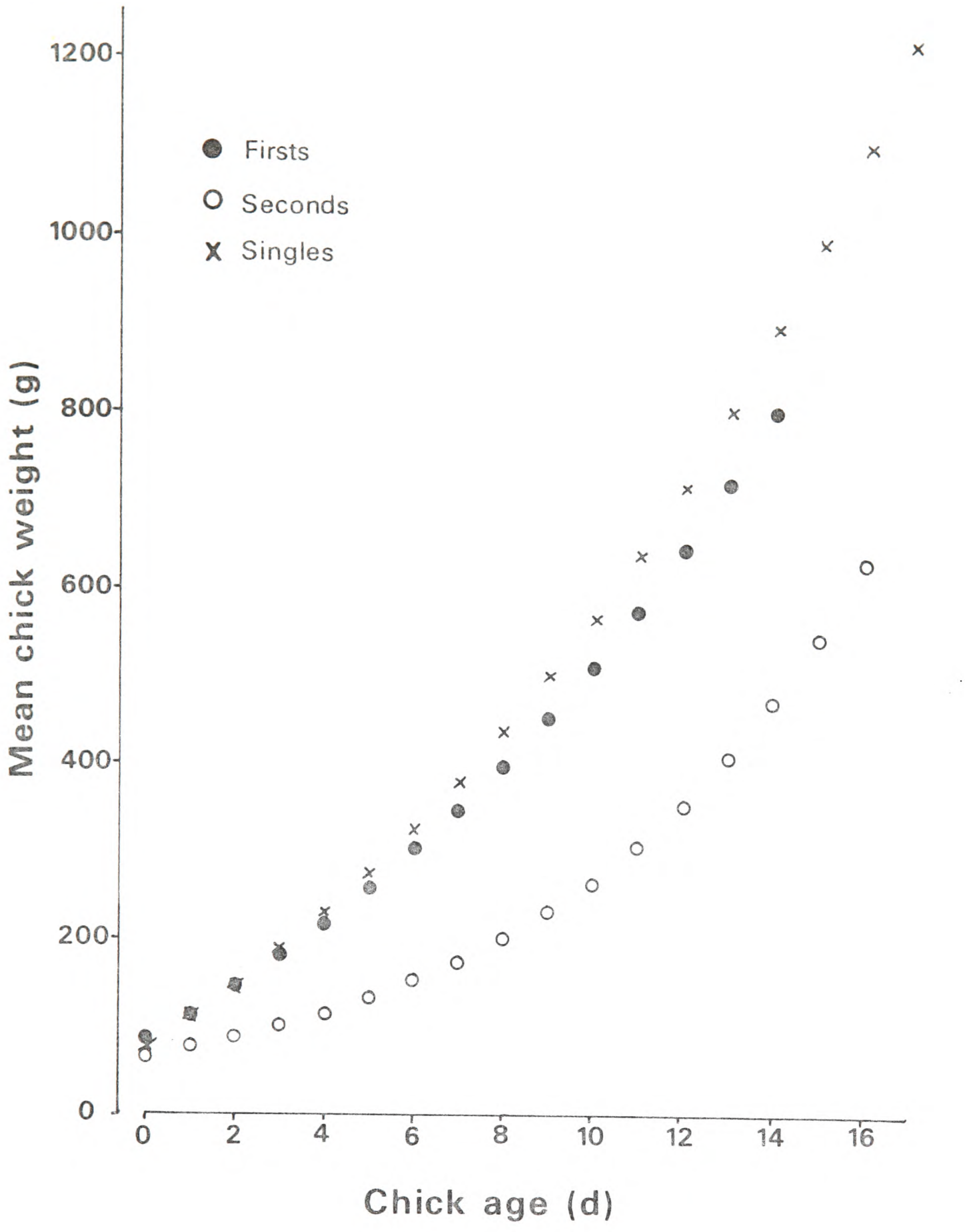



Figure 5.11. Growth curves fitted to the exponential growth phase of Adélie chicks in 1981/82.

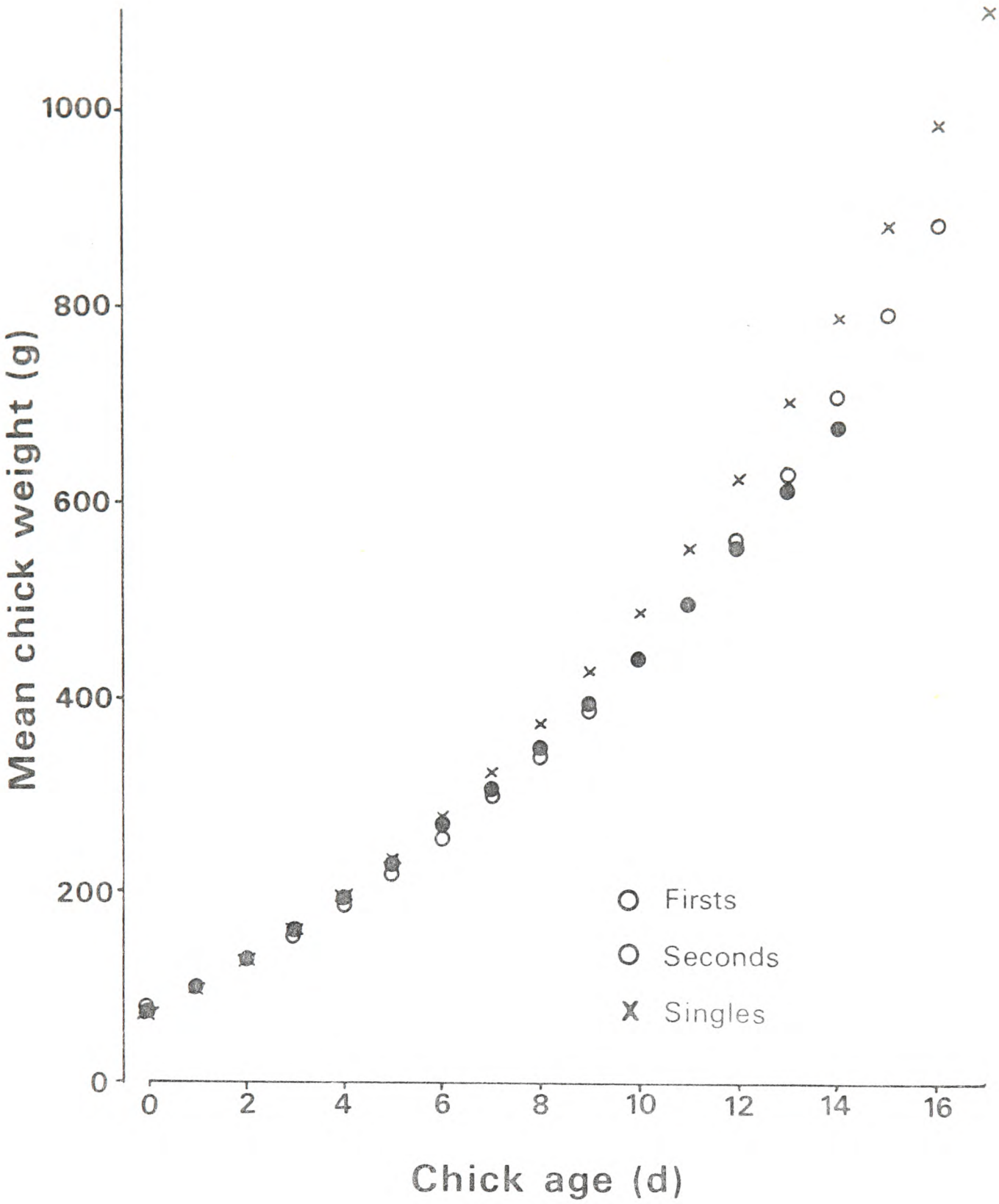



Figure 5.12. Growth curves fitted to the exponential growth phase of chinstrap chicks in 1981/82.

| Species | Year | Chick status | $exp^{-k}$ | B | A |
|---|---|---|---|---|---|
| Adélie | 1980/81 | First | 1.0989 | 0.30 | -0.22 |
| | | Second | 1.1016 | 0.27 | -0.19 |
| | | Single | 1.1118 | 0.33 | -0.26 |
| Adélie | 1981/82 | First | 1.0825 | 0.31 | -0.22 |
| | | Second | 1.1584 | 0.16 | -0.10 |
| | | Single | 1.0797 | 0.35 | -0.27 |
| Chinstrap | 1981/82 | First | 1.0708 | 0.29 | -0.21 |
| | | Second | 1.0984 | 0.29 | -0.21 |
| | | Single | 1.0935 | 0.33 | -0.26 |

Table 5.3. The parameters of chick growth during the exponential growth phase.

| Species/ Year | Sample date | Chick status | Age (d) | Chick weight (g) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Control chick | | | | Study chick | | | |
| | | | | Mean | sd. | range | No | Mean | sd. | range | No |
| Adélie | 23/12 | First | 14 | 869 | 158 | 552-1100 | 10 | 817 | 133 | 580-975 | 14 |
| 1980/81 | | Second | 13 | 572 | 175 | 202-875 | 10 | 737 | 147 | 512-1002 | 13 |
| | | Single | 14 | 931 | 171 | 700-1325 | 10 | 916 | 193 | 607-1175 | 8 |
| | 04/01 | Single | 26 | 1196 | 399 | 570-2090 | 30 | 1524 | 283 | 1165-1810 | 5 |
| | 17/01 | Single | 39 | 1893 | 496 | 1060-2950 | 30 | 2207 | 447 | 1780-2675 | 6 |
| Chinstrap | 23/01 | First | 9 | 241 | 72 | 136-352 | 5 | 194 | 75 | 122-382 | 10 |
| 1980/81 | | Second | 9 | 169 | 47 | 135-254 | 5 | 179 | 74 | 103-380 | 10 |
| | | Single | 9 | 325 | 102 | 198-522 | 14 | 159 | 41 | 119-222 | 7 |

Table 5.4. A comparison of the weight of control and study chicks assumed to be of the same age.

rather than a gradual starvation and decreased growth rate caused by disturbed feeding of the chicks by the adults.

Culmen and flipper growth is shown in Figures 5.13-5.17 and the corresponding slopes and regression coefficients are given in Table 5.5. Culmen and flipper growth of all chicks was very similar, except that the rate of growth of chinstrap flippers was greater than that of Adélie flippers ($F=8.8$, $P<0.001$) and the growth rate of flippers of chicks of both species was much greater than the growth rate of culmens ($P<0.001$). The largest dimensions of the flipper and culmen of single chicks, calculated from the regression lines, are compared in Table 5.6 with the same dimensions of adults killed for the diet study. The regression lines are only representative of flipper and culmen growth over the period when dimensions were recorded, so it is not possible to determine the exact pattern of growth before and after this period. However, it appears that chicks fledged with almost fully grown flippers but with culmens that were substantially less than fully grown.

## DISCUSSION

### a. Overall growth pattern

The form of Adélie and chinstrap growth recorded here conformed to a sigmoid growth pattern. There was an initial period of slow growth, when the newly hatched chicks survive on the remainder of the energy reserves from the egg. When the parents begin regularly feeding the chicks, this is followed by a period of almost linear growth and then a decrease in growth rate toward an asymptotic weight. The first two of these stages together approximate to exponential growth. In some other penguin growth studies (Taylor and Roberts, 1962; Ainley and Schlatter, 1972; Volkman and Trivelpiece, 1980) a decrease in mean weight occurred after a peak weight

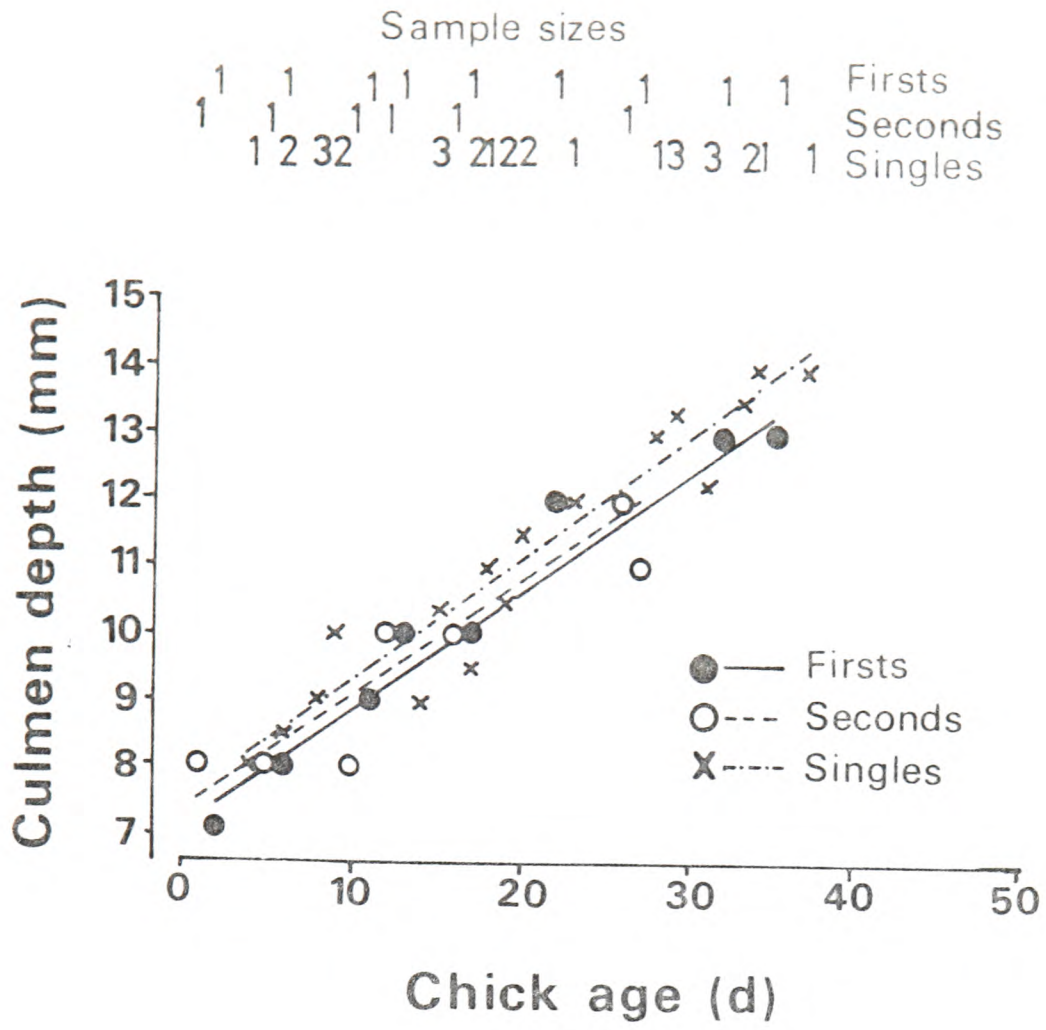



Figure 5.13. The change in culmen depth with age of chinstrap chicks in 1981/82.

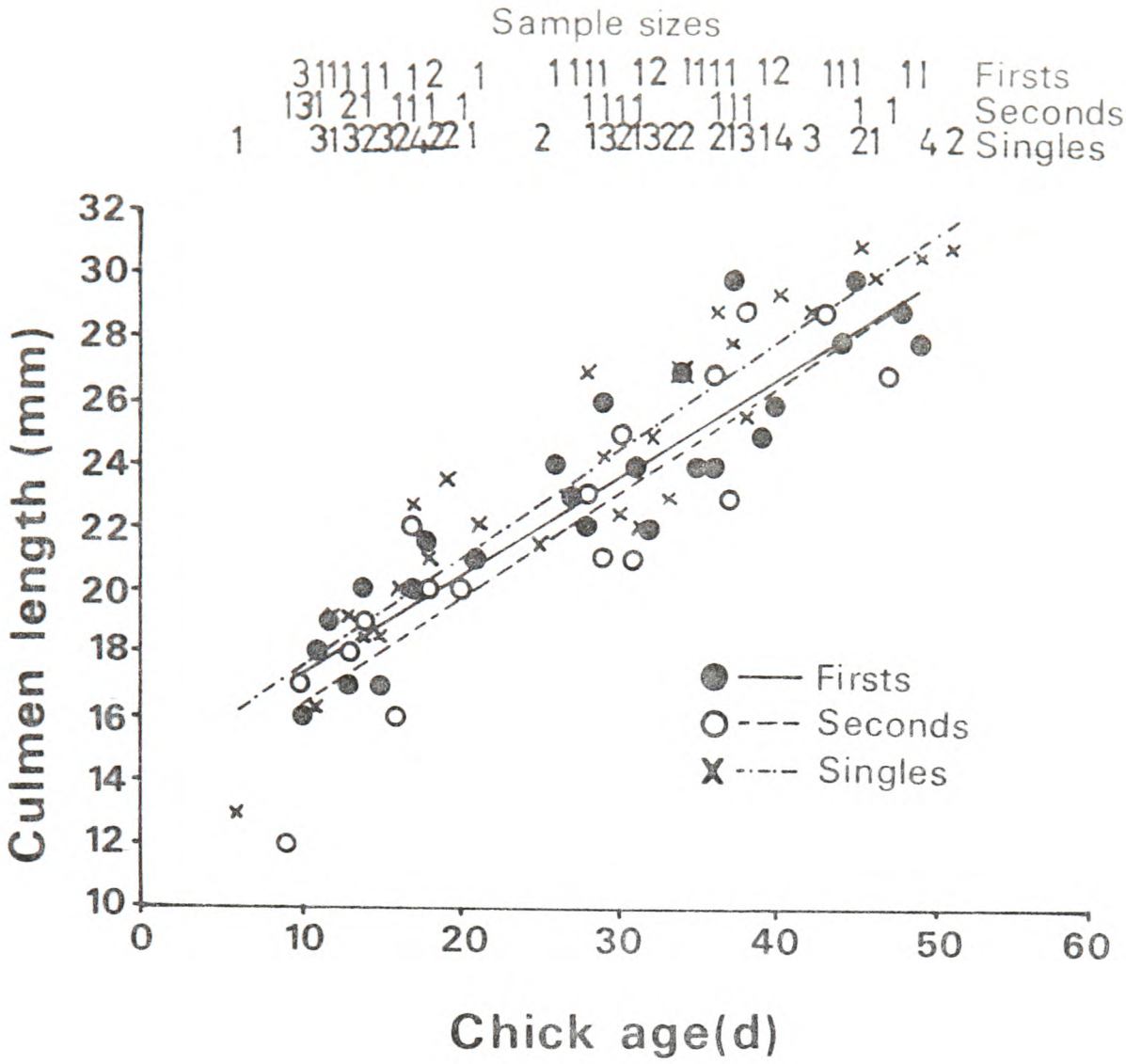



Figure 5.14. The change in culmen length with age of Adēlie chicks in 1980/81.

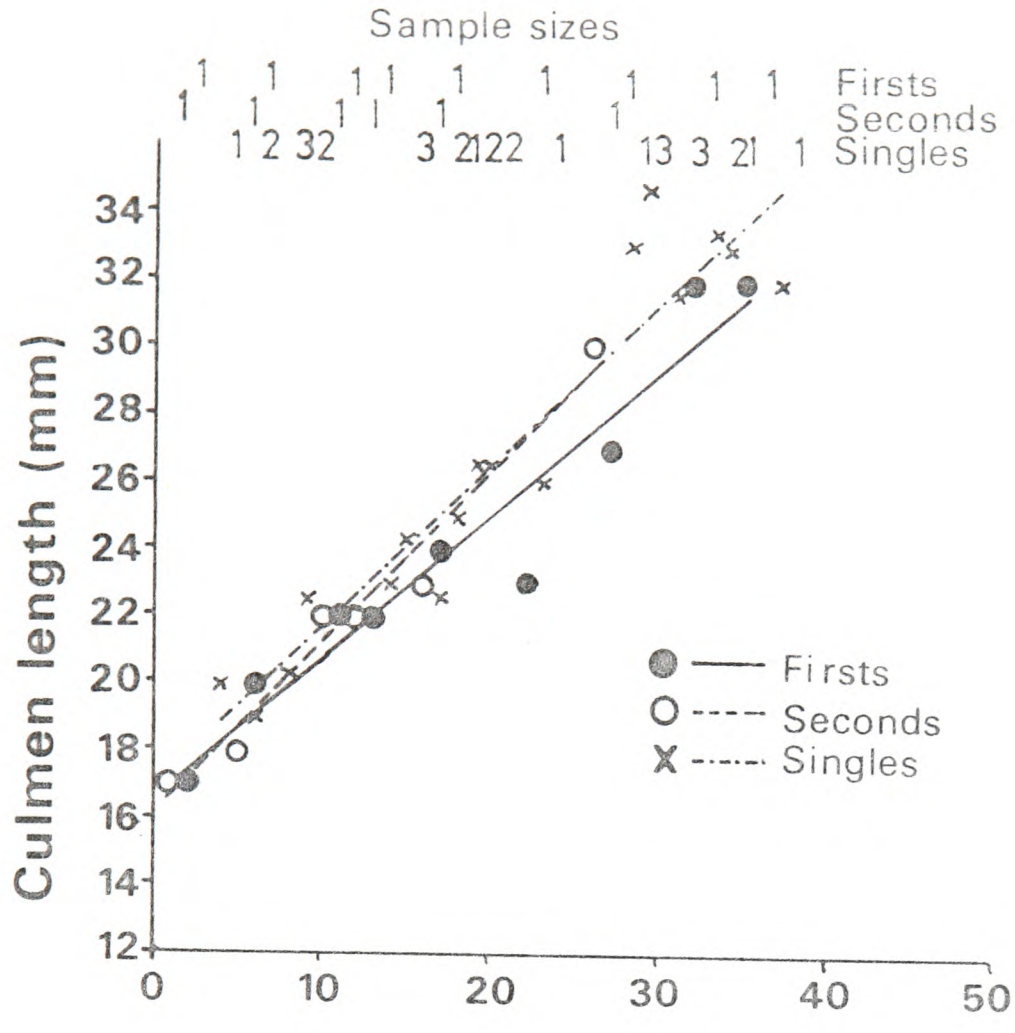



Figure 5.15. The change in culmen length with age of chinstrap chicks in 1981/82.

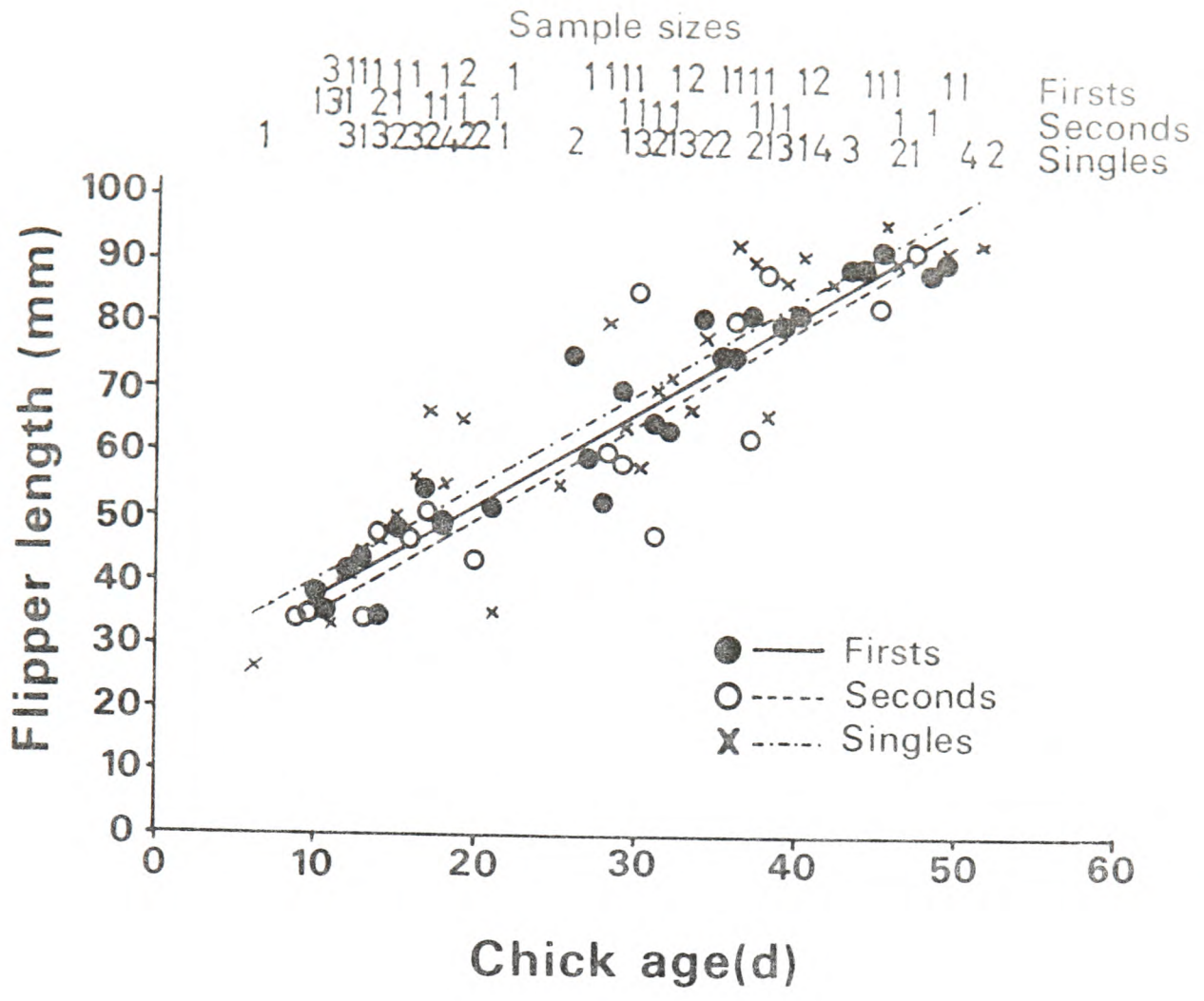



Figure 5.16. The change in flipper length with age of Adēlie chicks in 1980/81.

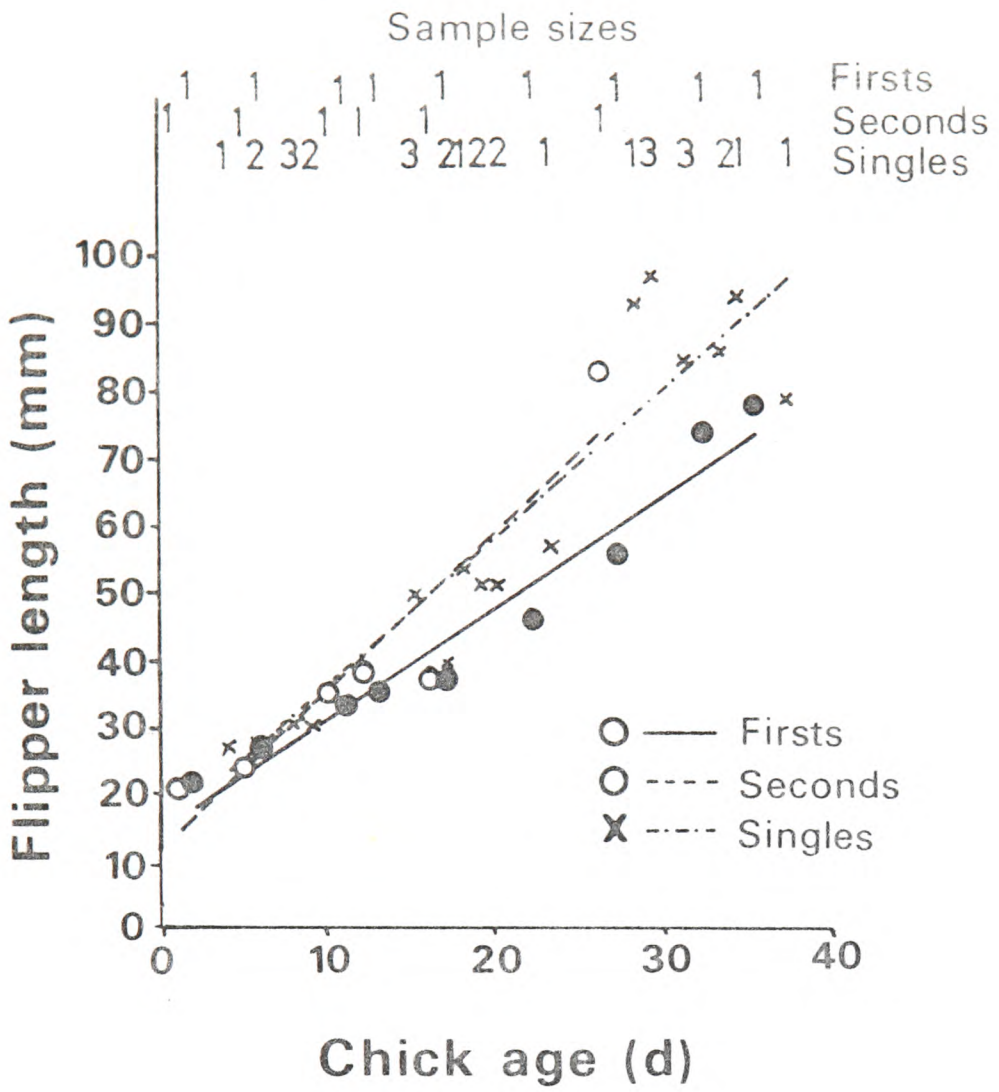



Figure 5.17. The change in flipper length with age of chinstrap chicks in 1981/82.

| Species/ Year | Chick status | Length (mm) Flipper Slope | r | No | Length (mm) Culmen Slope | r | No | Depth (mm) Culmen Slope | r | No |
|---|---|---|---|---|---|---|---|---|---|---|
| Adélie | First | 1.473 | 0.9577 | 26 | 0.316 | 0.9277 | 26 | | | |
| 1980/81 | Second | 1.486 | 0.8996 | 18 | 0.345 | 0.8941 | 18 | | | |
| | Single | 1.468 | 0.9015 | 29 | 0.347 | 0.9312 | 29 | | | |
| Chinstrap | First | 1.699 | 0.9277 | 9 | 0.430 | 0.9640 | 9 | 0.178 | 0.9642 | 9 |
| 1981/82 | Second | 2.388 | 0.9370 | 6 | 0.516 | 0.9846 | 6 | 0.173 | 0.9300 | 6 |
| | Single | 2.254 | 0.9331 | 16 | 0.482 | 0.9484 | 16 | 0.184 | 0.9592 | 16 |

Table 5.5. The slopes and regression coefficients (r) of Adélie and chinstrap culmen and flipper growth.

| Species/ Year | Sex | Flipper length (mm) Adult Mean | sd. | range | No | Chick[1] Mean | Chick age(d) | Proportion of adult dimension (%)[2] |
|---|---|---|---|---|---|---|---|---|
| Adélie 1980/81 | Male | 112.1 | 3.5 | 106-120 | 30 | 100.5 | 51 | 91 |
| | Female | 108.5 | 5.0 | 101-118 | 21 | | | |
| Chinstrap 1981/82 | Male | 116.9 | 3.7 | 108-124 | 40 | 96.5 | 37 | 84 |
| | Female | 113.5 | 3.6 | 108-123 | 25 | | | |
| **Culmen length (mm)** | | | | | | | | |
| Adélie 1980/81 | Male | 40.0 | 3.3 | 35-54 | 32 | 31.8 | 51 | 83 |
| | Female | 37.0 | 2.5 | 33-43 | 22 | | | |
| Chinstrap 1981/82 | Male | 49.8 | 2.4 | 44-55 | 39 | 32.8 | 37 | 69 |
| | Female | 45.4 | 2.0 | 41-50 | 24 | | | |
| **Culmen depth (mm)** | | | | | | | | |
| Chinstrap 1981/82 | Male | 18.8 | 0.7 | 18-20 | 39 | 14.5 | 37 | 81 |
| | Female | 17.3 | 0.9 | 16-19 | 24 | | | |

Notes :

[1] taken from Figures 5.13-5.17.

[2] taken as the mid-point of the male and female dimension.

Table 5.6. A comparison of adult and chick culmen and flipper growth.

had been reached. This has been found for the young of other species, though these are all either oceanic species or swallows and swifts, e.g.the cliff swallow Petrochelidon pyrrhonata, of which it is suggested that weight recession is due to plumage development (Ricklefs, 1968 b), but there may also be a decrease in feeding frequency during the last few days of the chick rearing period which could contribute to this.

b. Variations in growth pattern

Growth patterns vary in several ways: the length of the period of linear growth, the rate of growth, the stage at which growth rate begins to level off and the asymptotic weight are all variable. This variation can be both intra- and interspecific and it appears that there can be major differences in growth at different breeding localities. Volkman and Trivelpiece (1980), who carried out the only comparative growth study of all three pygoscelid penguins, found that growth followed the logistic curve more closely than the Gompertz. Taylor and Roberts (1962) found that the truncated normal curve described Adélie growth best and, in fact, only Despin (1977) has fitted the Gompertz curve to pygoscelid growth data, although the asymptotes obtained did not appear to reflect the empirical data.

In this study, exponential growth and asymptotes of single chicks were faster and greater, respectively, than first and surviving chicks. In addition, the exponential growth phase of Adélie second chicks was slower than that of first chicks, whereas exponential growth of chinstrap first and second chicks was the same. Thus, the main difference between the two species is that Adélies invest more in the first chick, while chinstraps invest equal amounts in both first and second chicks. Taylor and Roberts (1962) also showed that Adélie second chicks grow at a slower rate and suggested that this was because the older and, therefore, probably larger first chicks were able to get more food. The disparity in age is the time

interval between the hatching of first and second chicks. In this study, in 1981/82, mean Adélie hatching intervals were 1.86 days (see chapter 2), which may account for the faster growth and possibly higher asymptote of first chicks relative to second chicks for Adélies but similar growth rates of both chinstrap chicks. However, it is more likely that it is due to a greater investment in the first egg by Adélies, as shown by the first and second egg weight disparity (see chapter 2), compared with equal investment in first and second eggs by chinstraps. A similar situation to that of Adélies was demonstrated by Furness (1983) who showed that great skua Catharacta skua chicks from large eggs within a sample have higher asymptotes than chicks from small eggs. It was also found that large and small skua chicks grew at the same rate which differs from the Adélie situation since, although the data (in Figures 5.1 and 5.2) suggest that the asymptote of Adélie first chicks was higher than that of second chicks, the larger first chicks also grew at a faster rate than the smaller second chicks. In addition, the growth of Adélie survivors and first chicks was slower than that of single chicks and yet the asymptotes were also lower. Fast exponential growth combined with a high asymptote is a situation which appears to contradict Ricklefs (1973). However, it is possible that although an inverse correlation of growth rate to asymptotic weight applies to comparisons within groups of similar avian species, it need not necessarily apply to intraspecific comparisons.

Taylor (1962) and Taylor and Roberts (1962) also found that the asymptotic weights of survivors were lower than that of singles and first chicks and suggested that the loss of a chick was due to poor parental care which would also be detrimental to the survivor. This is certainly possible, but it may also be that chicks which hatched as singles are likely to have had parents which were even more inept at raising a brood of two chicks. It is surprising, therefore, that in this study the growth rate of the singles was greater than that of survivors. It could be

expected that survivors would have an advantage over twins since their parents, who have already shown an inability to raise a brood of two because they did not provide quite enough food for two chicks, should have been able to provide more than enough to feed a survivor.

Volkman and Trivelpiece (1980) found no overall intraspecific differences in pygoscelid growth and suggest that this was because there was an abundant food source available to the chick. The intraspecific differences shown at Signy may therefore indicate a variable or deficient food supply. This would have favoured first chicks, if they were already larger than second chicks, since they would have been better able to compete for the food provided by the parents. The amount of food received by each chick in a brood would therefore have been determined by differences in the size of the chicks.

Volkman and Trivelpiece (1980) suggested that having a low asymptotic weight and high growth rate is an adaptation by a species to the shorter breeding season associated with a higher latitudinal distribution. This makes sense as it is advantageous for a species to grow as fast as possible in the time available. Chicks of the emperor penguin, which has the most southerly breeding distribution of any bird, fledge at only 50 % of mean adult body weight (Stonehouse, 1953; Prévost and Sapin-Jaloustre, 1965), whereas the closely-related King penguin which breeds mainly in the Sub-Antarctic, fledges at about 90 % of mean adult body weight (Stonehouse, 1960). Adélies on the Antarctic Continent at Cape Crozier and Adélie Land, where the chick rearing period is only about 50 days, have been shown to fledge with low asymptotes of between 2.3 and 3.2 kg (Sapin-Jaloustre and Bourlière, 1951; Ainley and Schlatter, 1972). It seems unlikely, however, that having a low asymptotic weight and high growth rate is the only strategy employed in the maritime Antarctic where the breeding season is much longer. Although the asymptotic weight of Adélies was less than that of chinstraps at King George I (Volkman and Trivelpiece, 1980), this does

not necessarily imply that it is due to an adaptation by Adélies to a shorter breeding season. At Signy, which is only about 1.5° further north than King George I, there were no overall interspecific growth differences, but a tendency for chinstrap chicks more than 36 days old to be heavier than their Adélie counterparts.

A latitudinal variation in growth rate has been examined for Arctic and temperate finches (Maher, 1964), but no relationship was found. However, Ricklefs (1976) did find a slower growth rate amongst neotropical passerines when compared with temperate passerines. Within one breeding site, or at similar latitudes, it is possible that growth parameters are affected by differences in the environmental conditions of the breeding season (Stonehouse, 1970) and by variations in the availability of the preferred food, since it has been shown that, at very similar latitudes, there can be a very great range of asymptotic weights (Table 5.7). At Cape Royds, Adélie asymptotes were 4.05 kg, compared with a maximum mean weight of 3.2 kg reached by chicks at Cape Crozier. This is surprising considering that these two breeding sites are only about 80 km apart and birds from them may be feeding in the same area. At King George I, Adélie and chinstrap asymptotes were 3.94 and 4.02 kg, respectively, compared with 2.78 kg for Adélies and c.3.0 kg for chinstraps in 1981/82 at Signy (this study). In addition, at Signy, although initial exponential growth was similar in the two years, the overall growth parameters were even lower in 1980/81 when environmental conditions were poor, than in 1981/82. The optimum strategy for chicks of each species at each site would be to leave the colony as early as possible at the greatest weight attainable (Ricklefs, 1979 b), but this would be governed by the constraints imposed by the time available for breeding, the environmental conditions and the amount of food available.

The estimated and fitted asymptotes of Adélies and chinstraps at Signy were considerably lower than any others recorded, with the exception of

| Locality | Latitude °S | Asymptote (kg) | Reference |
|---|---|---|---|
| Adélie | | | |
| Signy I | 61° | 3.59 | Sladen (1958) |
| " | " | 2.23 | This study - 1980/81 |
| " | " | 2.78 | This study - 1981/82 |
| King George I | 62° | 3.41 | Volkman and Trivelpiece (1980) |
| Hope Bay | 63° | 3.94 | Sladen (1958) |
| Adélie Land | 66° | 2.31 | Sapin-Jaloustre & Bourlière (1951) |
| Cape Royds | 77° | 4.05 | Taylor and Roberts (1962) |
| Cape Crozier | 77° | 3.20 | Ainley and Schlatter (1972) |
| Chinstrap | | | |
| Signy I | 61° | 4.76 | Laws (in Conroy and others, 1975 a) |
| " | " | 3.78 | Despin (1977) |
| " | " | c3.00 | This study - 1981/82 |
| King George I | 62° | 4.03 | Volkman and Trivelpiece (1980) |

Table 5.7. Asymptotes of chicks from studies of Adélies and chinstraps.

Adélies at Adélie Land (Sapin-Jaloustre and Bourlière, 1951) (Table 5.7). In 1980/81, the Adélie asymptote was 44 % less than that at King George I in 1977/78. Even the less reliable estimate from 1981/82 was 29 % less than this value. The chinstrap asymptote (estimated as c 3.0 kg) was 26 % less than that of chinstraps at King George I. The ratios of asymptotic weight to the mean weight of adults (given by Stonehouse (1975)) was also calculated at King George I. These were much higher than the values calculated for Signy using the same adult weights (Table 5.8).

Ricklefs (1968 b) suggested that an absence of high peak chick weight and pre-fledging weight loss is due to one of three factors :
1. lightweight plumage, 2. a staggered development of plumage, 3. precocious plumage development so that decrease in feather weight is concealed by an increase in the weight of the rest of the chick. This must assume that other factors such as shortage of food, a decrease in feeding frequency, as found for guillemot Uria aalge chicks (Birkhead, 1977 a), or increased chick activity, as found for little auk chicks (Norderhaug, 1980), which might also cause pre-fledging weight loss, do not occur. The chick weights from this study levelled off below adult weight and growth was presumably completed after the young had left the colony. Ainley and Schlatter (1972) suggested that asymptotic weights less than adult weights (75-89 % of adult weight) indicate that successful foraging is probably not a great problem for fledglings. This may be so, but assumes that adults are allowing chicks to fledge at a low weight because enought food is available rather than the low fledging weight being a consequence of a poor food supply to the chicks during the chick rearing period. In contrast, Manx shearwater Puffinus puffinus chicks reach almost 150 % and fledge at 120 % of adult weight, which allows the chicks to survive if food supply is poor and the adults to vacate the colony early (Harris, 1966). From the results of this study, it is perhaps realistic to assume that fledglings weighing approximately 50 % of adult weight have, in fact, a very poor

| | Mean adult weight (kg)* | Chick asymptote (kg) | | Chick asymptote/adult wt. | |
|---|---|---|---|---|---|
| | | King George I | Signy I | King George I | Signy I |
| Adélie | 5.0 | 3.940 | 2.78 | 0.79 | 0.56 |
| Chinstrap | 4.5 | 4.025 | c3.00 | 0.89 | 0.67 |

* Weights used are those given by Stonehouse (1975)

Table 5.8. Ratio of chick asymptote to adult weight for Adélies and chinstraps at King George and Signy Is.

chance of surviving once they leave the breeding colony unless there is plenty of food available and they can easily learn to feed economically.

It is difficult to see exactly why growth of Adélies and chinstraps at Signy is rather different from anywhere else, but certain aspects of the feeding ecology and breeding biology suggest that it may be related to the demands on the local food supply made by the very large populations of penguins at the South Orkney Is. This will be discussed in greater detail in Chapter 8.

In both this and the King George I study, chick flippers grew at a faster rate than culmens. Wing and flipper growth is less susceptible than weight gain to changes in the food supply. This reflects the importance of enabling even underweight chicks to be able to fly, or in this case, swim at fledging which allows them at least a slight chance of survival (Harris, 1966). Volkman and Trivelpiece (1980) also suggested that rapid flipper (and foot) growth enables escape from and defence against predators to take place at an early age and permits the chicks to chase the parents for food. They also suggest that since culmens are not at a mature size at fledging, fledged chicks may only be able to feed on smaller food items at first. Chicks at King George I had flippers which were 75 % and 80 % and culmens which were 61 % and 60 % of adult length for Adélies and chinstraps, respectively, at the beginning of the crèche period. It is likely that chicks from this study fledged with almost fully grown flippers. However, although culmens were probably not fully grown when the chicks fledged, this does not imply that the size of prey they can consume is smaller than that taken by adults since adults may take prey much smaller than their culmen size will allow (see Chapter 3).

In retrospect, a different sampling procedure should perhaps be used to obtain growth data, provided that feeding frequency does not need to be recorded in the same sample of chicks. If chicks of each category were weighed by age rather than daily, large samples of chicks of the same age

would have their weights recorded. This need only be every two or three days for each chick, which would cause less disturbance in the colony. Many of the data from this study were eliminated because the samples weighed on each day had a wide range of ages. Since weights were not always recorded on a daily basis toward the end of the fledging period, the sample sizes for each age became very small. In most cases, Gompertz curves fitted data very well for the initial stages of growth, but the absence of data nearer to fledging, when growth rate decreased toward the asymptote, meant that curves were influenced by a few very varied data points and often gave unreliable asymptotes.

## CONCLUSIONS

Adélie and chinstrap chick growth at Signy I was characterized by low asymptotes compared with species elsewhere, which could perhaps be explained by a restriction in the food supply toward the end of the growth period.

No overall interspecific or between year growth differences were found, although chinstrap chicks of some ages were heavier than Adélie chicks and Adélie chicks of some ages were heavier in 1981/82 than in 1980/81. The most striking difference shown by the two species was the different investment in the growth of the two chicks in a brood. More was invested in Adélie first chicks and they grew at a faster rate than second chicks, whereas there was no difference in investment in chinstrap first and second chicks, and the growth rates were the same. For Adélies, this is probably an adaptation to a short breeding season, but may also have been caused by a restriction in the energy supply needed for growth. This may also have been the reason why single chicks of both species had a

higher growth rate than chicks from broods of two. Environmental conditions may also have affected growth of all chick categories, especially in 1980/81.

# Chapter Six

# Bioenergetics

# INTRODUCTION

Because birds as a class are small in size and they fly or swim for a lot of the time, their energy requirements are high.

A knowledge of bioenergetics is necessary to determine the role that energy utilisation plays in the evolution of a reproductive strategy. The availability of energy is one of the main selective pressures in this evolution since it can determine laying date, clutch size and the duration of the chick rearing period (Lack, 1968). Theoretically, there are optimum clutch sizes and laying dates for species which coincide with the availability of the preferred food, but in many cases parents delay laying to beyond the date giving maximum probability of chick survival (Murton, 1961; Lack, 1966; Perrins, 1970; Harris, 1969 b) and produce smaller clutches than the most productive one (Perrins and Moss, 1975). This is because there are also secondary factors, such as local environmental conditions and the condition of the parent, which could cause a decrease in reproductive success (Drent and Daan, 1980).

Energy can also influence reproduction by its rate of use, e.g.the time spent foraging determines the amount of food (energy) caught, the time spent brooding chicks during the guard period determines the time spent foraging, and the distance to the foraging area must be balanced by the time taken to reach it and the energy used to do so (Ricklefs, 1974). The ability of a bird to obtain all of its energy requirements determines most of the aspects of its ecology, e.g.distribution, abundance, timing and length of the breeding season and intra- and interspecific competition. All the aspects of breeding and feeding are interrelated so that a change of one will affect the whole energy budget.

To assess the part played by a species in the energy flow through an ecosystem and determine some of the ways in which the energy budget of a species is related to its breeding and feeding strategies, a daily energy

budget must be estimated. This is the energy consumed and then used for an activity or conserved in the form of fat (Kendeigh and others, 1977). If the energy equivalents of each activity during the breeding season are known, the total daily energy requirements can be estimated (Kendeigh, 1974; Ricklefs, 1974).

Information on the bioenergetics of seabirds is difficult to obtain empirically since there are many factors which influence the total energy requirements and which are almost impossible to record. However, using theoretical relationships between body weight and metabolism (Lasiewski and Dawson, 1967; Kendeigh and others, 1977), it is possible to use measurements of the body weight of birds recorded during certain activities to give an indirect approximation of energy requirements.

During incubation and pre-laying attendance, adult Adélies and chinstraps fast for long periods (see Chapter 2). The rate of weight loss during this time is determined by the rate of energy use in basal and resting metabolism (Kendeigh and others, 1977). The aim of this chapter is to present data on the rate of weight loss during a fast and to use these empirical data to estimate the energy used during pre-laying and incubation fasts by Adélies and chinstraps. In addition, an indication of the rate of use of one of the energy stores in the body will be determined from weights of the Pectoralis major muscle taken at several stages in the breeding season from the bodies of birds killed for diet studies.

## METHODS

Energy consumption during pre-laying attendance and incubation was recorded by monitoring the decline in weight of a sample of adults while incubating.

Preparation of study nests

Three colonies of each species were selected, and a study group of 20 nests established in each, according to the same criteria used for the establishment of nests in the breeding biology study (see chapter 2). Nests and birds were also prepared in the same way.

Data collection

Each bird at the nest was weighed on the day it was marked, and subsequently on every third or fourth day, using the method described in chapter 2. In 1980/81, most of the chinstrap study birds abandoned their nests, so the process was repeated in 1981/82 at different colonies.

The adults killed for diet studies (see chapter 3) were dissected to remove a Pectoralis major muscle and to measure the thickness of the layer of subcutaneous fat laying over the top of the sternum. The change in the weight of the P.major and the thickness of the fat layer were examined for indications of the rate and extent of use of energy stores in the body during the course of the breeding season.

Data analysis

When plotted graphically, adult weight loss during fasts was found to be exponential but with two fairly distinct phases. The initial phase of rapid weight loss is accounted for by assimilation of food and excretion of unassimilated food and is linear, ie. a constant proportion of body weight was lost per day. The second phase of gradual weight loss is accounted for by metabolism of stored energy. Adult weight loss during the pre-laying attendance and incubation fasts was analysed in three ways. The initial weight and rate of weight loss were estimated by regression of the logarithm of weight against time :

a) for all birds weighed near to the beginning and end of a fast,

b) for birds weighed at least four times during a fast and

c) for all the weights of the study birds taken during a fast (each sample was weighted by n, where n = sample size of birds weighed on each day of a fast).

Weight loss was described as an exponential function of time, $Wt = Wo.e^{-kt}$, where Wt is the weight t days after the start of a fast, Wo is the weight at the start of a fast and k is the proportion of the weight of the bird lost per day. Rates of weight loss were compared intra- and inter- specifically and between years. For each of the regressions of the logarithm of weight against time, calculated using the third analysis method, the slope of the regression, i.e.the regression coefficient, and the standard error of the regression coefficient were obtained. The significance of the regression coefficient was tested by determining the ratio of the deviation of the slope from zero to the standard error of the regression coefficient. If the probability that a slope deviated from zero was greater than 95 %, the slope was used in further comparisons of weight loss between sexes and between shifts.

Metabolic rates were estimated using the weight lost during each fast, calculated from the slopes of the regressions, and estimates of the energy content of the weight lost. Groscolas and Clement (1976), working with fasting emperor penguins, estimated that the composition of the material lost was 55 % fat and 9.2 % protein, with water comprising the residue. This is used here to calculate a lower limit to the energy costs of fasting by Adélies and chinstraps. The assumption that all material lost is fat is used to calculate an upper limit to energy costs. The energy content of fat and protein was taken as 39.7 kJ $g^{-1}$ and 16.7 kJ $g^{-1}$, respectively (Petrusewicz and Macfadyen, 1970). Using the weight at the mid-point of a fast, calculated from the regressions of the logarithm of weight against time, basal metabolic rate (BMR) and existence metabolic rate (EMR) were also estimated using the theoretical relationships for non-passerines at 0°C : $BMR = 4.18\ (0.5224\ Wt^{0.7347})$ and $EMR = 4.18\ (4.142\ Wt^{0.5444})$,

where metabolic rates are in kJ $d^{-1}$ and Wt is the weight in g at the mid-point of a fast (Kendeigh and others, 1977).

The second and third methods of analysis of rate of weight loss during fasts use data recorded throughout the whole of a fast, whereas the first method only analyses data using the weight of adults near the beginning and end of fasts. The first method is better for calculations of energy consumption since only the weights of birds for which the weights were taken at or near both the beginning and the end of a fast are used, which gives a more accurate estimate of the total weight lost during a fast.

## RESULTS

### 1. Weight loss during pre-laying attendance and incubation fasts

During the early part of the breeding season, both species fast for extended periods. During chick rearing, birds of either sex may remain at the nest and go without food for three or four days, but rarely for longer than this. The extended fasting periods by birds of each sex comprise a pre-laying fast and one (Adēlie) or two (chinstrap) fasts during incubation. The actual rate of weight loss and theoretical rate of energy consumption during each of these fasts was calculated using the three methods of analysis. Results are given in Appendices 6.1-6.3. The relationships between weight and time spent fasting, calculated using the second and third analysis methods, are given in Figures 6.1-6.6.

Because the sample sizes using the second analysis method were small, inter- and intraspecific comparisons of weight loss by chinstraps are not possible, but Appendix 6.2 shows that, in 1980/81, incubating Adēlie females lost weight at a rate of 2.0 % per day, which was nearly twice the rate of weight loss by incubating males ($P<0.001$). Analyses using the third method (Figures 6.4-6.6 and Appendix 6.3) show that, in 1980/81, the

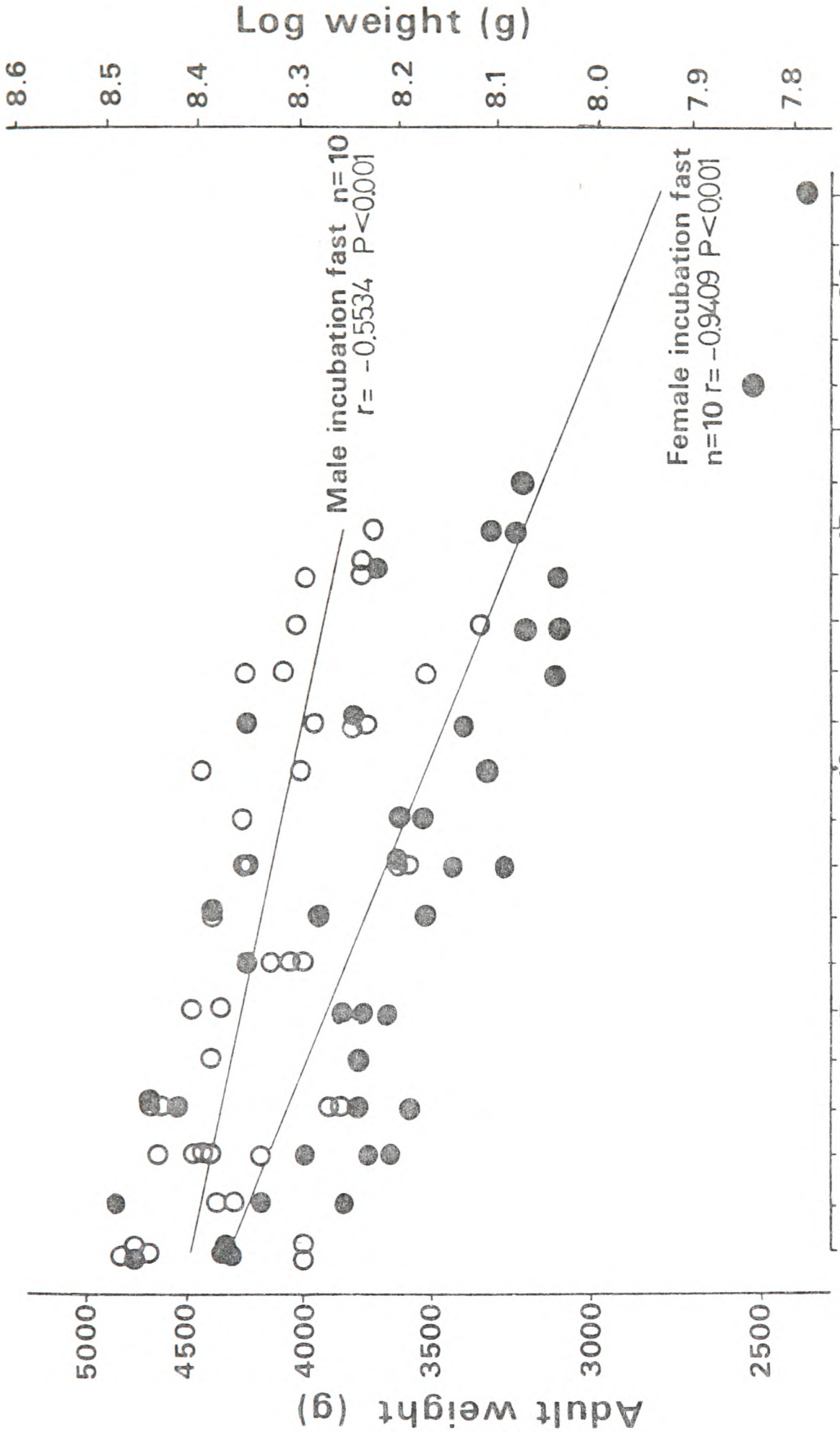



Figure 6.1. The weight loss of fasting Adélies in 1980/81 (each bird weighed at least four times during a fast). (s = rate of weight loss ($\%d^{-1}$).)

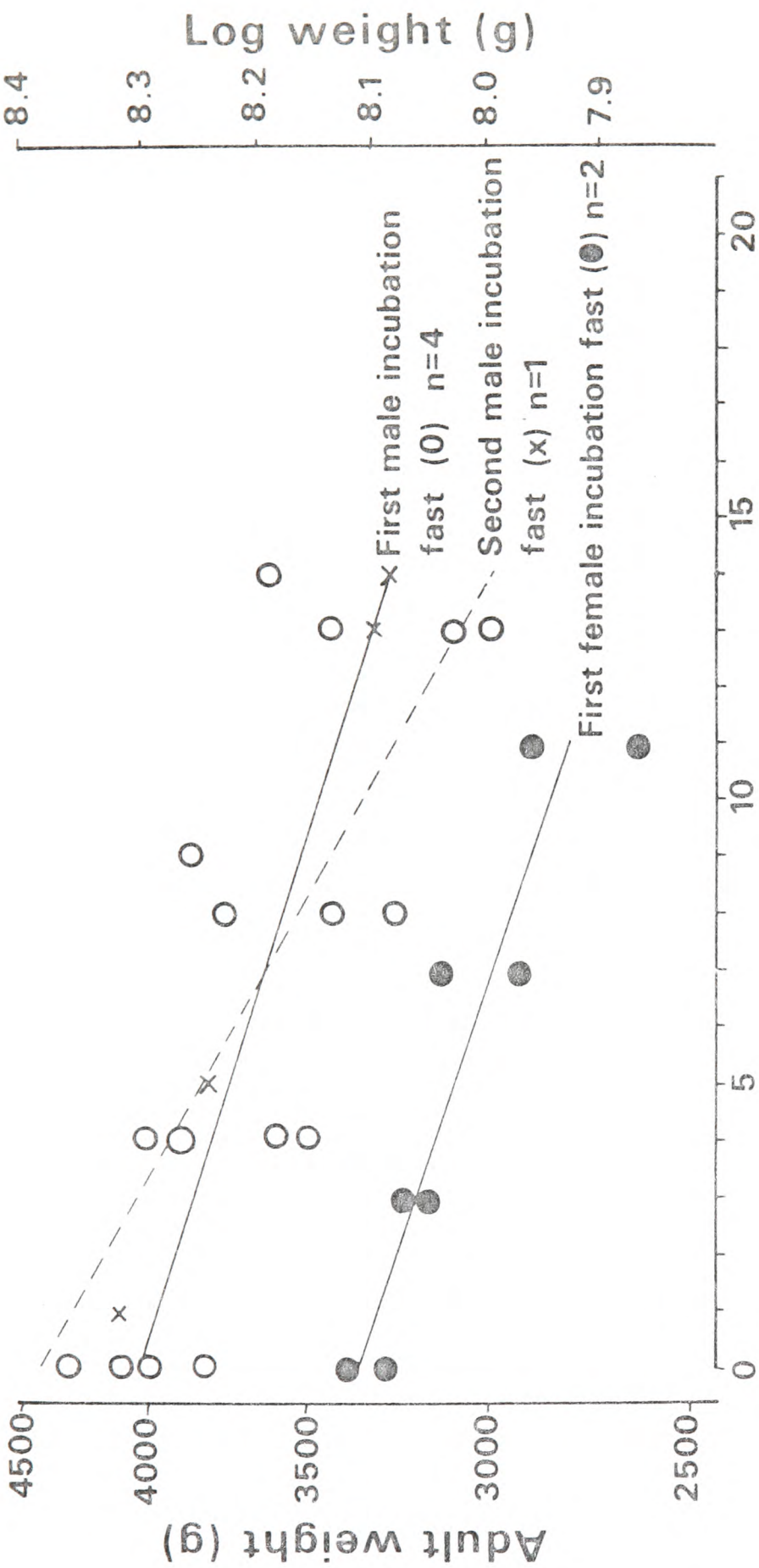



Figure 6.2. The weight loss of fasting chinstraps in 1980/81 (each bird weighed at least four times during a fast; first male incubation fast: $s = 1.85$; $r = -0.7539$, $P<0.001$; second male incubation fast: $s = 2.50$; $r = -0.9180$, $P<0.001$; first female incubation fast: $s = 1.68$; $r = -0.9108$, $P<0.02$; $s$ is rate of weight loss (% $d^{-1}$).)

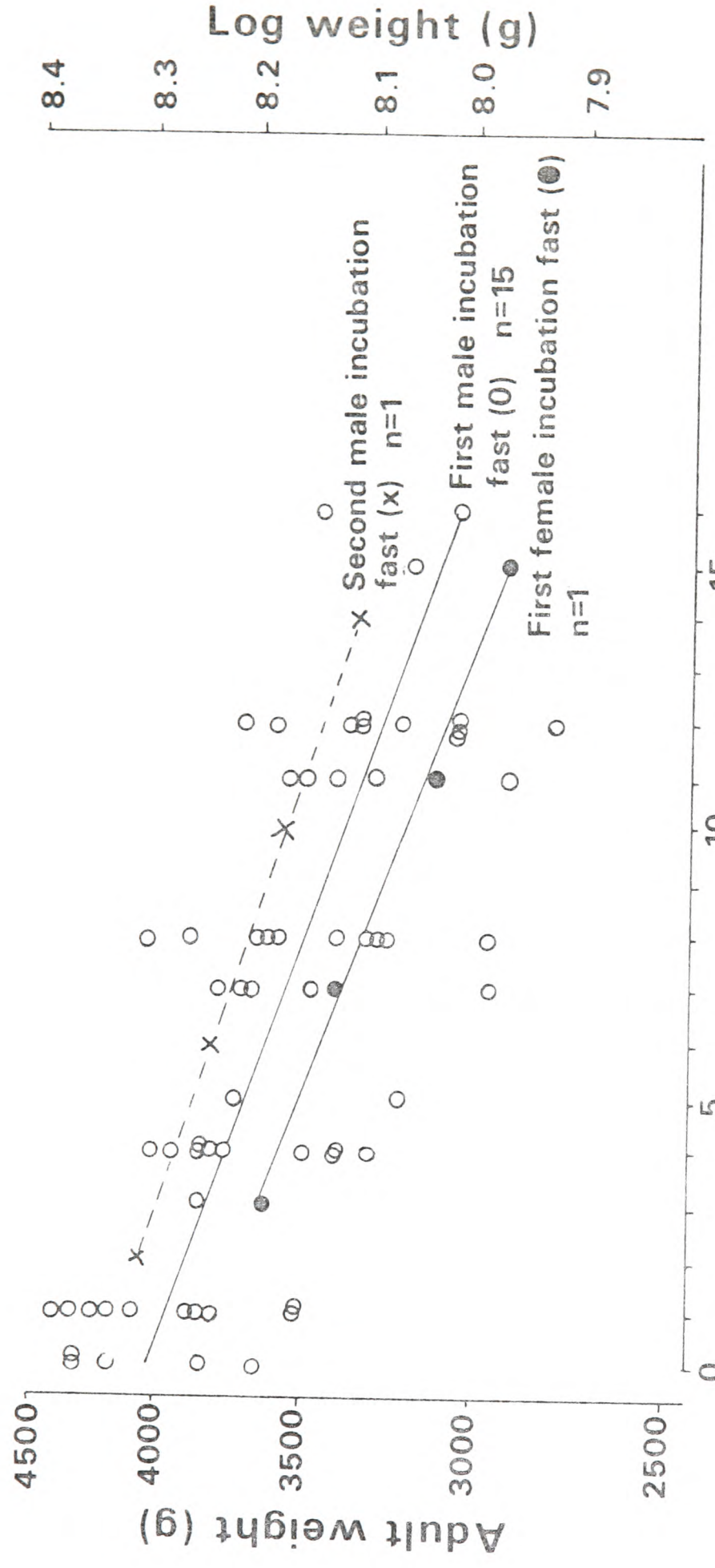



Figure 6.3. The weight loss of fasting chinstraps in 1981/82 (each bird weighed at least four times during a fast; first male incubation fast: $s = 1.75$; $r = -0.6892$, $P<0.001$; second male incubation fast: $s = 1.65$; $r = -0.9955$, $P<0.001$; first female incubation fast: $s = 1.90$; $r = -0.9984$, $P<0.001$; $s$ is rate of weight loss (% $d^{-1}$).)

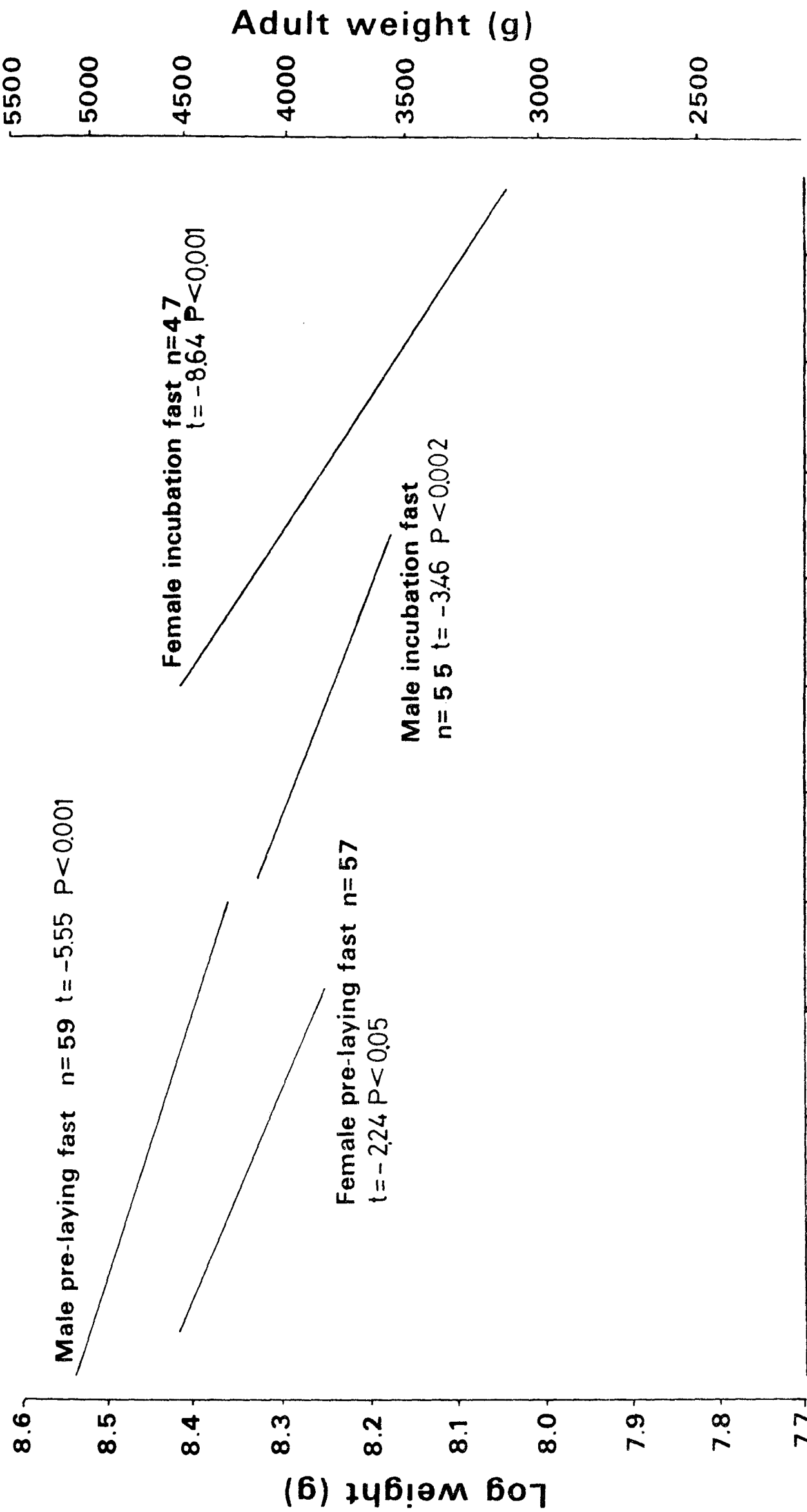



Figure 6.4. The weight loss of fasting Adélies in 1980/81 (regression of all the recorded adult weights). (n = number of recorded weights.)

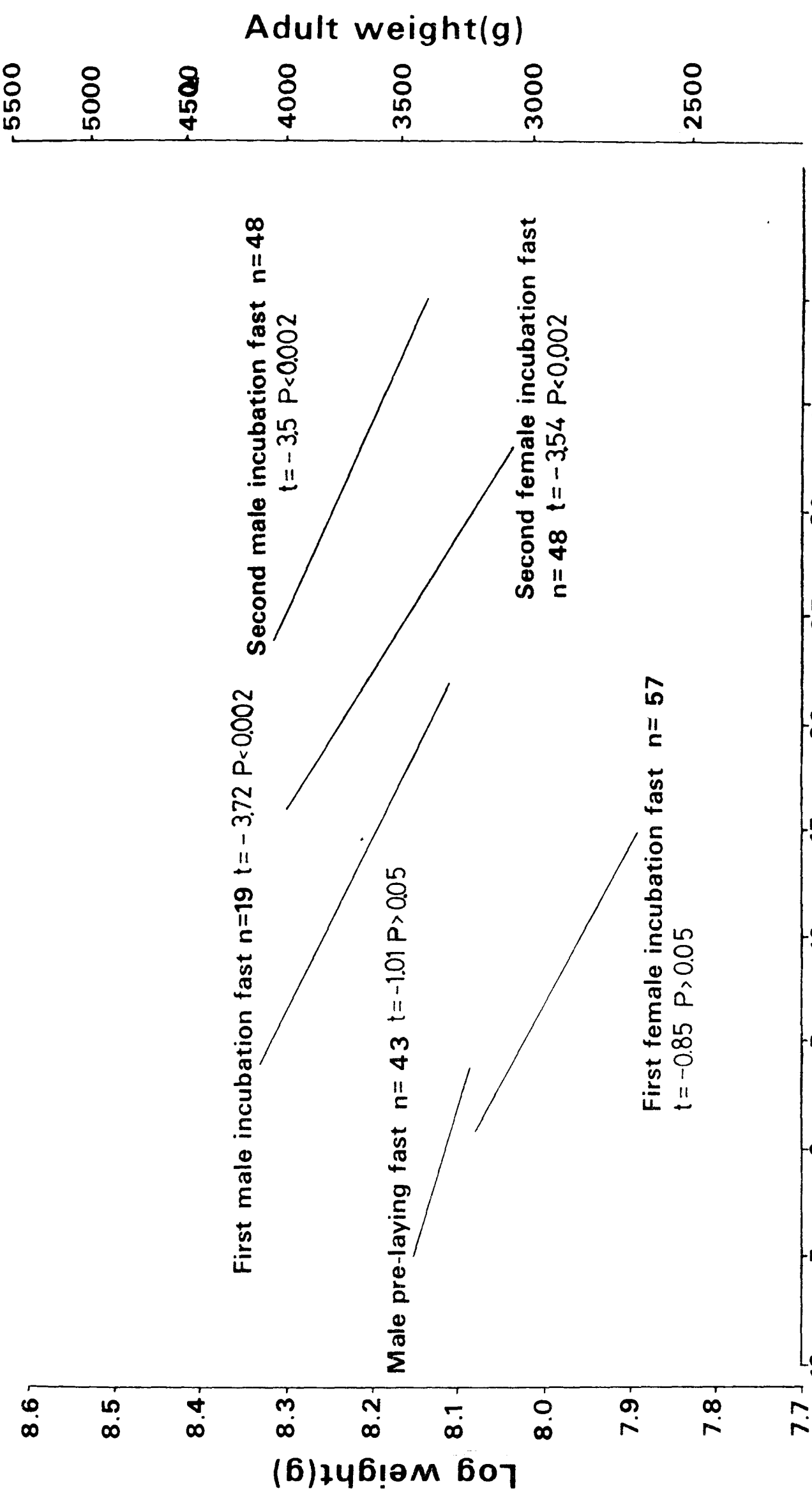



Figure 6.5. The weight loss of fasting chinstraps in 1980/81 (regression of all the recorded adult weights). Note: weight loss during the female pre-laying fast was not recorded; n = number of recorded weights.

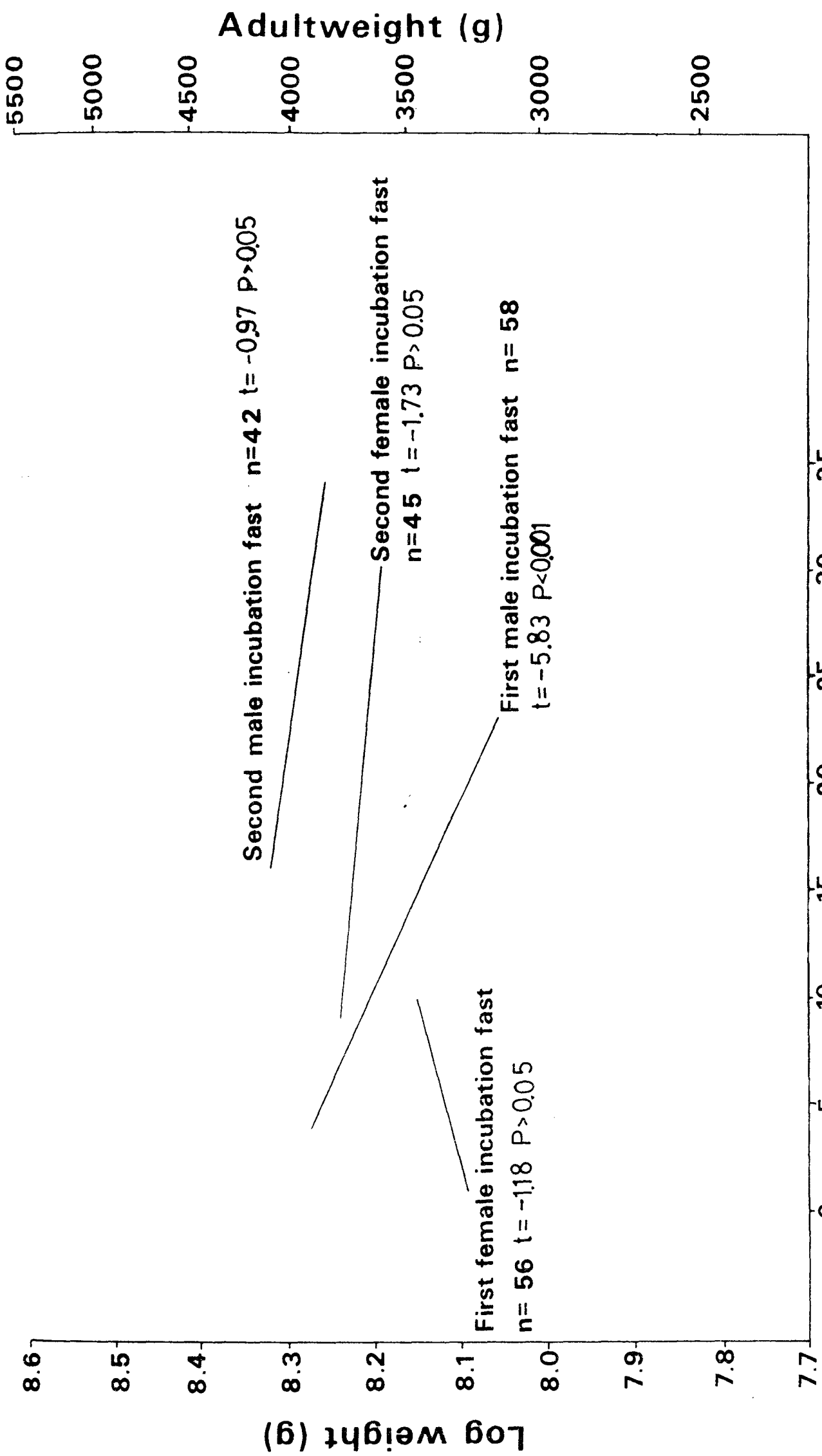



Figure 6.6. The weight loss of fasting chinstraps in 1981/82 (regression of all the recorded adult weights). (n = number of recorded weights.)

rate of weight loss was the same during all fasts by the same sex ($F = 0.234$, $P<0.05$), but that females lost weight faster than males (Adélies : females 1.58 % $d^{-1}$, males 0.84 % $d^{-1}$ ; chinstraps : females 1.45 % $d^{-1}$, males 1.10 % $d^{-1}$ ; $F = 5.97$, $P<0.05$). In 1981/82, chinstrap female weight appears to increase during a fast. This probably occurred because some birds were not reweighed at the end of a fast which resulted in a sample with a biased distribution of weights. Between years, male chinstraps lost weight faster in 1980/81 (1980/81 : 1.10 % $d^{-1}$, 1981/82 : 0.98 % $d^{-1}$; $F = 6.66$, $P<0.05$).

The values for energy consumption during fasts, from the first analysis method, are given in Table 6.1. These were obtained from large sample sizes in all cases, unlike those from the second analysis method, and do not contain any biased results, as is the case for chinstrap females in 1981/82 calculated using the third analysis method. Metabolic rates calculated by the first analysis method are therefore used in further comparisons and calculations. All the upper values are greater than theoretical EMR but all the lower values are within 37% and, for all except three of them, this is closer than the upper values to theoretical EMR. The exceptions are Adélie males and chinstrap males in pre-laying attendance. In 1980/81, the energy consumption of females of both species was usually greater than that of males, but there was no overall difference between the species. Between years, the energy consumption of chinstrap males was greater in 1981/82 than in 1980/81. The heaviest sex of both species has a lower rate of energy consumption, but the relationship between body weight and theoretical BMR gives the opposite result. Thus, within each species, the heavier sex has a lower ratio of recorded values of metabolic rate to theoretical BMR (Table 6.2). The same is also true for the heavier species since, if it is assumed that the recorded lower values of energy consumption represent the daily energy cost of incubation, in 1980/81 the energy consumption (cost) of chinstraps during incubation

| Species/ Year | Sex/ Fast* | Energy consumption ($kJd^{-1}$) Calculated Lower | Calculated Upper | Theoretical Basal | Theoretical Existence | Wt. (g) at mid-point of fast | Specific EMR($Wkg^{-1}$) | Mean for each: Sex | Mean for each: Species |
|---|---|---|---|---|---|---|---|---|---|
| Adélie | F 1 | 1515 | 2548 | 982 | 1647 | 4081 | 4.67 | | |
| | | | | | | | | | 4.52 |
| 1980/81 | M 1 | 1197 | 2017 | 1093 | 1781 | 4724 | 4.36 | | |
| | F 2 | 1665 | 2803 | 965 | 1580 | 3987 | 4.59 | | |
| | | | | | | | | | 4.58 |
| | M 2 | 1105 | 1858 | 969 | 1585 | 4010 | 4.57 | | |
| Chinstrap | M 1 | 1092 | 1837 | 917 | 1545 | 3721 | 4.81 | | 4.88 |
| 1980/81 | F 2 | 1761 | 2966 | 801 | 1376 | 3093 | 5.15 | | |
| | | | | | | | | 5.05 | |
| | F 3 | 1674 | 2820 | 849 | 1437 | 3351 | 4.96 | | |
| | | | | | | | | | 4.86 |
| | M 2 | 1485 | 2502 | 915 | 1519 | 3708 | 4.74 | | |
| | | | | | | | | 4.67 | |
| | M 3 | 2146 | 3615 | 956 | 1569 | 3938 | 4.61 | | |
| Chinstrap | F 2 | 1134 | 1908 | 854 | 1442 | 3373 | 4.95 | | |
| | | | | | | | | 4.84 | |
| 1981/82 | F 3 | 1795 | 3021 | 916 | 1519 | 3713 | 4.73 | | |
| | | | | | | | | | 4.77 |
| | M 2 | 1841 | 3100 | 898 | 1498 | 3615 | 4.80 | | |
| | | | | | | | | 4.71 | |
| | M 3 | 2054 | 3456 | 954 | 1569 | 3925 | 4.63 | | |

* Fast 1 is pre-laying attendance, fasts 2 and 3 are incubation fasts.

Table 6.1. The calculated and theoretical values of energy consumption during pre-laying and incubation fasts (first analysis method). (Lower values of energy consumption were calculated on the basis that the consumption of the material lost during fasting was 55% fat and 9.2% protein and upper values assuming all material lost is fat; theoretical energy consumption was calculated using the weight at the mid-point of a fast and theoretical equations for BMR and EMR; specific EMR was calculated using the weight at the mid-point of a fast; W = watts.)

| Species | Year | Sex/ Fast* | Ratio calculated MR : BMR | | |
|---|---|---|---|---|---|
| | | | Mean | Sex mean | Species/year mean |
| Adélie | 1980/81 | F 1 | 1.57 | 1.64 | 1.39 |
| | | F 2 | 1.71 | | |
| | | M 1 | 1.24 | 1.14 | |
| | | M 2 | 1.03 | | |
| Chinstrap | 1980/81 | F 2 | 2.20 | 2.06 | 1.86 |
| | | F 3 | 1.92 | | |
| | | M 1 | 1.27 | 1.72 | |
| | | M 2 | 1.62 | | |
| | | M 3 | 2.28 | | |
| Chinstrap | 1981/82 | F 2 | 1.33 | 1.65 | 1.87 |
| | | F 3 | 1.96 | | |
| | | M 2 | 2.05 | 2.10 | |
| | | M 3 | 2.15 | | |

* Fast 1 is pre-laying attendance, fasts 2 and 3 are incubation fasts.

Table 6.2. The ratios of calculated and predicted metabolic rates.

was 1.9 times theoretical BMR and the cost to the heavier Adélie was 1.4 times theoretical BMR. The value for Adélies is similar to that for Adélie males calculated from Bougaeff (1975) in Croxall (1982). The value for chinstraps is higher than the range of 1.33-1.60 given for incubating and fasting penguins in Croxall (1982). However, in terms of energy use per kg of body weight, the metabolic rate of the two species is very similar. If the mean weight of Adélies and chinstraps during incubation is taken as 4.0 and 3.5 kg, respectively, and the average BMR during incubation in 1980/81 is taken as 967 kJ $d^{-1}$ for Adélies and 880 kJ $d^{-1}$ for chinstraps (mean theoretical BMR estimated from all incubation fasts - see Table 6.1), the weight-specific metabolic rates are 2.8 W $kg^{-1}$ and 2.9 W $kg^{-1}$, respectively. Specific existence metabolic rate (EMR) during pre-laying attendance and incubation can be calculated in a similar way. The values of these for males and females of both species are given in Table 6.1.

During fasts, birds lost up to 29 % of their body weight. However, Table 6.3 shows that there was no major decline in weight over the period from laying to hatching. This is because most of the reserves consumed during each fast are replenished before the next fast.

2. Energy supply during pre-laying attendance and incubation fasts.
The energy expended during fasting, brooding and foraging is supplied from the metabolic breakdown of fat deposits and muscle protein. Measurement of the thickness of subcutaneous fat of both species showed that the layer decreased from about 7 mm to zero during a breeding season.

There was also a significant decrease in the weight of the Pectoralis major muscle during the breeding season (Figure 6.7), except for Adélies in 1980/81. The weight of the P.major was compared with body weight (Figure 6.8) to determine how this decrease was related to the overall decline in adult body weight during the breeding season. In both years, chinstrap P.major, as a proportion of body weight, decreased significantly (1980/81 :

| Fast | | Adélie 1980/81 Female Mean sd. No | Adélie 1980/81 Male Mean sd. No | Chinstrap 1980/81 Female Mean sd. No | Chinstrap 1980/81 Male Mean sd. No | Chinstrap 1981/82 Female Mean sd. No | Chinstrap 1981/82 Male Mean sd. No |
|---|---|---|---|---|---|---|---|
| Pre-laying | Start | 4522 271 57 | 5105 198 59 | No data | No data | No data | No data |
| | Finish | 3631 253 27 | 4343 298 49 | | 3321 273 20 | | |
| | Length(d) | 22.0 | 16.0 | | | | |
| | Decrease(%)* | 19.7 | 14.9 | | | | |
| First incubation | Start | | 4339 225 48 | 3384 301 37 | | 3541 360 15 | |
| | Finish | | 3681 206 | 2803 278 | | 3206 221 | |
| | Length(d) | | 15.0 | 9.4 | | 7.5 | |
| | Decrease(%)* | | 15.2 | 17.2 | | 9.5 | |
| First incubation | Start | 4424 191 44 | | | 4056 350 17 | | 4053 294 15 |
| | Finish | 3550 171 | | | 3369 327 | | 3178 338 |
| | Length(d) | 13.6 | | | 12.3 | | 13.7 |
| | Decrease(%)* | 19.8 | | | 16.9 | | 21.6 |
| Second incubation | Start | | | 3626 310 10 | | 3851 - 1 | |
| | Finish | | | 3076 309 | | 2733 - | |
| | Length(d) | | | 9.6 | | 19.0 | |
| | Decrease(%)* | | | 15.2 | | 29.0 | |
| Second incubation | Start | | | | 4394 420 9 | | 4189 - 1 |
| | Finish | | | | 3482 453 | | 3165 - |
| | Length(d) | | | | 10.6 | | 18.0 |
| | Decrease(%)* | | | | 20.8 | | 24.4 |

* percentage of body weight lost during a fast

Table 6.3. The weight of adults at the start and finish of pre-laying and incubation fasts, the mean length of each fast and the mean percentage of body weight lost during each fast.

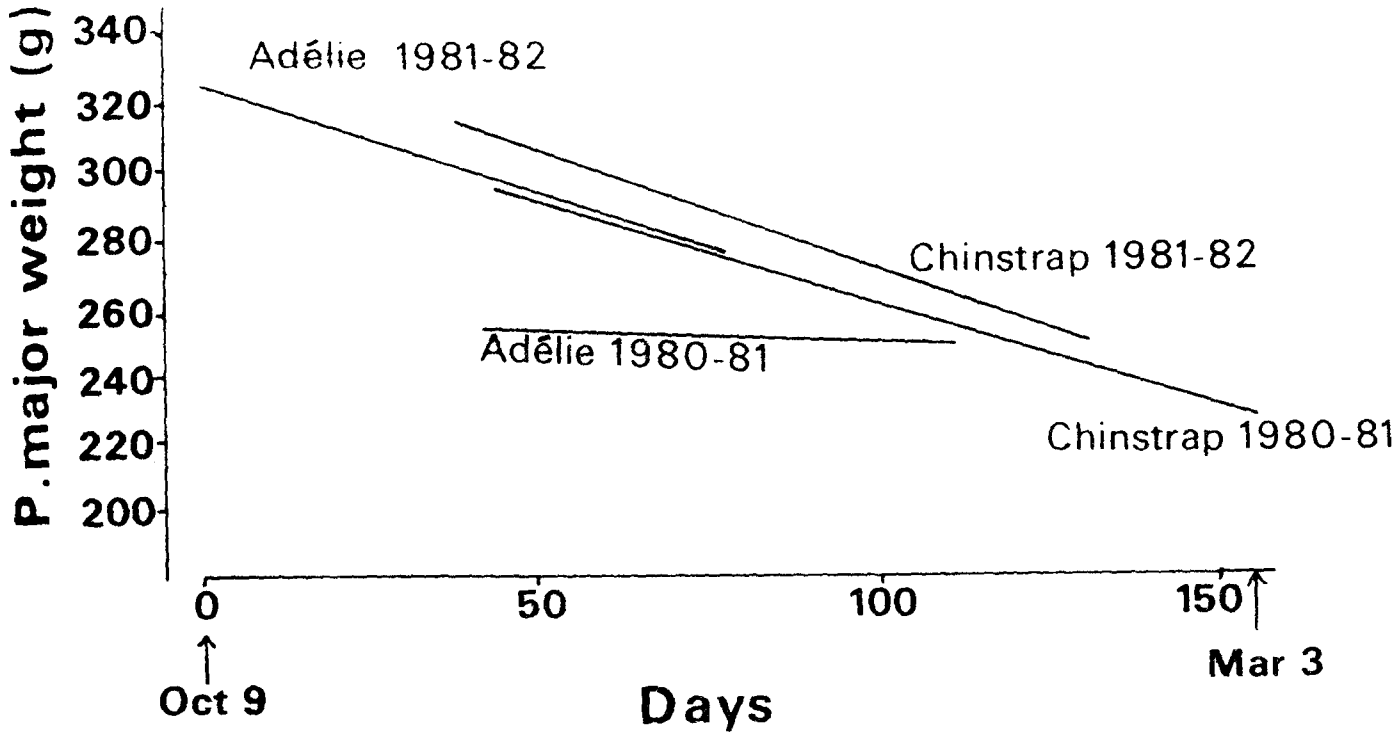



Figure 6.7. The weight loss of the Pectoralis major muscle during the breeding season. (s = rate of weight loss (g $d^{-1}$).)

| | | n | r | P | s |
|---|---|---|---|---|---|
| Adélie | 1980/81 | 18 | 0.045 | >0.05 | -0.07 |
| | 1981/82 | 25 | 0.495 | <0.01 | -0.60 |
| Chinstrap | 1980/81 | 28 | 0.469 | <0.01 | -0.58 |
| | 1981/82 | 25 | 0.675 | <0.001 | -0.69 |

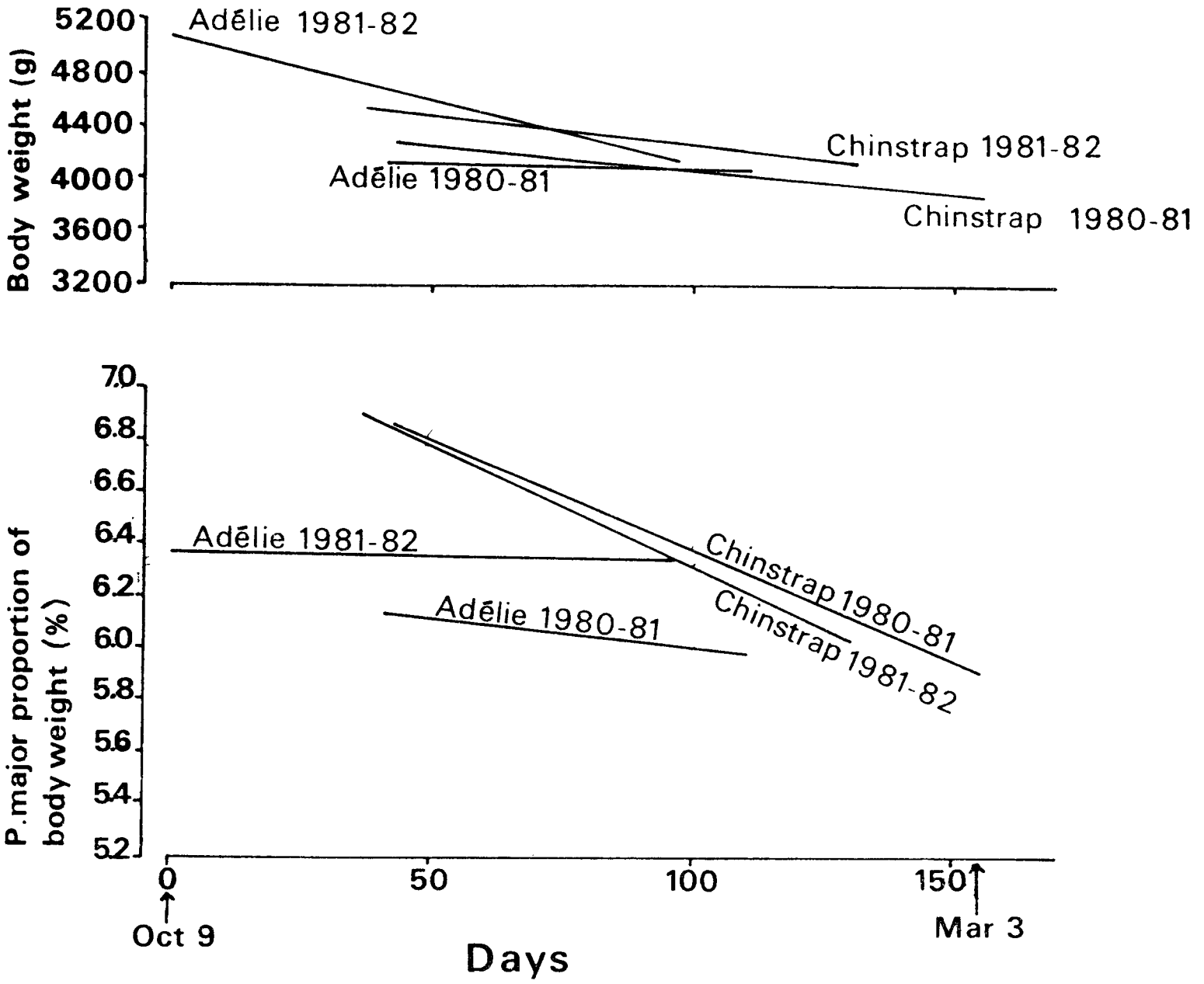



Figure 6.8. Body weight loss and proportional Pectoralis major weight loss. (s = rate of weight loss (g $d^{-1}$ and % $d^{-1}$).)

| | | Body weight | | | | P.major proportion | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | n | r | P | s | n | r | P | s |
| Adélie | 1980/81 | 27 | 0.121 | >0.05 | -0.89 | 18 | 0.087 | >0.05 | -0.002 |
| | 1981/82 | 25 | 0.621 | <0.001 | -8.82 | 25 | 0.004 | >0.05 | -0.0002 |
| Chinstrap | 1980/81 | 40 | 0.096 | >0.05 | -3.56 | 28 | 0.501 | <0.01 | -0.008 |
| | 1981/82 | 25 | 0.401 | <0.05 | -4.74 | 25 | 0.664 | <0.001 | -0.009 |

$P<0.01$ ; 1981/82 : $P<0.001$). Chinstrap body weight decreased significantly in 1981/82 but not in 1980/81 (Figure 6.8), so the decrease in P.major weight was greater in relation to body weight in 1980/81. Body and P.major weight of Adélies both decreased significantly at similar rates in 1981/82, so P.major weight as a proportion of body weight remained the same. In 1980/81, body and P.major weight of Adélies remained the same, and so, therefore, did the proportion of P.major weight.

## DISCUSSION

### 1. Weight loss

Adélies and chinstraps both lost about 1.2 % of their body weight per day during pre-laying and incubation fasts. This is close to the results of studies on Adélie (Bougaeff, 1975) and macaroni penguins (Croxall, 1982) and similar to results from a study of the incubation weight loss of black-browed and grey-headed albatrosses at Bird I (Prince and others, 1981). These two species are of similar weights to Adélies and chinstraps (3.6-3.9 kg) and lost 1.0-1.3 % of body weight per day. The heavier wandering albatross Diomedea exulans (7.4-10.6 kg) loses 0.8-1.0 % of body weight per day during incubation (Croxall and Ricketts, 1983). These values and those for Adélies and chinstraps from this study are close to predictions from theoretical equations (Lasiewski and Dawson, 1967; Kendeigh, 1970; Kendeigh and others, 1977) that metabolic rate of species, and hence rate of weight loss, decreases with increase in body weight of species. Male chinstraps lost weight during incubation fasts at a faster rate in 1980/81 than in 1981/82. It is likely that this was due to the ice conditions in 1980/81. The fat content of incubating male Adélies decreases from 45 % of dry weight on arrival at the colony to c20 % after 27 d (Johnson and West, 1973). Although it is likely that most of this fat

is replenished before the next fast, it is unlikely that it would be restored to the same level in the relatively short time between fasts, especially if the fasts have been unusually long. Bougaeff (1975) shows that the rate of weight loss by Adélies during incubation increases after a certain number of days, possibly due to the exhaustion of lipid reserves and the onset of protein metabolism. Under normal circumstances, birds are relieved at the nest and finish fasting before this stage is reached. However, in 1980/81, some chinstrap males fasted for as long as 23 days and then abandoned the nest after losing 38% of body weight. If protein was metabolised during the last few days of these long fasts, this might account for the greater overall rate of weight loss in 1980/81.

Of the calculated values of energy consumption, the lower values were usually close to the theoretical values of EMR. The lower values were calculated on the basis that the composition of material lost comprised 55.5 % fat and 9.2 % protein (Groscolas and Clement, 1976). Where there is close agreement between the calculated and theoretical values it is likely that the theoretical values are a reasonable approximation to the actual proportion of fat and muscle broken down to provide energy during fasting. The mean ratio of calculated metabolic rate to theoretical BMR for chinstraps is 1.9, compared with 1.4 for Adélies. While this may be partly due to the lighter species having a higher metabolic rate, as ratios are 1.3-1.6 for most other penguins (Croxall, 1982), then it is possible that the assumption that the material lost by chinstraps comprised 55.5 % fat and 9.2 % protein is incorrect, and that it perhaps comprised smaller proportions of fat and protein. There is no evidence to support this, however.

2. Energy supply

Although there is no reason to suggest that there is a difference in the proportion of fat and muscle stores used by the two species, it appears

that there was some difference in the method of energy supply. In 1981/82, the gradual decrease in body weight indicates that both species were using up stored energy reserves. P.major weight also decreased, so at least some of the energy supply came from this muscle, although it is not known what proportions of the material lost were fat and protein. Since chinstrap P.major weight decreased at a greater rate than body weight, it is likely that the P.major was used as a major source of energy supply. Adélie P.major weight decreased at the same rate as body weight, which suggests energy was supplied from the P.major but to a lesser extent than in chinstraps. In 1980/81, chinstrap P.major weight again decreased at a greater rate than body weight, so the method of energy supply was probably the same. Adélie P.major and body weight remained the same, which suggests that enough food was caught to make the use of stored energy reserves unnecessary. However, it seems strange that this should happen in a year with adverse ice conditions, but not in a normal ice year.

## CONCLUSIONS

Adélies and chinstraps undertake long incubation and pre-laying fasts which, for Adélies, may be an adaptation to breeding where ice conditions can delay travel between colony and foraging area. Fast length may also be determined by metabolic rate since it has been suggested that the composition of the weight lost during a fast changes from mainly fat to mainly protein after a certain time. Weight lost through protein metabolism is probably more difficult to replace than that lost during fat metabolism, so adults may finish incubating before protein metabolism starts.

Both species lost about 1.2 % of their body weight on each day of a fast which is close to results of studies on other birds of similar

weight. Ice conditions were probably the cause of an increase in weight loss rate by chinstraps in 1980/81. The estimated fasting energy consumption of Adēlies is close to predictions from theoretical equations but that of chinstraps was higher in both years, a possible explanation being that the composition of the material lost was different from the estimates used. The source of the material lost by the two species may also have been different, with the P.major being used by chinstraps for an energy supply but with relatively less use being made of stored energy reserves by Adélies.

# Chapter Seven

## Food consumption and energy requirements

# INTRODUCTION

Since the energy requirements of birds is high, they may consume a disproportionate amount of food for their size, such that their consumption of organisms from lower trophic levels is greater than that of other animals of the same size. The diet and activities of Adélie and chinstrap penguins outside the breeding season are almost totally unknown, so the complete energy budget cannot be determined. However, using information gathered on the costs of activities, duration of each activity and population sizes, most of the adult energy requirements during the breeding season can be estimated and used to determine the total amount of krill that might be consumed by Adélies and chinstraps during the breeding season.

The aims of this chapter are to estimate the energetic cost of various activities during the breeding season, to determine how the energy budget of Adélies and chinstraps may be related to their breeding and feeding strategies, and compare the energy consumption values interspecifically and with those estimated for Adélies at other breeding localities; the energy consumption values presented here for chinstraps are the first to be recorded for the species.

The importance of penguins as consumers of krill in the South Orkneys will also be examined, by using the estimates of the energy consumption of various activities during the breeding season, the duration of each activity and the population of Adélies and chinstraps in the South Orkneys and determining the impact of Adélies and chinstraps in relation to the other krill-eating species breeding in the South Orkneys.

The adult energy budget during the breeding season comprises the energy used during a) pre-laying attendance, b) egg laying, c) incubation, d) brooding, e) the pre- and post-fast accumulation of fat reserves, f) foraging (both for the bird itself and for the chick) and g) post-fledging moult (although, strictly, this is not during the breeding season). All

the energy comes from the food caught during foraging.

Many of these components have been calculated or estimated here, with the exception of the cost of egg laying to the female. Since Adélies do not moult at Signy, and it proved impossible to collect data on chinstrap moult, the costs of moult by Adélies and chinstraps at Signy are also still unknown.

An energy budget includes the energy requirements of growing chicks, which must be satisfied by the adults. Data on chick meal size and feeding frequency were used to calculate the total food intake of chicks. The energy equivalent of this was compared with estimates of the total foraging energy expenditure of adults. While it was possible to record the total food intake of chicks, the proportion of that food partitioned into energy for growth, energy for existence metabolism and waste products in the form of respiratory heat and faeces cannot be determined without the use of the results of studies of the calorific content of chicks at all stages of development, and these could not be carried out in the field.

The diet of Adélies and chinstraps at Signy consists almost entirely of krill and the consumption of krill during the breeding season by an individual of each species is estimated in this chapter. To assess the relative importance of the role played by Adélies and chinstraps in predation of the food resources of the South Orkneys, it is necessary to estimate the total consumption of food by all species feeding there. Several computer simulation models have been used to calculate the daily energy requirements of seabirds (Wiens and Scott, 1975; Furness, 1978). The most recent of these is an evaluation of the food consumption of the breeding population of seabirds and seals on the marine resources of the Scotia Sea (Croxall and others, in press c). This same model has been used here, using input data for seabirds breeding at the South Orkneys, to assess the krill consumption of Adélies and chinstraps, in particular, and the variation of this consumption during an annual cycle.

# METHODS

## 1. Energy consumption

### a. Adults

Apart from energy consumption during pre-laying attendance and incubation, which was estimated using empirical data in chapter 6, breeding penguins fast when at the nest during the guard period. The weight loss during all these fasts is replaced while foraging at sea. Foraging to replace this weight and for the chick also uses energy. Energy consumption between return to the colony at the start of the breeding season and chick fledging thus comprises four types of energy cost: pre-laying existence metabolic rate (PEMR), incubation existence metabolic rate (EMR), brooding existence metabolic rate (BEMR) and average daily metabolic rate (ADMR).

The daily energetic cost of brooding (BEMR) was calculated theoretically using $4.18(a - bt)$, where $a = 4.142\ Wt^{0.5444}$, $b = 0.2761\ Wt^{0.2818}$, t is the ambient temperature in °C and Wt is the average adult weight during brooding (Kendeigh and others, 1977). It is assumed that adults restore the weight lost during brooding fasts in the same way that they do so after incubation fasts. However, since there tends to be a gradual loss of weight by the adults as the breeding season progresses, the weights of adults returning from foraging trips (Table 7.1 - data from chapter 3), rather than the incubation weights recorded earlier in the breeding season, are used in the estimations of BEMR. Similarly, where empirical data were absent, the pre-laying attendance metabolic rate (PEMR) was calculated in this way, using the average adult weight during the pre-laying attendance period.

The ADMR at sea comprises the energetic costs to the adult of foraging for the chick and itself and the replacement of weight lost during fasts, and depends on the calorific composition of the diet. It was found (by Davis and others (1983)) to be 2.9 times standard metabolic rate (SMR)

| Species | Year | | Adult weight (kg) Female | Male |
|---|---|---|---|---|
| Adélie | 1980/81 | Mean | 3.843 | 4.356 |
| | | sd. | 0.253 | 0.345 |
| | | No | 6 | 14 |
| Chinstrap | 1980/81 | Mean | 3.671 | 4.273 |
| | | sd. | 0.397 | 0.217 |
| | | No | 8 | 14 |
| Chinstrap | 1981/82 | Mean | 3.750 | 4.279 |
| | | sd. | 0.071 | 0.249 |
| | | No | 3 | 7 |

Table 7.1. The weight of adults on return from foraging trips made during the chick rearing period.

(effectively equal to BMR (Kendeigh and others, 1977)) for the macaroni penguin, which is a krill-eating penguin of similar mass to the Adélie and chinstrap penguin. It was therefore assumed that Adélie and chinstrap ADMR was also equal to 2.9 times SMR. To estimate ADMR, BMR was recalculated using the weights given in Table 7.1, since the birds lose some weight between incubation and foraging.

To estimate the total energy requirement of each sex of both species during the breeding season, the energy costs (PEMR, EMR, BEMR and ADMR) were multiplied by the amount of time spent in each activity. The length of each fast was recorded by daily observation of the bird at the nest, and the number of foraging trips and time spent foraging was determined from the feeding frequency and the length of the guard and crêche periods. Since there was fairly close agreement of theoretical EMR's and those calculated from actual weight loss data, and assuming that material lost comprised 55.5 % fat and 9.2 % protein, fasting EMR's calculated from emprical data in chapter 6 were used in the estimates of total energy requirements. It was assumed that foraging and brooding were shared equally between the sexes during the guard period and that adults spent a negligible amount of time in the colony during the crêche period.

The amount of krill needed to replace the energy lost due to fasting and foraging was calculated from the calorific value of krill, which equals 4.6 kJ $g^{-1}$ wet weight (Clarke and Prince, 1980), and assuming an 80 % assimilation efficiency. This value was based on energy assimilation measurements of Adélie chicks (Costa in Kooyman and others, 1982).

b. Chicks

Meal size and frequency of feeds to chicks were calculated from daily weighings in chapter 4. These were used to calculate the total chick food intake from adults over the whole of the fledging period. This was then compared with estimates of the total amount of food provided by adults over

the fledging period, obtained from the weight of krill in the stomachs of birds killed in the course of diet studies (chapter 3).

2. Consumption of krill by Adélies and chinstraps

Much of the data used in the model to determine the amount of krill consumed by Adélies and chinstraps at the South Orkneys was similar to that used by Croxall and others (in press c). Thus, population estimates are from Croxall and others (in press b); sex specific weights during the various activities of the breeding season are from this study, for Adélies and chinstraps, and B.A.S. (unpublished data) for the other species; diet compositions (by weight) are from this study and from Croxall and Prince (1980 b), Croxall (1983) and Shaw (unpublished data); empirical energy consumption values are, with the exception of moult, from this study for Adélies and chinstraps and from Croxall (1982), Davis and others (1983) or B.A.S. (unpublished data) for Adélie and chinstrap moult and the values for the other species; theoretical energy consumption values are based on equations from Kendeigh and others (1977), as described in Croxall and Prince (1982), and the nature and timing of the activities in the annual cycle are from this study or Croxall and others (in press d). Data on the mortality rates of eggs and chicks from Pinder (1966), Beck and Brown (1972), Croxall and Prince (1980 a) and B.A.S. (unpublished data) were taken into account when estimating foraging energy expenditure. Migratory species were assumed to leave the South Orkneys after their chicks had fledged, but penguins were assumed to remain and forage in the vicinity throughout the non-breeding period. This could overestimate annual food consumption, but is probably balanced by the consumption of failed breeders, pre-breeding and non-breeding birds, which were not accounted for.

Input data were used to calculate the energy consumption at the South Orkneys on each day of the year of each sex of each species breeding there. This was converted to food consumption using the composition and

energy values of the diet of each species, and assuming an average assimilation efficiency of 75 % (although Costa in Kooyman and others (1982) estimated the assimilation efficiency of Adélies as 80 %).

## RESULTS

### 1. Adults

#### a. Brooding fasts

BEMR and estimates of the specific metabolic rate during brooding are given in Table 7.2. For Adélies and chinstraps, with a mean weight during brooding in 1980/81 of 4.1 and 4.0 kg, the average BEMR was 1604 and 1574 kJ $d^{-1}$, repectively, and the specific BEMR was 4.6 W $kg^{-1}$ for both species. In 1981/82, average chinstrap BEMR and specific BEMR (1574 kJ $d^{-1}$ and 4.6 W $kg^{-1}$) were both lower than in 1980/81 (1558 kJ $d^{-1}$ and 4.5 W $kg^{-1}$).

#### b. Foraging

The ADMR of each sex of both species and an estimate of the specific metabolic rate during foraging is given in Table 7.3. Differences in ADMR between and within species and between years are caused by differences in weight of the two sexes, the two species and of different birds of the same category. Since it takes into account any differences in body weight, the specific metabolic rate provides a better comparison. There is no difference between the two species, but the specific ADMR of males is consistently less than that of females. This is also the case for specific PEMR and BEMR and, to a lesser extent, for specific EMR. The overall trend is for the heavier sex, ie. males, of both species, to use energy at a slower rate per kg of body weight than females.

| Species/ Year | Sex | Assumed[1] mean brooding wt.(kg) | Theoretical BEMR(kJ $d^{-1}$) | Specific MR(W $kg^{-1}$) | Mean[2] for each Species/year |
|---|---|---|---|---|---|
| Adēlie | Male | 4.4 | 1657 | 4.4 | 4.6 |
| 1980/81 | Female | 3.8 | 1548 | 4.7 | |
| Chinstrap | Male | 4.3 | 1632 | 4.4 | 4.6 |
| 1980/81 | Female | 3.7 | 1502 | 4.7 | |
| Chinstrap | Male | 4.3 | 1614 | 4.4 | 4.5 |
| 1981/82 | Female | 3.8 | 1501 | 4.6 | |

[1] uses data from Table 7.1.

[2] mean of the values for each sex

Table 7.2. Estimates of energy consumption calculated from theoretical values for brooding fasts.

| Species/ Year | Sex | Assumed[1] mean foraging wt.(kg) | Theoretical BMR($kJ\ d^{-1}$) | ADMR at sea($kJd^{-1}$)[2] | Specific ADMR($Wkg^{-1}$) | Mean[3] for each Species/year |
|---|---|---|---|---|---|---|
| Adélie | Male | 4.4 | 1030 | 2987 | 7.9 | 8.1 |
| 1980/81 | Female | 3.8 | 939 | 2724 | 8.3 | |
| Chinstrap | Male | 4.3 | 1015 | 2943 | 7.9 | 8.1 |
| 1980/81 | Female | 3.7 | 908 | 2633 | 8.2 | |
| Chinstrap | Male | 4.3 | 1017 | 2949 | 7.9 | 8.1 |
| 1981/82 | Female | 3.8 | 923 | 2677 | 8.2 | |

[1] uses data from Table 7.1.

[2] equivalent to 2.9 times BMR (Davis and others, 1983).

[3] mean of the values for each sex.

Table 7.3. Estimates of energy consumption calculated from theoretical values for foraging at sea.

c. Total energy consumption and food requirements

The totals of the energy used during each activity over the whole breeding cycle are shown in Table 7.4, together with an estimation of the total amount of krill which each category of bird must consume to replace the energy lost between the start of pre-laying attendance and the end of chick rearing. For Adélies, this is between 53 and 54 kg and for chinstraps between 47 and 53 kg. For chinstraps in all years, the total amount of food consumed was greater for males than females, but it was nearly the same for Adélies of both sexes in 1980/81. The trend in specific metabolic rates also applies to krill consumption per kg of body weight. Thus, the heavier males of each species require less krill per kg of body weight than females to sustain the existence of themselves over the whole of the breeding season, although this difference is more marked between Adélie males and Adélie females than between chinstraps of either sex. The amount of krill available to sustain the chicks in a brood is small in comparison and the amount provided does not appear to differ greatly for each parent (see chapter 3).

Food consumption per day, averaged over the whole of the breeding season, is estimated as 586-603 g for Adélies and 559-627 g for chinstraps. During foraging, it is 740-812 g for Adélies and 716-801 g for chinstraps (see Table 7.4). The actual weight of food brought ashore by birds after foraging trips made during the chick rearing period in 1981/82 (see Appendix 3.5) was 441-540 g for Adélies and 457-563 g for chinstraps. If it is assumed that the food brought ashore was caught as part of the daily consumption of a parent, 34-40 % of food caught by Adélies and 30-36 % of food caught by chinstraps was utilised by the adult before reaching land. It is also noticeable that although Adélies consume slightly more per day than chinstraps during foraging, at the end of a foraging trip they actually bring slightly less food ashore than chinstraps.

| Sex | Pre-laying fasts PEMR[3] | Days | Energy consumed (kJ) | Incubation fasts EMR | Days | Energy consumed (kJ) | Brooding fasts BEMR | Days | Energy consumed (kJ) | Foraging ADMR | Days | Energy consumed (kJ) | Total energy consumed (kJ) | Amount of krill required (kg) | Krill required per kg body weight (kg)[2] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Adélie 1980/81 | | | | | | | | | | | | | | | |
| Male | 1197 | 18 | 21,546 | 1105 | 17 | 18,785 | 1657 | 8.5 | 14,085 | 2987 | 47.5 | 141,882 | 196,298 | 53.34 | 12.25 |
| Female | 1515 | 18 | 27,270 | 1665 | 18 | 29,970 | 1548 | 8.5 | 13,158 | 2724 | 47.5 | 129,390 | 199,788 | 54.29 | 14.13 |
| Chinstrap 1980/81 | | | | | | | | | | | | | | | |
| Male | 1092 | 14 | 15,288 | 1816 | 19 | 34,504 | 1632 | 12.5 | 20,400 | 2943 | 40.5[1] | 119,191 | 189,383 | 51.46 | 12.04 |
| Female | 1495 | 14 | 20,930 | 1718 | 16 | 27,488 | 1502 | 12.5 | 18,775 | 2633 | 40.5[1] | 106,636 | 173,829 | 47.24 | 12.87 |
| Chinstrap 1981/82 | | | | | | | | | | | | | | | |
| Male | 1534 | 14 | 21,476 | 1948 | 18 | 35,064 | 1614 | 12.5 | 20,175 | 2949 | 40.5 | 119,434 | 196,149 | 53.30 | 12.46 |
| Female | 1484 | 14 | 20,776 | 1465 | 17 | 24,905 | 1501 | 12.5 | 18,762 | 2677 | 40.5 | 108,418 | 172,861 | 46.97 | 12.53 |

[1] uses days foraging in 1981/82, since no chicks survived to crèche age in 1980/81

[2] uses weights of adults on return from foraging trips (see Table 7.1)

[3] metabolic rates are $kJd^{-1}$.

Table 7.4. Estimates of the total energy consumption and total krill requirements during the breeding season.

2. Chicks

Estimates of mean meal size and feeding frequency are given in Appendix 4.5. Feeding frequency calculated from daily weighings and chick meal sizes calculated from the regression of daily weight increase against chick age, corrected for possible underestimation (by 196 g for Adēlies and 172 g for chinstraps - see chapter 4) were used to calculate total chick food intake (Table 7.5) which was then compared with the amount of food brought ashore by the adults (Table 7.6) in Table 7.7.

The total food intake of chicks was very similar, with a range of 10.7-13.4 kg, but second chicks received 0.2-2.8 kg less than chicks in other categories. The values for the total food available to a brood are 15-40 % greater than the estimated intake of single and surviving chicks, with the exception of chinstraps in 1980/81 which was just less than the value for singles intake but which should not really be considered realistic anyway, because the figures were calculated using data from 1981/82. The estimated intake of twins is 41-64 % greater than that of food available to the brood (again with the exception of chinstraps in 1980/81), but the values for the intake of one chick from a brood of two, i.e. the twins' intake halved, are 18-30 % less than that for food available.

3. The consumption of krill by Adēlies and chinstraps

From Table 7.8 it can be seen that the chinstrap penguin is the single most important avian consumer in the South Orkneys. It comprises nearly 65 % of the avian biomass and is responsible for 59 % of the krill consumed and nearly 57 % of all consumption that takes place. Adēlie penguins are the second most important avian consumer, taking nearly 20 % of the krill consumed. Together, Adēlies and chinstraps comprise over 85 % of the avian biomass at the South Orkneys and are responsible for nearly 80 % of the krill consumption. The division of a year into the breeding season and the

| Species/ Year | Chick status | Food intake (kg) Guard period | Crēche period | Total chick intake | Total brood intake | Notes |
|---|---|---|---|---|---|---|
| Adēlie | First | 3.00 | 9.05 | 12.05 | 23.49 | Based on a fledging |
| 1980/81 | Second | 2.86 | 8.58 | 11.44 | | period of 56 days. |
| | Single | 3.33 | 8.28 | 11.61 | 11.61 | |
| | Survivor | 3.58 | 8.07 | 11.65 | 11.65 | |
| Adēlie | First | 3.53 | 9.83 | 13.36 | 25.45 | Based on a fledging period |
| 1981/82 | Second | 3.03 | 9.06 | 12.09 | | of 61 days. Crēche period |
| | Single | 4.02 | 8.88 | 12.90 | 12.90 | data, except period |
| | Survivor | 4.16 | 8.66 | 12.82 | 12.82 | lengths, from 1980/81. |
| Chinstrap | First | 1.85 | 9.62 | 11.47 | 22.13 | Guard and crēche period |
| 1980/81 | Second | 1.97 | 8.69 | 10.66 | | lengths and crēche period |
| | Single | 2.72 | 9.43 | 12.15 | 12.15 | data from 1981/82. |
| | Survivor | 2.78 | 8.42 | 11.20 | 11.20 | |
| Chinstrap | First | 3.76 | 9.62 | 13.38 | 25.81 | Based on a fledging period |
| 1981/82 | Second | 3.74 | 8.69 | 12.43 | | of 53.3 days. |
| | Single | 5.62 | 9.43 | 15.05 | 15.05 | |
| | Survivor | 6.84 | 8.42 | 15.26 | 15.26 | |

Table 7.5. Estimates of the total chick food intake during the fledging period.

| Species/ Year | Sex | Stomach contents (g) | Guard period Feeds | Guard period Krill (kg) available | Crēche period Feeds | Crēche period Krill (kg) available | Total (kg) |
|---|---|---|---|---|---|---|---|
| Adélie | Male | Mean 463 | 5.25 | 2.43 | 12.2 | 5.65 | 8.08 |
| 1980/81 | | sd. 155 | | | | | |
| | | No 14 | | | | | |
| | Female | Mean 356 | 5.25 | 1.87 | 12.2 | 4.34 | 6.21 |
| | | sd. 62 | | | | | |
| | | No 6 | | | | | |
| Adélie | Male | Mean 571 | 5.63 | 3.22 | 12.2 | 6.99 | 10.21 |
| 1981/82 | | sd. 71 | | | | | |
| | | No 3 | | | | | |
| | Female | Mean 456 | 5.63 | 2.57 | 12.2 | 5.56 | 8.13 |
| | | sd. 158 | | | | | |
| | | No 7 | | | | | |
| Chinstrap | Male | Mean 353 | | 1.85* | | 3.95* | 5.80* |
| 1980/81 | | sd. 171 | | | | | |
| | | No 14 | | | | | |
| | Female | Mean 362 | | 1.90* | | 4.05* | 5.95* |
| | | sd. 187 | | | | | |
| | | No 8 | | | | | |
| Chinstrap | Male | Mean 459 | 7.70 | 3.54 | 11.2 | 5.14 | 8.68 |
| 1981/82 | | sd. 192 | | | | | |
| | | No 9 | | | | | |
| | Female | Mean 468 | 7.70 | 3.60 | 11.2 | 5.24 | 8.84 |
| | | sd. 84 | | | | | |
| | | No 3 | | | | | |

* calculated using crēche period lengths in 1981/82.

Table 7.6. An estimate of the weight of krill available from parents during the fledging period.

| Species/ Year | | | Guard period (kg) | Crēche period (kg) | Total (kg) | Notes |
|---|---|---|---|---|---|---|
| Adélie | Available from adults | | 4.30 | 9.99 | 14.29 | = total food available/brood |
| 1980/81 | Received | Firsts | 3.00 | 9.05 | 23.49 | = estimated twins intake |
| | by : | Seconds | 2.86 | 8.58 | | |
| | | Singles | 3.33 | 8.28 | 11.61 | = estimated singles intake |
| | | Survivors | 3.58 | 8.07 | 11.65 | = estimated survivors intake |
| Adélie | Available from adults | | 5.55 | 12.53 | 18.08 | = total food available/brood |
| 1981/82 | Received | Firsts | 3.53 | 9.83 | 25.45 | = estimated twins intake |
| | by : | Seconds | 3.03 | 9.06 | | |
| | | Singles | 4.02 | 8.88 | 12.90 | = estimated singles intake |
| | | Survivors | 4.16 | 8.66 | 12.82 | = estimated survivors intake |
| Chinstrap | Available from adults | | 3.75 | 8.00 | 11.75 | = total food available/brood |
| 1980/81 | Received | Firsts | 1.85 | 9.62 | 22.13 | = estimated twins intake |
| | by : | Seconds | 1.97 | 8.69 | | |
| | | Singles | 2.72 | 9.43 | 12.15 | = estimated singles intake |
| | | Survivors | 2.78 | 8.42 | 11.20 | = estimated survivors intake |
| Chinstrap | Available from adults | | 7.14 | 10.38 | 17.52 | = total food available/brood |
| 1981/82 | Received | Firsts | 3.76 | 9.62 | 25.81 | = estimated twins intake |
| | by : | Seconds | 3.74 | 8.69 | | |
| | | Singles | 5.62 | 9.43 | 15.05 | = estimated singles intake |
| | | Survivors | 6.84 | 8.42 | 15.26 | = estimated survivors intake |

Table 7.7. A comparison of total chick food intake and the amount of food available from the parents.

| Species | Percentage of total biomass | Percentage of krill consumed | Percentage of all consumption |
|---|---|---|---|
| Chinstrap penguin *Pygoscelis antarctica* | 64.930 | 59.230 | 56.690 |
| Adelie penguin *P.adēliae* | 21.790 | 19.410 | 18.570 |
| Antarctic fulmar *Fulmarus glacialoides* | 10.620 | 18.230 | 20.540 |
| Southern giant petrel *Macronectes giganteus* | 1.060 | 0.780 | 0.940 |
| Cape pigeon *Daption capense* | 0.580 | 1.280 | 1.440 |
| Gentoo penguin *P.papua* | 0.530 | 0.320 | 0.450 |
| Dove prion *Pachyptila desolata* | 0.230 | 0.510 | 0.840 |
| Blue-eyed shag *Phalacrocorax atriceps* | 0.147 | - | 0.200 |
| Snow petrel *Pagodroma nivea* | 0.087 | 0.210 | 0.250 |
| Antarctic tern *Sterna vittata* | 0.014 | 0.009 | 0.059 |
| Wilson's storm petrel *Oceanites oceanicus* | 0.009 | 0.017 | 0.025 |
| Macaroni penguin *Eudyptes chrysolophus* | 0.002 | 0.002 | 0.002 |
| Black-bellied storm petrel *Fregetta tropica* | 0.001 | 0.002 | 0.004 |
| Total biomass,krill, food (tonnes) | 7,296,612 | 447,704 | 467,801 |

Table 7.8. The proportional biomass (B.A.S. data) and krill and food consumption of birds breeding in the South Orkneys.

remainder of the year is approximately 35-40 % and 60-65 %, respectively, for both species, but the average daily consumption does not vary greatly between these two periods, being 49.9 tonnes $d^{-1}$ outside and 43.2 tonnes $d^{-1}$ during the breeding season for the South Orkney Adēlie population and 103.5 tonnes $d^{-1}$ outside and 90.5 tonnes $d^{-1}$ during the breeding season for the South Orkney chinstrap population. The daily consumption per bird works out as 583 g $d^{-1}$ for Adēlies and 565 g $d^{-1}$ for chinstraps. These last figures are within the range of those calculated in section 1.c of this chapter, but include the moult period which could have been expected to reduce the average daily consumption calculated over a year.

Figures 7.1-7.3 show the variation of krill consumption by Adēlies and chinstraps during an annual cycle at Signy and the consumption of krill relative to other prey items by all birds breeding in the South Orkneys. The size of impact varies according to the activity being undertaken, but was at its maximum on February 5 when food was being consumed by birds breeding in the South Orkneys at the rate of 1427 tonnes $d^{-1}$. At Signy, the maximum impact by Adēlies was on December 26, at the rate of 55 tonnes $d^{-1}$, and that by chinstraps was on February 3, at the rate of 117 tonnes $d^{-1}$.

## DISCUSSION

### 1. Adults

From the theoretical equation for EMR it can be predicted that a heavy bird uses energy at a lower rate per kg of body weight than a light bird. This was true for Adēlies and chinstraps, but only intraspecifically and in each year rather than interspecifically and between years. It is possible that any differences in total energy consumption and food requirements of

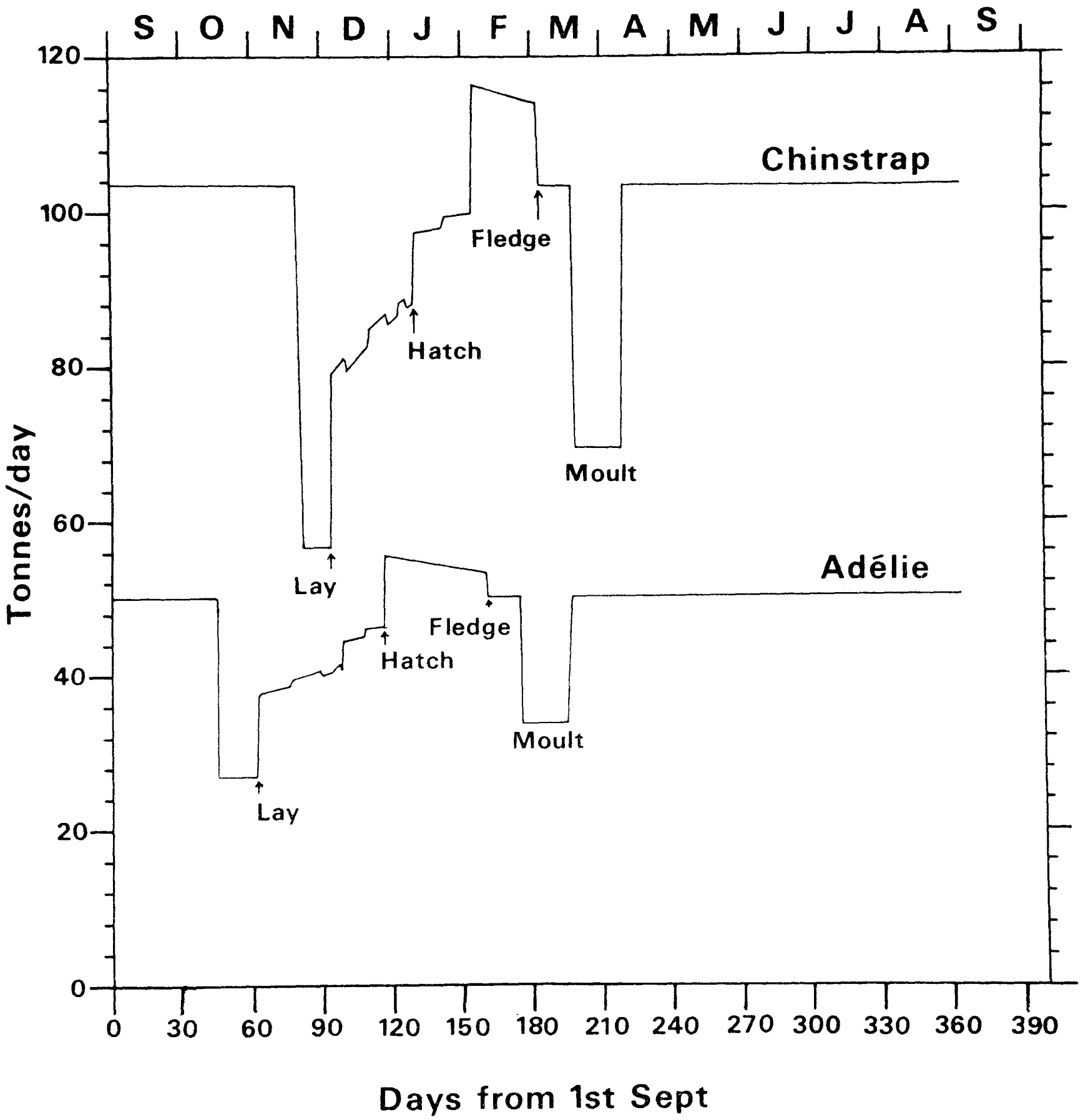



Figure 7.1. The variation during the breeding season of krill consumption by Adélies and chinstraps at Signy I. (See page 229 for explanation of model and sources of data.)

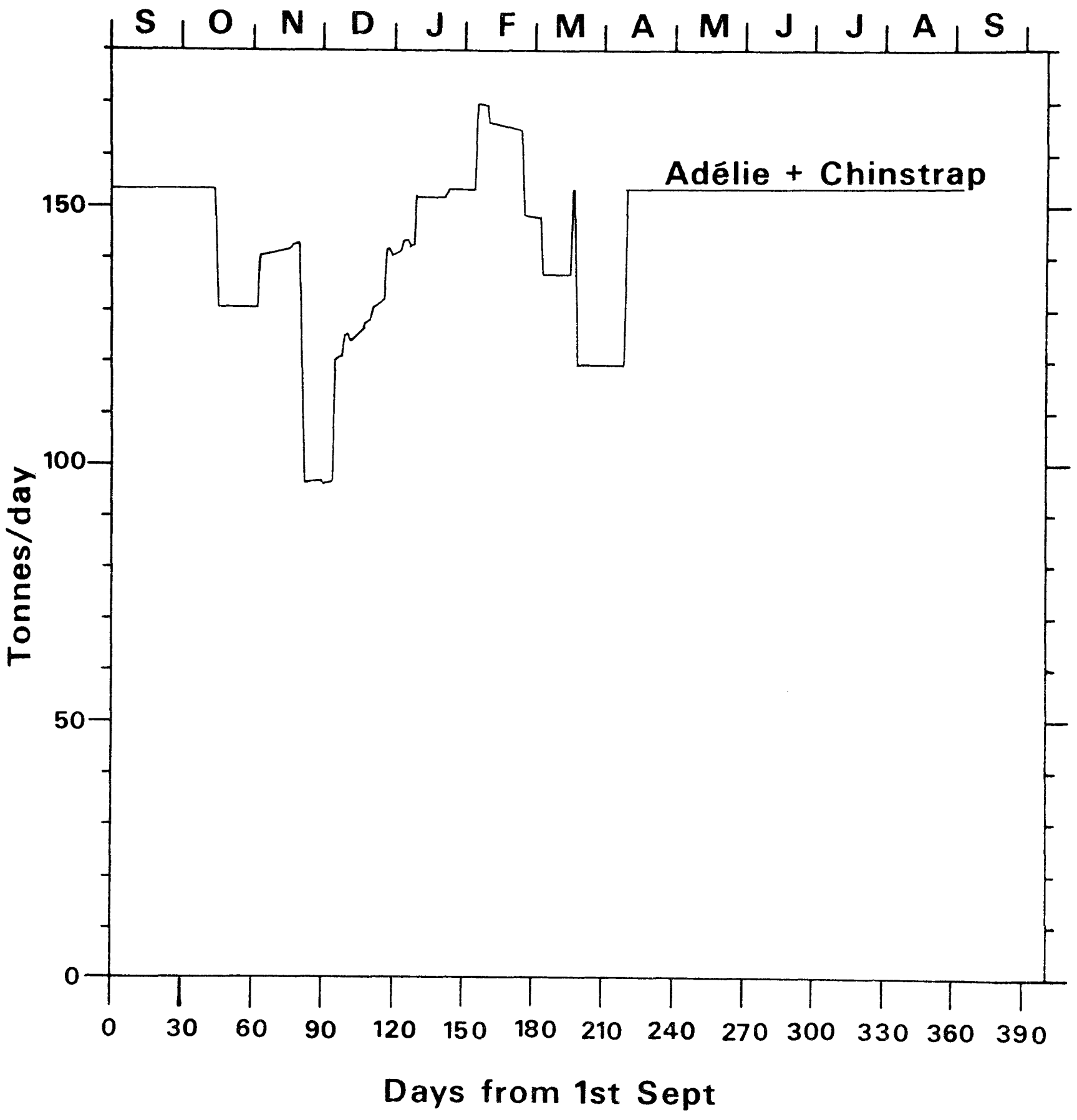



Figure 7.2. The consumption of krill by Adélies and chinstraps combined at Signy I. (See page 229 for explanation of model and sources of data.)

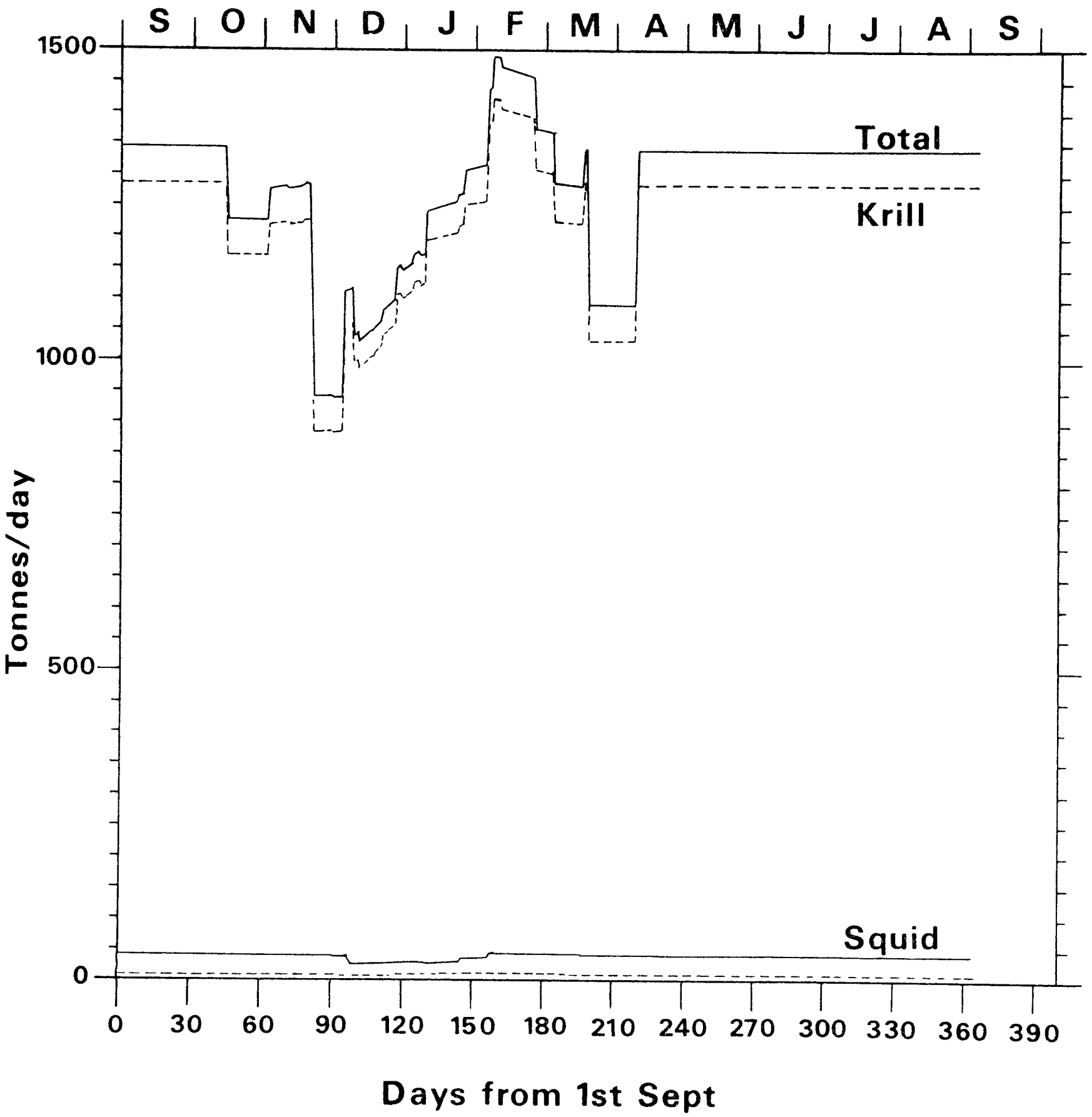



Figure 7.3. The variation during the breeding season of food consumption by all seabirds breeding at the South Orkney Is. (See page 229 for explanation of model and sources of data.)

Adélies and chinstraps of similar weight are due to differences in the length of the breeding season of each species.

It has been suggested (chapter 4) that Adélies spend more time swimming between the foraging area and the colony. A longer time at sea would mean that more energy is needed to sustain the adult and less is made available to the chicks. Consequently, krill would need to be provided over a longer period so that chicks could reach a viable weight at fledging, and this might account for the tendency of Adélies to consume more energy than chinstraps. In terms of the energetic costs of breeding, however, the two species need very similar amounts of krill per day.

2. Chicks

The difference between food available and intake of singles and survivors may partly be because chick stomach capacity is smaller during the guard period, so less of the food provided can be eaten, but it may also be that much of the food which is brought ashore but not given to chicks is used for the parents' own maintenance. Inter- and intra-specifically there were no major differences in food intake per chick, except that chinstrap singles and survivors received more food than chicks in broods of two from 1981/82. This could be expected since if parents are theoretically able to bring ashore enough food to raise two chicks to fledging, this amount of food should be available to a brood of only one chick. However, singles and survivors of both species did not receive so very much more food than chicks in broods of two and it appears that twins would together consume much more than that which was available from adults. The values for the estimated intake of twins do not refer to chicks from the same brood, since almost no two-chick broods survived to fledging. The values simply represent what might be required by two chicks in a brood if they were both to survive to fledging, assuming that meal size and feeding frequency remain similar to those used in the calculations. Since considerably less

than this amount of food was available from adults, it seems possible that Adélies and chinstraps at Signy, during both seasons studied, were unable to rear two chicks to fledging and were bringing ashore only enough food to properly sustain and raise one chick to fledging. This illustates how a lack of food can reduce the number of chicks raised (Lack, 1954; Ricklefs, 1965).

From the estimates of total chick food intake during the fledging period, it was found that chinstrap chicks consumed 12.4 - 15.3 kg of krill in 1981/82. Myrcha and Kaminski (1982) estimated, from changes in the calorific content of growing chinstrap chicks, that about 35,280 kJ (8400 kcal) are used in growth of the body. Assuming an 80 % assimilation efficiency of the food received, chinstrap chicks from this study used 45,632 - 56,304 kJ. Thus, it is possible that 63-77 % of food assimilated by chicks is used for growth and the remainder is used in resting metabolism. Assuming a chinstrap fledging period of 53 days, chick EMR may therefore be 195-397 kJ $d^{-1}$.

3. Consumption of krill by Adélies and chinstraps

The peak of food consumption during the breeding season by birds breeding in the South Orkneys was in early February. This coincides with ovarian lipogenesis in female krill, when their energy content may increase by 60 % (Clarke, 1980; in press). The short breeding season of most species allows flexibility in the timing of breeding, and enables this potential peak in energy supply to be exploited. Despite potential flexibility in the timing of its breeding at Signy and the obvious benefits to be gained from feeding on the most energy-rich krill, the timing of the Adélie breeding season means it cannot fully exploit this energy source. The selection pressures determining the breeding strategy of Adélies must be strong for this to occur. It may be that the reduction in competition gained by breeding early is an advantage which is greater than the benefits from breeding

later. Alternatively, Adélies may be conditioned to breed earlier by adaptations to harsh environmental conditions or the availability of small krill. This will be discussed in more detail in chapter 8.

Annual krill consumption by birds and seals breeding on the islands of the Scotia Sea (but not including South Georgia) has been estimated at $9.4 \times 10^6$ tonnes, and Adélies and chinstraps are responsible for an estimated 45 % of this (40 % chinstrap, 5 % Adélie). These two species are consequently the most important avian predators of krill in the Scotia Sea. The other main predator is the crabeater seal Lobodon carcinophagus, which consumes 45 % (Croxall and others, in press c). The consumption of krill by seals at the South Orkneys is unlikely to be of this order, since there are no major breeding populations. The absence of seals could be due to there being insufficient krill to support large numbers of seals, though other reasons, such as ice conditions or lack of suitable breeding beaches, are perhaps more likely. The influence of penguins, and especially chinstraps, on the stock of krill in the seas around the South Orkneys may therefore be even more important than at some of the other sites in the Scotia Sea where large numbers of birds breed. If seal consumption is relatively small, this may mean that consumption of krill by Adélies and chinstraps accounts for nearly all the consumption of krill by predators in the South Orkneys.

## CONCLUSIONS

Heavier male Adélies and chinstraps use less krill per kg of body weight than lighter females and Adélies tend to consume more than chinstraps during the breeding season. These differences probably reflect the slower metabolic rate of a heavier bird and differences of the length of the breeding season of the two species. Within each species, Adélie males

consumed less krill in total than females, but chinstrap males consumed more krill than females in both seasons studied. For Adēlies, this may reflect that fact that females lost weight at nearly twice the rate of males during incubation in 1980/81, although the reason for this is unclear. For chinstraps, it is possible that, although the food consumption per kg of males was less than that of females, being heavier birds, they require more krill overall than females.

Estimates of total chick food intake were not always the same as estimates of the amount of food available from adults. Where chick intake was less than this amount, it is likely that either some of the food provided could not be eaten because the chick was already satiated or some of the food brought ashore was for the parents' maintenance energy requirements. Since the estimated chick intake of twins was more than the amount provided and singles and survivors did not receive twice the amount received by twins, it is concluded that the Adēlies and chinstraps under study did not provide enough food to raise two chicks. Whether this was caused by a lack of food or by a strategy to ensure that one chick survived against all eventualities is uncertain, but the former is perhaps more likely since reduction in brood size has been previously shown to occur in response to a lack of food.

The consumption of krill by Adēlies and chinstraps may account for nearly all the consumption of krill by predators in the South Orkneys, unlike other sites, where crabeater seals may be the single most important consumer. The peak in consumption occurs in February when the energy content of krill may increase by 60 %. It seems possible that flexibility in the timing of breeding allows chinstraps to exploit this potential energy source but that there are strong selection pressures which prevent Adēlies from doing so. These may be adaptations either to the availability of small krill, to earlier breeding in response to environmental conditions or to reduce competition with chinstraps.

# Chapter Eight

# Discussion

## The Spheniscidae

There are 16 species of penguin in the Spheniscidae and each is adapted to its particular environment, usually in a fairly specific way. There are, however, groups of penguin species which possess several adaptations in common. This chapter will briefly examine the characteristics of these groups. Adēlies and chinstraps will then be examined in more detail to establish and account for the important features which separate the two species ecologically.

### 1. General similarities

In common with most seabirds, penguins have small clutch sizes, relatively high adult survival rates and sexual maturity deferred until age two to eight years (Croxall, 1982; 1984). A small clutch size is probably an adaptation to the largest number of young for which the parents can normally provide enough food (Lack, 1954). Although penguins presumably exploit large areas of ocean outside the breeding season, the need regularly to return to the colony to feed chicks means that they are restricted to feeding in the vicinity of the breeding site during the breeding season. This may act to promote intraspecific competition for food in the vicinity of the breeding site, which may restrict clutch sizes and cause reproductive failure of those individuals which cannot obtain adequate food for their chicks in the face of such competition (Ashmole, 1963). Low reproductive success means that recruitment into the population will be low, so for the population to remain stable, adult survival will be high.

Efficiency in obtaining enough food to breed successfully is presumably only acquired after several years of experience, so breeding is deferred to avoid high reproductive mortality in adults breeding early (Ashmole, 1963; Lack, 1968). The advantages of deferred breeding and of having breeding experience have been demonstrated for Adēlie penguins.

Older birds breeding for the first time raise a significantly larger number of chicks than younger birds breeding for the first time, and first time breeders of all ages have a lower breeding success than those with breeding experience (Ainley and others, 1983).

Penguins have several other features in common. Notably, a long, slender culmen used in prey capture, a shape which makes them efficient, streamlined swimmers, and temperature control features such as waterproof, feather coat, subcutaneous fat layer and heat exchange systems in the nasal passages, flippers and legs, all basically adaptations to life in cold environments.

2. Species groups with different adaptations

From the available information on the breeding, feeding, distribution and demography of penguins (Appendix 8.1), several groups can be distinguished on the basis of a particular combination of breeding and feeding adaptations (Table 8.1). Although there are four of these groups, that of the large emperor and king penguins is probably the most distinctive.

a. Emperor and king penguins

These differ greatly from the other penguins, being very much larger and heavier, laying one egg instead of two and taking a long time to raise their chick to fledging. To ensure this occurs in the summer, when food resources are abundant, they have evolved peculiar breeding cycles. The emperor penguin breeds annually, laying in the autumn and rearing its chick throughout the winter to fledge the following summer. King penguins breed twice in every three years, taking longer than emperors to raise a chick, but also rearing them throughout the winter so that chicks fledge before the following winter. Both species are pelagic, returning to feed their chicks no more than every three or four days.

| Species group | Breeding season | Age of first breeding | Eggs | Incubation fasts | Feeding |
|---|---|---|---|---|---|
| Aptenodytes | long, peculiar | 3-6 | 1 | long | offshore, pelagic |
| Eudyptes | short, annual | 7-8 | 2(1) | long - intermediate | offshore, semi-pelagic |
| Adēlie, chinstrap | short, annual | 3-7 | 2 | intermediate | offshore, semi-pelagic |
| Gentoo, Spheniscus, Eudyptula, Megadyptes | short, annual | 2-4 | 2 | short | inshore |

Table 8.1. Breeding and feeding adaptations characteristic of four groupings of penguin species.

b. Other penguins

The remaining penguin species differ from emperor and king penguins in three respects. They are much smaller and lighter, they lay two eggs and they breed at least annually, taking less than four-five months to do so. They can be further divided into three groups, reflecting ecological and demographic characteristics as well as taxanomic ones. These are the crested penguins (Eudyptes), a group comprising the genera Spheniscus, Eudyptula and Megadyptes, and also the gentoo penguin and, as an intermediate group, the Adélie and chinstrap penguins. It is convenient to characterise the other two groups by their Antarctic members whose distribution overlaps in part that of both Adélies and chinstraps.

1. Macaroni penguins

This is a migratory species, commencing breeding fairly late in the spring, in late November. They lay two eggs, but normally only one (the second) hatches, the first egg probably acting as insurance against loss of the much larger second egg. Incubation fasts are long and chicks are fed about every two days, which presumably enables them to feed offshore at some distance from the colony, perhaps increasing the chances of finding krill. Breeding is deferred until age seven or eight years.

2. Gentoo penguins

The gentoo penguin is very different. It is a non-migratory species which starts breeding early in the spring, in October. Parents change over at the nest each day, and chicks are fed daily. The parents feed inshore and supplement their krill diet with fish. First breeding may occur at the age of two.

The later onset of sexual maturity of macaroni penguins, compared with gentoos, might be explained by greater intraspecific competition for food. Croxall and Prince (1980 b) suggest that, when rearing chicks, macaronis at

South Georgia may forage in a volume of sea which is more than 13 times that at the disposal of gentoos. The macaroni population there is more than 50 times that of gentoos, so intraspecific competition for food by macaronis could be greater.

The significance of the difference in the timing of breeding by macaronis and gentoos and of the fact that the former is migratory and the latter a resident species is unclear. By being resident all year, gentoos are likely to be well acquainted with their feeding grounds and able to use this experience to obtain enough food to raise two chicks in seasons when food is in particularly plentiful supply and breeding early would allow more time for two chicks to fledge. Experience gained by being resident may be another factor which is responsible for the early onset of sexual maturity of gentoo penguins.

Being later in the summer, macaroni breeding would coincide with an increase in food availability similar to that which it is suggested occurs with chinstrap breeding at the South Orkneys but this would also leave insufficient time to raise two chicks before the supply of food diminishes.

In general terms, the macaroni penguin is well adapted to forage over a wide area, although competition for food is perhaps the cause of deferred sexual maturity. Gentoo penguins are adapted to inshore feeding and, since breeding is only deferred until age two to four, may experience relatively little intraspecific competition for food.

Adēlies and chinstraps

Adēlies and chinstraps are intermediate between the two groups represented by gentoos and macaronis, possessing some features of each. Thus, they lay two eggs, both of which may hatch, but seem rarely to rear two chicks to fledging. Incubation fasts are intermediate in length, chicks are fed every 1.5-2.0 days and parents forage offshore, travelling some distance

from the colony to do so. The age of first breeding is also intermediate, at three to four years. Other features common to both species were found in this study, and are summarised in Table 8.2, together with the main differences.

1. Differences between Adélies and chinstraps

Despite many similarities, Adélies and chinstraps are very different in many aspects of breeding and feeding. These are the important ones:

a. Breeding

1. Adélies start breeding one month before chinstraps,
2. Adélie first eggs are heavier and larger than second eggs, chinstrap eggs have the same measurements,
3. Adélie incubation shifts are longer than those of chinstraps,
4. Adélie first chicks grow faster than second chicks, chinstrap first and second chicks grow at the same rate,
5. Adélie breeding success was higher than chinstraps in both seasons studied.

b. Feeding

1. Adélies always consumed the same mean length of krill, chinstraps consumed larger krill as the season progressed,
2. Adélies consumed considerably more juvenile krill than chinstraps,
3. Adélie feeding frequencies may have been lower and the maximum foraging range greater than for chinstraps.

Apart from the first one, these differences have not so far been supported by other studies, so it is conceivable that some of them may be peculiar to Signy or to the seasons in which the work was carried out.

| DIFFERENT | ADELIE | CHINSTRAP |
|---|---|---|
| **General** | | |
| Distribution (Antarctic) | Continent; Peninsula | Peninsula; Scotia Sea |
| Pairs breeding (Signy) | 37 000, up to 300% in 30 yrs. | 80 000, up to 800% in 30 yrs |
| **Breeding biology** | | |
| All events | Start c. 1 month earlier | |
| Return date vs. latitude | Positive correlation | No relationship |
| Laying date vs. latitude | Positive correlation | No relationship |
| Egg weight | Heavier: first>second | Both same weight |
| Egg volume | Larger: first>second | Both same size |
| Egg weight loss | 15.7 % | 17.4 % |
| Incubation shifts | Longer: first by male | First by female |
| Hatch date vs. latitude | Positive correlation | No relationship |
| Hatching interval | 1981/82: 1.9 d | 1.3 d |
| Hatching weights | Heavier: first>second | Both same weight |
| Crêche age | High synchrony; 16-21 d | Low synchrony; 23-29 d |
| Crêche formation | Tight, large | Loose, small |
| Fledging periods | Longer; 1980/81: 56 d; 81/82: 61 d | 1981/82: 53 d |
| Disturbance | Affected more | |
| Breeding success | Higher; 1980/81: 0.15 | 1980/81: 0.016 |
| (chicks/pair) | 1981/82: 0.41 | 1981/82: 0.36 |
| Predation | Mainly by skuas | Mainly by sheathbills |
| Nest desertion | Lower; 80/81: 7%; 81/82: 2.5% | 80/81: 43%; 81/82: 24% |
| **Diet** | | |
| Mean krill length | Same all season | Larger through season |
| Length-frequency distribution | Higher proportion, or even majority juvenile | Mainly sub-adult or adult, few juvenile |
| Digestion of krill | Perhaps more digested | |
| Culmen lengths | | Longer |
| **Feeding ecology** | | |
| Meal size | Larger 1980/81; same 1981/82 | |
| Feeding frequency | 1980/81: more frequent | 81/82: singles more frequent |
| Foraging distance | Part of range further | |
| **Chick growth** | | |
| Rate | First greater than second | Both same rate |
| Comparative weights | | 81/82: older were heavier |
| **Bioenergetics** | | |
| Incubation weight loss | | Perhaps faster |
| Energy consumption | 1.4 times BMR | 1.9 times BMR |
| Fasting energy supply | *P. major* relatively unused | *P. major* may be used |
| **Food consumption** | | |
| Total | Slightly more | |
| Weight specific | Females more than males | Same (to less extent) |
| South Orkney consumers | Second most important | Most important |
| Date of maximum impact | December 26 | February 5 |

| SIMILAR | |
|---|---|
| **General** | |
| Conditions | 1980/81: pack ice until Feb<br>1981/82: pack dispersed Nov |
| **Breeding biology** | |
| Pre-laying | Males return first |
| Laying synchrony | Highly synchronous |
| Laying interval | 3 d |
| Eggs | c. 3 % of female weight |
| Incubation length | First eggs longer than second |
| Hatching date | 81/82: 1st earlier; 80/81: both same |
| Crêche age | Single chicks begin latest |
| Disturbance effect | Most during chick rearing |
| Mortality | 80/81: high, especially second chicks during guard period |
| Breeding success | Unaffected by colony size, nest position, laying date |
| **Diet** | |
| Composition | Mainly krill (<1% fish & amphipods) |
| Mean krill length | Longer in 1980/81 |
| Wt. and no. of krill | Sharp increase after hatching |
| Culmen depths | Males > females |
| **Feeding ecology** | |
| Meal size | Increase in guard, steady in creche period |
| Intraspecific meal size | Twins>singles, singles>one twin |
| Foraging distance | Considerable overlap |
| Chick feeding time | Perhaps late afternoon |
| Diving | Perhaps both shallow and at night |
| **Chick growth** | |
| Curve | Gompertz fitted better than logistic |
| Asymptotes | Singles highest; all lower than elsewhere |
| Rates | Firsts>seconds |
| Body growth rate | Flippers>culmen (full grown at fledging) |
| **Bioenergetics** | |
| Incubation weight loss | Female faster than males, no overall decline |
| Energy consumption | Males lower rate |
| **Food consumption** | |
| Daily intake (adults) | c. 600 g |
| Chick intake | Seconds receive less |
| Food provided | Not enough to raise two chicks |

Table 8.2 Summary of major differences between Adélie and chinstraps breeding at Signy Island in 1980/81 and 1981/82.

2. Reasons for differences

Adélies breeding at Signy can be characterized as early breeders with eggs which are dimorphic in size and weight, long incubation shifts and low provisioning rate to chicks and consumers of mainly juvenile krill. Chinstraps breed later, and take mainly mature krill, their eggs are not dimorphic, incubation shifts are shorter and feeding frequencies may be higher.

The degree to which these differences are determined by adaptations developed in response to conditions typically prevailing at the centre of the species range of distribution, to the availability of food and to competition between the two species is discussed below.

a. Environmental conditions

The two species may breed at different times and take different sized krill because each is optimally adapted to the environment in which it mainly occurs. The centre of Adélie distribution is probably on the Antarctic continent and especially in the Ross Sea, where over 40 % of the world annual breeding population occurs (Ainley and O'Connor, in press). Adélies are well adapted to breeding in more southerly latitudes by having a breeding strategy which copes with the short summer and the prolonged presence of ice. Thus, breeding occurs as early as possible, which ensures that chicks can fledge while supplies of food remain available, more is invested in the first egg and chick than the second (allowing brood reduction if environmental conditions dictate it) and incubation shifts are long to permit travel for long distances over ice. In contrast, chinstraps are more or less confined to the Scotia Arc and are most abundant at the South Sandwich Is. Signy I is thus near the centre of their range of distribution. They have a breeding strategy adapted to a less extreme Antarctic climate where the summer is longer and ice less likely to be present. Thus, breeding usually begins after ice has dispersed

from the breeding site, there is equal investment in both eggs and both chicks, so the only brood reduction mechanisms are laying and hatching intervals, and incubation shifts are shorter than those of Adēlies. In a normal breeding season, it would appear, therefore, that chinstraps are better adapted to breeding at Signy than Adēlies. However, 1980/81 was an abnormal season and, in 1981/82, although ice-free for much of the time, there was ice around Signy until the middle of November 1981. In both seasons, Adēlie breeding success was higher than that of chinstraps, so although primarily adapted to breeding further south, Adēlies were able to do better than chinstraps under conditions which were more like those at the centre of their range of distribution. Chinstraps, without adaptations such as longer incubation shifts and different sized eggs and chicks, consequently did worse than Adēlies under adverse conditions, and especially those of 1980/81.

b.Food availability

If Adēlie and chinstrap breeding strategies are largely determined by environmental conditions, then many differences in their feeding ecology may simply be a consequence of the breeding strategy. At Signy, this consequence may be more applicable to Adēlies than to chinstraps. The time of peak Adēlie energy demand in the Ross Sea coincides with the presence of mature E.crystallorophias (Emison, 1968). These are of a similar size to the juvenile E.superba which are important only to Adēlies at Signy I. Breeding adaptations of pelagic seabirds are thought to reflect certain characteristics of the food supply such as availability, quantity or quality (Ashmole, 1971; Ashmole and Ashmole, 1967; Lack, 1968) so it is conceivable that Adēlies breed early in the season at Signy because they are primarily adapted to feed on small krill, which may be less available later in the season (Stepnik, 1982). Juvenile E.superba are, however, a generally less economic resource than mature E.superba since, for example,

approximately seven krill of 25 mm in length must be caught to obtain the same weight of one krill of 45 mm in length, so Adēlies do not appear to be feeding on the best food resource at Signy. Adaptation of breeding by Adēlies to such feeding would seem unlikely, and is therefore probably only a consequence of a breeding strategy determined by environmental conditions.

The time of peak chinstrap energy demand at Signy coincides with the abundant presence of mature E.superba, which may either be entirely fortuitous or might suggest a relationship between breeding time and krill availability. In either case, chinstraps are probably feeding on a better food resource than Adēlies. This may only be possible at Signy because the summer is not so short that it is necessary to breed as early as possible to allow chicks to fledge before winter. A species is probably well adapted to the environment it experiences at the centre of its range of distribution, but each set of adaptations may ultimately depend on the most important factor which determines breeding success. Thus, the chinstrap breeding timetable may be primarily adapted to food availability, since adaptation to harsh environmental conditions and a short summer are relatively unnecessary at Signy, and the earlier breeding by Adēlies may only be possible because they have retained adaptations to the harsh Antarctic environment at the centre of their range of distribution, though an adaptation by Adēlies in the Ross Sea to the peak availability of E.crystallorophias cannot be discounted.

c. Competition

The feeding and breeding strategy demonstrated by Adēlies could be the result of competition between the two species. If chinstraps are better suited to breeding at Signy, they would probably have a competitive advantage over Adēlies. Feeding on less economic juvenile krill would therefore be an example of niche-shift by Adēlies in the face of such

competition. There have been no studies of the breeding and feeding strategies of Adélies carried out where they are not breeding sympatrically with chinstraps, but are feeding on E.superba, so this can only be inferred. However, various combinations of breeding and feeding differences have certainly been suggested to reduce competition between several other pairs of seabird species (Berruti, 1979; Prince, 1980 a; 1980 b; Croxall and Prince, 1980 a; 1980 b; Thomas, 1982).

In conclusion, it seems likely that Adélies are primarily adapted to breeding further south than chinstraps and that chinstraps are better adapted to breeding at Signy than Adélies, except when unusually harsh environmental conditions prevail. It may well be that Adélie and chinstrap breeding and feeding strategies at Signy are governed by differing degrees of adaptation to food availability, environmental conditions and competition between the two species rather than to one single factor.

3. Differences in Adélie and chinstrap breeding and feeding strategies between this study and previous ones

Whenever possible, the results of each aspect of this study have been compared with those of previous studies of Adélies and chinstraps. There are many similarities, but a pattern of differences has also emerged :

1. chinstrap chick feeding frequencies were higher at Elephant I in two breeding seasons studied: 1970/71 (Conroy and others, 1975 b) and 1976/77 (Croxall and Furse, 1980),
2. Adélie meal sizes may have been greater at Signy thirty years ago (Sladen, 1958),
3. Adélies and chinstraps took very few juvenile krill at King George I in 1977/78 (Volkman and others, 1980).
4. Adélie and chinstrap breeding success was higher at King George I in 1976/77 and 1977/78 (Trivelpiece, 1981), and Adélie breeding success was also higher at Cape Crozier in all years between 1967 and 1974 (Ainley and others, 1983),

5. Adēlie chick asymptotes were much higher at Cape Royds in 1959/60 and King George I in 1976/77 and 1977/78 (Taylor and Roberts, 1962; Volkman and Trivelpiece, 1980) and at Signy thirty years ago (Sladen, 1958); chinstrap chick asymptotes and growth rates were much higher at King George I 1976/77 and 1977/78 (Volkman and Trivelpiece, 1980).

Studies of other species have shown differences, similar to those found here, in breeding and feeding strategies at different breeding localities. Thus, puffins Fratercula arctica breeding on St.Kilda fledged chicks with lower weights than those breeding on the Isle of May, and it was suggested that this was due to poorer feeding conditions at St. Kilda (Harris and Hislop, 1978); and Thomas and others (1983) found differences in the chick growth pattern of light-mantled sooty albatrosses breeding on South Georgia and at Marion I. It was suggested that these were related to diet and chick feeding frequency differences. The differences found between this study and other Adēlie and chinstrap studies may also relate to differences in feeding aspects. Either quantity or availability of food, or a combination of these could influence the nature of the components of the breeding and feeding strategies.

At King George I, Adēlies caught considerably more mature krill than they did at Signy. If mature krill were largely unavailable to Adēlies at Signy, by feeding on juvenile krill they might have contributed to the low asymptotes of their chicks and poor breeding performance. A relationship between food quality and breeding success would not account, however, for the poor breeding performance of chinstraps since they were feeding on mature krill.

It has been indicated (Croxall and Furse, 1980) that chinstraps at Elephant I may feed c. 50 km from the island at the edge of the continental shelf. In chapter four of this thesis it was suggested that Adēlies and chinstraps travel between 130 and 240 km during a foraging trip. If significant numbers of krill only occur at such distances from Signy, one

could reasonably expect the chicks of both species to be adapted to a low rate of energy supply and a longer fledging period to enable chicks to reach adult weight before fledging. Growth rates at Signy are not comparable with those recorded elsewhere because different growth curves were used, so the relationship between chick growth rates at Signy and elsewhere is unknown. However, the fledging periods of Adēlies and chinstraps at Signy are similar to those previously recorded and chicks that did fledge had completed moult. It is likely, therefore, that they had developed to the same extent physiologically by the end of the fledging as chicks from other studies. However, Adēlie and chinstrap chicks at Signy reached lower asymptotes before fledging, and presumably therefore received less food during the fledging period. There are two possible reasons why adults did not feed their chicks for longer so that they might reach adult weight before fledging. Firstly, food may become relatively unavailable, especially to chinstraps, toward the end of the breeding season. Secondly, parents may stop feeding their chicks in order to increase their own body weight before they start to moult. The second of these reasons is perhaps more likely since it is equally applicable to both species.

Feeding on juvenile krill may be partially responsible for the low asymptotes of Adélie chicks, but this would not account for low chinstrap chick asymptotes, even though their feeding may have been affected early in both seasons by ice. It is possible that the quantity of krill available at the South Orkneys is insufficient at the times when energy demands of Adēlies and chinstraps are at a maximum. Over the past 30 years, there has been a huge increase in the number of Adēlies and chinstraps breeding at Signy (Croxall and others, 1981), and there is no reason to doubt that the same has occurred in the South Orkneys as a whole. However, data from counts of selected colonies at Signy from 1978 to the present show no indication of any continuing increase. The numbers have remained

approximately stable. In contrast to this, the populations of Adélies and chinstraps at Point Thomas, King George I have increased at much slower rates and are at much lower levels than at Signy (Trivelpiece and Volkman, 1979; Croxall and Kirkwood, 1979). It may be that krill in the waters off the South Orkneys cannot support a further increase in the numbers of breeding birds or even provide sufficient energy to allow the number of chicks being reared at present to fledge with asymptotes which are close to adult weight. Adélie chick asymptotes were higher at Signy thirty years ago (Sladen, 1958), so the low asymptotes of chicks of both species may be a recent phenomenon caused by large numbers of birds attempting to rear chicks using food resources which are temporarily depleted due to heavy competition for the available food.

In conclusion, it appears that Adélies and chinstraps at Signy are at present breeding under conditions which cause chicks to fledge with asymptotes which are much lower than most of those previously recorded at Signy and at other breeding localities. This may be due to the distance of the food from the colony, but it is perhaps more likely that food is at present in short supply due to the combined and simultaneous impact of a greatly increased breeding population.

# ACKNOWLEDGEMENTS

I would like to thank the British Antarctic Survey and its Director, Dr. R.M. Laws, CBE, FRS, for providing me with the opportunity and facilities to undertake and produce this thesis. I would particularly like to thank Dr. J.P. Croxall for his constant help, advice and supervision while I was in the field and when writing up in the UK. My university supervisor, Dr. C.M. Perrins, also provided much help and advice, for which I am very grateful.

I have benefited greatly from discussions with various members of the Life Sciences Division at the British Antarctic Survey. For this, I am grateful to Nigel Bonner, John Croxall, Peter Prince, Chris Ricketts, Bill Doidge, Steve Hunter and Seamus McCann. I would also like to thank Dr. J.P. Croxall, Dr. C.M. Perrins and Prof. E.C. Young for reading and commenting on a final draft of this manuscript, and Dr. C. Ricketts for invaluable computing and statistical help and advice.

I thank the captains, officers and crews of R.R.S. John Biscoe and R.R.S. Bransfield for getting me to Signy Island, and a helicopter crew of H.M.S. Endurance for enabling me to take aerial photographs of penguin colonies.

Due to ice conditions, it was not possible for me to reach Signy at the start of the 1980/81 breeding season, so I spent one month at South Georgia. I would like to thank the base commander at South Georgia, Pete Witty, for providing accomodation and facilities for me to prepare equipment for the field. While I was at South Georgia, the work for this thesis was begun at Signy. For this, I would like to thank Doug Allan, Paul Drummond, Neil Fitch and Phil Sharples, but especially Rick Price, the biological assistant, who made an excellent job of preparing the Adélie study nests and carefully recording laying dates, adult weights and incubation shift lengths. During the remainder of the season and that of

1981/82, Rick Price, Bob Forster, Ken Cameron, Alan Hemmings, Mark Redpath, Adrian Overbury, Mick Brothers, John Fleming and Wally Hamilton provided much needed assistance. I would like to thank these and all other Base members for contributing to the enjoyment of all and making my time at Signy the most memorable experience of my life.

For preparing the captions for the illustrations, I would like to thank Tony Sylvester and Roger Missing, and for help with obtaining references I thank Christine Phillips. Ellen Bailey typed some of the tables and corrected and produced the thesis on word processor, for which I am extremely grateful.

Finally, I would like to thank my parents and friends for their constant help and encouragement, and especially Carol for her support and encouragement whenever the light at the end of the tunnel seemed a long way off.

# REFERENCES

ADAMS, N.J. and BROWN, C.R. (in press). Diving depths of the gentoo penguin, Pygoscelis papua. Condor.

AINLEY, D.G. 1975. Displays of Adélie penguins: a re-interpretation. (In STONEHOUSE, B., ed., The biology of penguins. London, MacMillan, 503-534.)

AINLEY, D.G. 1978. Activity patterns and social behaviour of non-breeding Adélie penguins. Condor, 80, 138-146.

AINLEY, D.G. and DEMASTER, D.P. 1980. Survival and mortality in a population of penguins. Ecology, 61, 522-530.

AINLEY, D.G. and EMISON, W.B. 1972. Sexual size dimorphism in Adélie penguins. Ibis, 114, 267-271.

AINLEY, D.G. and LERESCHE, R.E. 1973. The effects of weather and ice conditions on breeding in Adélie penguins. Condor, 75, 235-239.

AINLEY, D.G. and O'CONNOR, E.F. (in press). The marine ecology of birds in the Ross Sea, Antarctica. American Ornithological Union Monograph.

AINLEY, D.G. and SCHLATTER, R.P. 1972. Chick raising ability in Adélie penguins. Auk, 89, 559-566.

AINLEY, D.G., LERESCHE, R.E. and SLADEN, W.J.L. (1983). Breeding biology of the Adélie penguin. Los Angeles, University of California Press.

AINLEY, D.G., WOOD, R.C. and SLADEN, W.J.L. 1978. Bird life at Cape Crozier, Ross Island. Wilson Bulletin, 90, 492-510.

ASBIRSK, S. 1979. The adaptive significance of the reproductive pattern in the black guillemot Cepphus grylle. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København, 141, 29-80.

ASHMOLE, N.P. 1962. The black noddy Anous tenuirostris on Ascension Island. Part I, General biology. Ibis, 103b, 235-273.

ASHMOLE, N.P. 1963. The regulation of numbers of tropical oceanic birds. Ibis, 103b, 458-473.

ASHMOLE, N.P. 1971. Seabird ecology and the marine environment. (In FARNER, D.S. and KING, J.R., eds., Avian biology, Vol.I. New York, Academic Press, 223-286.)

ASHMOLE, N.P. and ASHMOLE, M.J. 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. Bulletin of the Peabody Museum of Natural History, 24, 1-131.

ASHMOLE, N.P. and TOVAR, S.H. 1968. Prolonged parental care in royal terns and other birds. Auk, 85, 90-100.

ASHWORTH, P.G. 1963. Ornithological report, Deception Island. Falkland Islands Dependencies Scientific Bureau, Q/1963/B (Unpublished).

AUSTIN, O.L. 1945. The role of longevity in successful breeding by the common tern Sterna hirundo. Bird Banding, 16, 21-28.

BAGSHAWE, T.W. 1938. Notes on the habits of the gentoo and ringed or Antarctic penguins. Transactions of the Zoological Society of London, 24, 185-306.

BARRAT, A. 1976. Quelques aspects de la biologie et de l'écologie du manchot royal (Aptenodytes patagonicus) des Iles Crozet. Comité National Francais des Réchérches Antarctiques, 40, 9-52.

BECK, J.R. and BROWN, D.W. 1972. The biology of Wilson's storm petrel Oceanites oceanicus (Kuhl) at Signy Island, South Orkney Islands. British Antarctic Survey Scientific Report 69, 54 pp.

BEDARD, J. 1969 a. Adaptive radiation in Alcidae. Ibis, 111, 189-198.

BEDARD, J. 1969 b. Feeding of the least, crested and parakeet auklets around St. Lawrence Island, Alaska. Canadian Journal of Zoology, 47, 1025-1050.

BERNACCHI, L. 1901. To the south polar regions. Expedition of 1898-1900. London, Hurst and Blackett, 348 pp.

BERRUTI, A. 1979. The breeding biologies of the sooty albatrosses Phoebetria fusca and P.palpebrata. Emu, 79, 161-175.

BIOMASS, 1982. Post-FIBEX data interpretation workshop. BIOMASS Report Series, 20, 38 pp.

BIRKHEAD, T.R. 1977 a. Adaptive significance of the nestling period of guillemots Uria aalge. Ibis, 119, 544-549.

BIRKHEAD, T.R. 1977 b. The effect of habitat and density on breeding success in the common guillemot Uria aalge. Journal of Animal Ecology, 46, 751-764.

BIRKHEAD, T.R. and NETTLESHIP, D.N. 1981. Reproductive biology of thick-billed murres Uria lomvia: an inter-colony comparison. Auk, 98, 258-269.

BOERSMA, P.D. 1976. An ecological and behavioural study of the Galapagos penguin. The Living Bird, 15, 43-93.

BOERSMA, P.D. 1978. Breeding patterns of Galapagos penguins as an indicator of oceanographic conditions. Science, 200, 1481-1483.

BOGDANOV, M.A., ORADOVSKIY, S.G., SOLYANKIN, Ye.V. and KHVATSKIY, N.V. 1969. On the frontal zone of the Scotia Sea. Okeanologiya, 9, 777-783.

BONNER, W.N. 1968. The fur seal of South Georgia. British Antarctic Survey Scientific Report, No.56, 81 pp.

BOSWELL, J. and MACIVER, D. 1975. The magellanic penguin Spheniscus magellanicus. (In STONEHOUSE, B., ed., The biology of penguins, London, MacMillan, 271-305.)

BOUGAEFF, S. 1975. Variations pondérales et evaluation de la dépense énergétique chez le manchot Adélie Pygoscelis adeliae. Comptes rendus, Academie des Sciences Paris, Série D, 280, 2373-2376.

BROWN, L.H. and ROOT, A. 1971. The breeding behaviour of the lesser flamingo Phoeniconaias minor. Ibis, 113, 147-173.

BROWN, L.H. and URBAN, E.K. 1969. The breeding biology of the great white pelican Pelicanus onocrotalus roseus at Lake Shala, Ethiopia. Ibis, 111, 199-237.

BURGER, A.E. 1979. Breeding biology, moult and survival of lesser sheathbills Chionis minor at Marion Island. Ardea, 67, 1-14.

BUTLER, P.J. and JONES, D.R. 1982. The comparative physiology of diving in vertebrates. (In LOWENSTEIN, O., ed., Advances in comparative physiology and biochemistry, 8, 180-364.)

BUTLER, R.G. and MULLER-SCHWARZE, D. 1977. Penguin census by aerial photographic analysis at Cape Crozier, Ross Island. Antarctic Journal of the United States, 22, 24-27.

CAIRNS, D. 1981. Breeding, feeding and chick growth of the black guillemot Cepphus grylle in Southern Quebec. Canadian Field Naturalist, 95, 312-318.

CARRICK, R. 1964. Breeding biology of Eudyptes. (In THOMSON, A.L., ed., A new dictionary of birds, London, Nelson, 614pp.)

CARRICK, R. 1972. Population ecology of the Australian black-backed magpie, royal penguin and silver gull. (In United States Department of the Interior Wildlife Research Report, No. 2, Population ecology of migratory birds: a symposium, 41-99.)

CASE, T.J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Quarterly Review of Biology, 53, 243-282.

CLARK, B.D. and BEMIS, W. 1979. Kinematics of swimming of penguins at the Detroit Zoo. Journal of Zoology, 188, 411-428.

CLARKE, W.E. 1906. Ornithological results of the Scottish National Antarctic Expedition. II. On the birds of the South Orkney Islands. Ibis, 8, 145-187.

CLARKE, A. 1980. The biochemical composition of krill Euphausia superba Dana from South Georgia. Journal of Experimental Marine Biology and Ecology, 43, 221-236.

CLARKE, A. (in press). Lipid content and composition of Antarctic krill Euphausia superba Dana. Journal of Crustacean Biology.

CLARKE, A. and PRINCE, P.A. 1980. Chemical composition and calorific value of food fed to mollymauk chicks at Bird Island, South Georgia. Ibis, 122, 488-494.

CONROY, J.W.H. 1975. Recent increases in penguin populations in Antarctica and the sub- Antarctic. (In STONEHOUSE, B., ed., The biology of penguins. London, Macmillan, 321-336.)

CONROY, J.W.H., DARLING, O.H.S. and SMITH, H.G. 1975 a. The annual cycle of the chinstrap penguin Pygoscelis antarctica on Signy Island, South Orkney Islands. (In STONEHOUSE, B., ed., The biology of penguins. London, Macmillan, 353-362.)

CONROY, J.W.H., WHITE, M.G., FURSE, J.R. and BRUCE, G. 1975 b. Observations on the breeding biology of the chinstrap penguin Pygoscelis antarctica, at Elephant Island, South Shetland Islands. British Antarctic Survey Bulletin, 40, 23-32.

COOPER, J. 1980. Breeding biology of the jackass penguin with special reference to its conservation. Proceedings of the 4th Pan-African Ornithological Congress, 227-231.

COOPER, J. and MORANT, P.D. 1981. The design of stainless steel flipper bands for penguins. Ostrich, 52, 119-123.

COOPER, J., WILLIAMS, A.J. and BRITTON, P.L. In press. Distribution, population sizes and conservation of breeding seabirds in the Afrotropical region. (In CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, R.W., eds., The status and conservation of seabirds. ICBP, Croom Helm.)

COULSON, J.C. 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake Rissa tridactyla. Journal of Animal Ecology, 35, 269-279.

COULSON, J.C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature, 217, 478-479.

COULSON, J.C. and WHITE, E. 1956. A study of colonies of the kittiwake Rissa tridactyla. Ibis, 98, 63-79.

COULSON, J.C. and WHITE, E. 1960. The effect of age and density of breeding birds on the time of breeding of the kittiwake Rissa tridactyla. Ibis, 102, 71-93.

COULTER, M. In press. Seabird conservation in the Galapagos Is, Equador. (In CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, R.W., eds., The status and conservation of seabirds. ICBP, Croom Helm.)

CROXALL, J.P. 1982. Energy costs of incubation and moult in petrels and penguins. Journal of Animal Ecology, 51, 177-194.

CROXALL, J.P. 1983. Prey samples from blue-eyed shags Phalacrocorax atriceps, Bird Island, South Georgia, 1982-83. British Antarctic Survey unpublished report.

CROXALL, J.P. 1984. Seabird ecology. (In LAWS, R.M., ed., Antarctic Ecology, London, Academic Press.)

CROXALL, J.P. and FURSE, J.R. 1980. Food of chinstrap penguins Pygoscelis antarctica and macaroni penguins Eudyptes chrysolophus at Elephant Island, South Shetland Islands. Ibis, 122, 237-245.

CROXALL, J.P. and KIRKWOOD, E.D. 1979. The distribution of penguins on the Antarctic Peninsula and islands of the Scotia Sea. Cambridge, British Antarctic Survey, 186 pp.

CROXALL, J.P. and PRINCE, P.A. 1979. Antarctic seabird and seal monitoring studies. Polar Record, 19, 573-595.

CROXALL, J.P. and PRINCE, P.A. 1980 a. The food of the gentoo penguins Pygoscelis papua and macaroni penguins Eudyptes chrysolophus at South Georgia. Ibis, 122, 2, 245-253.

CROXALL, J.P. and PRINCE, P.A. 1980 b. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biological Journal of the Linnean Society, 14, 103-131.

CROXALL, J.P. and PRINCE, P.A. 1982. A preliminary assessment of the impact of seabirds on marine resouces at South Georgia. Comitê National Francais des Rêchêrches Antarctiques, 51, 501-509.

CROXALL, J.P. and PRINCE, P.A. 1983. Antarctic penguins and albatrosses. Oceanus, 26, 18-27.

CROXALL, J.P. and RICKETTS, C. 1983. Energy costs of incubation in the wandering albatross Diomedea exulans. Ibis, 125, 33-39.

CROXALL, J.P., ROOTES, D.M. and PRICE, R.A. 1981. Increases in penguin populations at Signy Island, South Orkney Islands. British Antarctic Survey Bulletin, 54, 47-56.

CROXALL, J.P., EVERSON, I., KOOYMAN, G.L., RICKETTS, C. and DAVIS, R.W. (in press a). Fur seal diving behaviour in relation to krill vertical distribution. Polar Biology, 2, 41-46.

CROXALL, J.P., PRINCE, P.A., HUNTER, I., McINNES, S. and COPESTAKE, P.G. (in press b). The seabirds of the Antarctic Peninsula, islands of the Scotia Sea and Antarctic Continent between 80°E and 20°W: their status and conservation. (In CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, R.W., eds., The status and conservation of seabirds. ICBP.)

CROXALL, J.P., PRINCE, P.A. and RICKETTS, C. (in press c). Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. Proceedings of the Fourth SCAR Symposium on Antarctic Biology.

CROXALL, J.P., PRINCE, P.A. and RICKETTS, C. (in press d). Impact of seabirds on marine resources, especially krill, of South Georgia waters. (In WHITTOW, G.C. and RAHN, A., eds., Seabird Energetics. New York, Plenum.)

CROXALL, J.P., PRINCE, P.A. and McINNES, S. (in press e). The status and conservation of seabirds at the Falkland Islands. (In: CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, W.R., eds., The status and conservation of seabirds. ICBP, Croom Helm.)

DARLING, F.F. 1938. Bird flocks and the breeding cycle: a contribution to the study of avian sociality. London, Cambridge University Press.

DAVIS, J.W.F. 1976. Breeding success and experience in the Arctic skua Stercorarius parasiticus. Journal of Animal Ecology, 45, 531-535.

DAVIS, L.S. 1980. Egg and chick survival of the Adēlie penguin Pygoscelis adeliae at Cape Bird, Antarctica. Unpublished Msc.Thesis, University of Canterbury, Christchurch, New Zealand.

DAVIS, L.S. 1982 a. Crēching behaviour of Adēlie penguin chicks Pygoscelis adeliae. New Zealand Journal of Zoology, 9, 279-286.

DAVIS, L.S. 1982 b. Timing of nest relief and its effect on breeding success in Adēlie penguins Pygoscelis adeliae. Condor, 84, 178-183.

DAVIS, R.W., KOOYMAN, G.L. and CROXALL, J.P. 1983. Water flux and estimated metabolism of free-ranging gentoo and macaroni penguins at South Georgia. Polar Biology, 2, 41-46.

DERENNE, P., MOUGIN, J-L., STEINBERG, C. and VOISIN, J.F. 1976. Les oiseaux de l'Ile aux Cochons, Archipel Crozet (46°06'S.,50°14'E). Comitē National Francais des Rēchērches Antarctiques, 40, 107-148.

DERKSEN, D.V. 1977. A quantitative analysis of the incubation behaviour of the Adēlie penguin. Auk, 94, 552-566.

DESPIN, B. 1977. Croissances comparées des poussins chez les manchots du genre Pygoscelis. Comptes rendus, Academie des Sciences Paris, Série D, 285, 1135-1137.

DOWNES, M.C., EALEY, E.H.M., GWYNN, A.M. and YOUNG, P.S. 1959. The birds of Heard Island. Australian National Antarctic Research Expedition Report, Series B, 1, 1-135.

DRENT, R.H. and DAAN, S. 1980. The prudent parent: energetic adjustments in avian breeding. (In KLOMP, H. and WOLDENDORP, J.W., eds., The integrated study of bird populations. Ardea, 225-252.)

DUFFY, D.C., HAYS, C. and PLENGE, M.A. (in press). The conservation of Peruvian seabirds. (In: CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, W.R., eds., The status and conservation of seabirds. ICBP, Croom Helm.)

ELIZAROV, A.A. 1971. Distinctive features of water dynamics in areas of mass krill concentrations. Trudy VNIRO, 79, 31-39.

EMISON, W.B. 1968. Feeding preferences of the Adélie penguin at Cape Crozier, Ross Island. (In AUSTIN, O.L. Jr., ed., Antarctic bird studies, 12, 191-212. Washington, American Geophysical Union.)

EVERSON, I. 1982. Diurnal variations in mean volume backscattering strength of an Antarctic krill Euphausia superba patch. Journal of Plankton Research, 4, 155-162.

EVERSON, I. 1983. Variations in vertical distribution and density of krill swarms in the vicinity of South Georgia. (In NEMOTO, T. AND MATSUDA, T., eds., Proceedings of the BIOMASS colloquium in 1982, 84-92.)

EWER, J.P. and ANDERSON, J.H. 1948. Bird report, Signy and Laurie Islands. Falkland Islands Dependencies Scientific Bureau No. 57/48 (Unpublished), 9 pp.

FALLA, R.A. 1937. British, Australian and New Zealand Antarctic Research Expedition report, 1929-1931 (Adelaide), Birds, Series B, 2, 1-288.

FLETT, W.R. 1944. Biological report, Deception Island. Operation Tabarin Report No 215 (Unpublished).

FURNESS, R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. Journal of Animal Ecology, 47, 39-53.

FURNESS, R.W. 1983. Variations in size and growth of great skua Catharacta skua chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. Journal of Zoology, 199, 101-116.

GAIN, L. 1913. The penguins of the antarctic regions. Report of the Smithsonian Institute, 1912, 475-482.

GOCHFELD, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. (In BURGER, J., OLLA, B.L. and WINN, H.E., eds., Behaviour of marine animals, New York, Plenum Press, 515pp.)

GOLDSMITH, R. 1962. Reproductive behaviour and adaptation in the Adélie penguin Pygoscelis adeliae. Journal of Reproduction and Fertility, 4, 237-238.

GRAILEY-PHIPPS, J. 1978. A world survey of penguins in captivity. International Zoo Yearbook, 18, 7-13.

GROSCOLAS, R. and CLEMENT, C. 1976. Utilisation des réserves énergétiques au cours du jeune de la réproduction chez le manchot empereur Aptenodytes forsteri. Comptes rendus, Academie des Sciences Paris, Série D, 282, 297-300.

GWYNN, A.M. 1953. The egg laying and incubation periods of rockhopper, macaroni and gentoo penguins. Australian National Antarctic Research Expedition Report, Series B, 1, 1-19.

HAMILTON, J.E. 1939. The leopard seal Hydrurga leptonyx (De Blainville). Discovery Reports, 18, 239-264.

HARRIS, M.P. 1966. Breeding biology of the Manx shearwater Puffinus puffinus. Ibis, 108, 17-33.

HARRIS, M.P. 1969 a. The biology of storm petrels in the Galapagos Islands. Proceedings of the Californian Academy of Sciences, Fourth Series, 37, 95-166.

HARRIS, M.P. 1969 b. Effect of laying date on chick production in oystercatchers and herring gulls. British Birds, 62, 70-75.

HARRIS, M.P. 1969 c. Factors influencing the breeding cycle of the red-billed tropicbird in the Galapagos Islands. Ardea, 57, 149-157.

HARRIS, M.P. and HISLOP, J.R.G. 1978. The food of young puffins Fratercula arctica. Journal of Zooloogy, 185, 213-236.

HODGES, B. and FERRAR, J.E. 1961. Ornithological report, Deception Island. Falkland Islands Dependencies Scientific Bureau, Q/1961/B (Unpublished).

HOWE, H.F. 1976. Egg size, hatching asynchrony, sex and brood reduction in the common grackle. Ecology, 57, 1195-1207.

HUNTER, S. 1983. The food and feeding ecology of the giant petrels Macronectes halli and M.giganteus at South Georgia. Journal of Zoology, 200, 521-538.

JACKSON, F., SIEGFRIED, W.R. and COOPER, J. 1976. A simulation model for the population dynamics of the jackass penguin. Transaction of the Royal Society of South Africa, 42, 11-21.

JAZDZEWSKI, K. 1981. Amphipod crustaceans in the diet of pygoscelid penguins of King George Island, South Shetland Islands, Antarctica. Polish Polar Research, 2, 133-144.

JOHNSON, S.R. and WEST, G.C. 1973. Fat content, fatty acid composition and estimates of energy metabolism of Adēlie penguins Pygoscelis adeliae during the early breeding season fast. Comparative Biochemistry and Physiology, 45B, 709-719.

JONES, N.V. 1963. The sheathbill Chionis alba (Gmelin) at Signy Island, South Orkney Islands. British Antarctic Survey Bulletin, 2, 53-71.

JONES, N.V. and PINDER, R. W. 1962. Ornithological report, Signy Island. Falkland Islands Dependencies Scientific Bureau, Q/1961/H (Unpublished).

JOUVENTIN, P. and MOUGIN, J-L. 1981. Les strategies adaptives des oiseaux de mer. Revue d'écologie (Terre et Vie), 35, 217-272.

JOUVENTIN, P., MOUGIN, J.L., STAHL, J.C. and WEIMERSKIRSH, H. (in press). The seabirds of the French Subantarctic islands and Adēlie Land: Their status and conservation. (In: CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, W.R., eds., The status and conservation of seabirds. ICBP, Croom Helm.)

KALINOWSKI, J. and WITEK, Z. 1980. Diurnal vertical distribution of krill aggregations in the western Antarctic. Polish Polar Research, 1, 127-146.

KENDEIGH, S.C. 1970. Energy requirements for existence in relation to size of bird. Condor, 72, 60-65.

KENDEIGH, S.C. 1974. Seasonal allocation of time and energy resources in birds. (In PAYNTER, R.A. Jr., ed., Avian energetics. Publications of the Nuttall Ornithological Club, 15, 152-297.)

KENDEIGH, S.C., DOL'NIK, V.R. and GAVRILOV, V.M. 1977. Avian energetics. (In PINOWSKI, J. and KENDEIGH, S.C., eds., Granivorous birds in ecosystems. Cambridge, Cambridge University Press, 127-204.)

KINSKY, F.C. 1960. The yearly cycle of the northern blue penguin Eudyptula minor novaehollandiae in the Wellington Harbour area. Records of the Dominion Museum, Wellington, 3, 145-218.

KOJIMA, I 1978. Breeding Humboldt's penguins Spheniscus humboldtii at Kyoto Zoo. International Zoo Yearbook, 18, 53-59.

KOOYMAN, G.L. 1975. The physiology of diving in penguins. (In STONEHOUSE, B., ed., The biology of penguins. London, Macmillan, p.115-137.)

KOOYMAN, G.L., BILLUPS, J.O. and W.D.FARWELL. 1983. Two recently developed recorders for monitoring diving activity of marine birds and mammals. (In MACDONALD, A.G. and PRIEDE, I.G., eds., Experimental biology at sea. New York, Academic Press.)

KOOYMAN, G.L., DAVIS, R.W. and CROXALL, J.P. (in press). Diving behaviour of the Antarctic fur seal Arctocephalus gazella. (In KOOYMAN, G.L. and GENTRY, R.L., eds., Fur seals: maternal strategies on land and at sea, Princeton, Princeton University Press.)

KOOYMAN, G.L., DRABEK, C.M., ELSNER, R. and CAMPBELL, W.B. 1971. Diving behaviour of the emperor penguin Aptenodytes forsteri. Auk, 88, 775-795.

KOOYMAN, G.L., DAVIS, R.W., CROXALL, J.P. and COSTA, D.P. 1982. Diving depths and energy requirements of king penguins. Science, 217, 726-727.

KYTE, G.F. 1962. Ornithological report, Deception Island. Falkland Islands Dependencies Scientific Bureau, Q/1962/B (Unpublished).

LACK, D. 1947. The significance of clutch size. Parts I and II. Ibis, 89, 302-352.

LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press, 343 pp.

LACK, D. 1966. Population studies of birds. Oxford, Clarendon Press, 341 pp.

LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen, xii + 409 pp.

LACK, D. 1971. Ecological isolation in birds. Oxford, Blackwell, 404 pp.

LASIEWSKI, R.C. and DAWSON, W.R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor, 69, 13-23.

LAWS, R.M. 1949. Preliminary biological report, Signy Island, October-November 1948. Falkland Islands Dependencies Scientific Bureau No. 51/49 (Unpublished), 37 pp.

LAWS, R.M. 1977. Seals and whales in the Southern Ocean. Philosophical Transactions of the Royal Society of London, B, 279, 81-96.

LEMAHO, Y. 1977. The emperor penguin: a strategy to live and breed in the cold. American Science, 65, 680-693.

LERESCHE, R.E. and SLADEN, W.J.L. 1970. Establishment of pair and breeding site bonds by young known-age Adélie penguins Pygoscelis adeliae. Animal Behaviour, 18, 517-526.

LEVICK, G.M. 1914. Antarctic penguins: a study of their social habits. London, Heinemann, 140 pp.

LEVICK, G.M. 1915. Natural history of the Adélie penguin. British Antarctic Terra Nova Expedition 1910. Natural History Report, Zoology, 1, 55-84.

LOCKYER, C. 1973. Wet weight, volume and length correlation in the Antarctic krill Euphausia superba. (In MACKINTOSH N.A., Distribution of post-larval krill in the Antarctic. Discovery Reports, 36, 152-155.)

MACKINTOSH, N.A. 1973. Distribution of post-larval krill in the Antarctic. Discovery Reports, 36, 95-156.

MAHER, W.J. 1964. Growth rate and development of endothermy in the snow bunting Plectrophenax nivalis and Lapland bunting Calcarius lapponicus at Barrow, Alaska. Ecology, 45, 520-528.

MARR, J.W.S. 1962. The natural history and geography of the Antarctic krill Euphausia superba Dana. Discovery Reports, 32, 33-464.

MAUCHLINE, J. and FISHER, L.R. 1969. The biology of euphausiids. Advances in Marine Biology, 7, 1-454.

MENEGAUX, A. 1907. Expedition Antarctique Francaise 1903-1905. Oiseaux, 4, 1-79.

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.

MILLER, R.S. 1973. The brood size of cranes. Wilson Bulletin, 85, 436-441.

MOUGIN, J-L. 1966. Observations écologique à la colonie de manchots empereur de Pointe Géologie (Terre Adélie) en 1964. Oiseau, 36, 167-226.

MOUGIN, J-L. 1967. Etude écologique des deux espèces de fulmars, le fulmar Atlantique Fulmarus glacialis et le fulmar Antarctique F.glacialoides. L'Oiseau et la Révue Francaise d'Ornithologie, 37, 57-103.

MOUGIN, J-L. 1968. Notes sur le cycle reproducteur et la mue du manchot Adélie Pygoscelis adeliae dans l'Archipel de Pointe Géologie (Terre Adélie). L'Oiseau et la Révue Francaise d'Ornithologie, 38, 89-94.

MULLER-SCHWARZE, D. and MULLER-SCHWARZE, C. 1975. A survey of twenty-four rookeries of pygoscelid penguins in the Antarctic Peninsula region. (In STONEHOUSE, B., ed., The biology of penguins. London, Macmillan, p. 309-320.

MUNRO, J. and BEDARD, J. 1977 a. Gull predation and crêching behaviour in the common eider. Journal of Animal Ecology, 46, 799-810.

MUNRO, J. and BEDARD, J. 1977 b. Crêche formation in the common eider. Auk, 94, 759-771.

MURRAY, J. 1909. Biology, Penguins. Appendix I to SHACKLETON, E.H., The heart of the Antarctic, 2, 243-260. London, Heinemann, 418 pp.

MURPHY, R.C. 1936. Oceanic birds of South America. New York, Macmillan, 1245 pp.

MURTON, R.K. 1961. Some survival estimates for the wood pigeon. Bird Study, 8, 165-173.

MYRCHA, A. and KAMINSKI, P. 1982. Changes in body calorific values during nestling development of penguins of the genus Pygoscelis. Polish Polar Research, 3, 81-88.

NAGY, K.A., SIEGFRIED, W.R., and WILSON, R.P. (in press). Energy utilization by free-ranging jackass penguins Sphensiscus demersus. Ecology.

NELSON, J.B. 1966. The breeding biology of the gannet Sula bassana on the Bass Rock, Scotland. Ibis, 108, 584-626.

NELSON, J.B. 1970. The relationship between behaviour and ecology in the Sulidae with reference to other seabirds. Oceanography and Marine Biology, 8, 501-574.

NELSON, J.B. 1977. Some relationships between food and breeding in the marine Pelecaniformes. (In STONEHOUSE, B. and PERRINS, C.M., eds., Evolutionary ecology. London, Macmillan, 77-87 pp.)

NELSON, J.B. 1978. The Sulidae. Oxford, Oxford University Press, 1012 pp.

NEMOTO, T. and NASU, K. 1975. Present status of exploitation and biology of krill in the Antarctic. (In Oceanology International 75. Conference papers. London, BPS Exhibitions, 353-360.)

NEMOTO, T., DAI, T. and NASU, K. 1981. Biological characteristics of krill caught in the Southern Ocean. (In BIOMASS, Vol II. Cambridge, SCAR/SCOR, 47-63.)

NEWTON, I. 1978. Breeding strategies in birds of prey. Living Bird, 16, 51-82.

NORDERHAUG, M. 1980. The breeding biology of the little auk Plautus alle in Svalbard. Skrifter Norsk Polarinstitutt, 173, 1-43.

O'CONNOR, R.J. 1977. Growth strategies in nestling passerines. The Living Bird, 16, 209-238.

O'CONNOR, R.J. 1978. Brood reduction in birds: selection for fratricide, infanticide or suicide? Animal Behaviour, 26, 79-96.

OELKE, H. 1975. Breeding behaviour and success in a colony of Adélie penguins Pygoscelis adeliae at Cape Crozier, Antarctica. (In STONEHOUSE, B., ed., The biology of penguins, London, MacMillan, 363-395.)

OELKE, H. 1978. Natural or human influences on population changes of Adélie penguins Pygoscelis adeliae in the Ross Sea sector of Antarctica. Journal für Ornithologie, 119, 1-13.

PATTERSON, I.J. 1965. Timing and spacing of broods in the black-headed gull Larus ridibundus. Ibis, 107, 433-459.

PAULIAN, P. 1953. Pinnipedes, cetacés, oiseaux des Iles Kerguelen et Amsterdam. Mission Kerguelen 1951. Membre de l'Institut Science de Madagascar, Série A, 8.

PENNEY, R.L. 1964. The Adélie penguin's faithfulness to territory and mate. Biologie Antarctique, 401-406.

PENNEY, R.L. 1968. Territorial and social behaviour in the Adélie penguin. (In AUSTIN, O.L. Jr., ed., Antarctic Research Series, 12. Washington, American Geophysical Union, 83-131.)

PENNEY, R.L. and LOWRY, G. 1967. Leopard seal predation on Adélie penguins. Ecology, 48, 879-882.

PERRINS, C.M. 1965. Population fluctuations and clutch size in the great tit Parus major L. Journal of Animal Ecology, 34, 601-647.

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

PERRINS, C.M. and MOSS, D. 1975. Reproductive rates in the great tit. Journal of Animal Ecology, 44, 695-706.

PETTINGILL, O.S. Jr. 1960. Crêche behaviour and individual recognition in a colony of rockhopper penguins. Wilson Bulletin, 72, 213-221.

PETRUSEWICZ, K. and MACFADYEN, A. 1970. Productivity of terrestrial animals: principles and methods. IBP Handbook 13. Oxford, Blackwell Scientific Publications, 190 pp.

PINDER, R.W. 1961. Ornithological report, Signy Island. Falkland Islands Dependencies Scientific Bureau, N1/1961/H (Unpublished).

PINDER, R.W. 1966. The cape pigeon Daption capensis Linnaeus at Signy Island, South Orkney Islands. British Antarctic Survey Bulletin, 8, 19-47.

PREVOST, J. 1961. Ecologie du manchot empereur. Paris, Hermann.

PREVOST, J. and SAPIN-JALOUSTRE, J. 1965. Ecologie des manchots Antarctiques. (In VAN OYE, P. and VAN MIEGHEN, J., eds., Biogeography and ecology in Antarctica. The Hague, Junk Monograph.)

PRINCE, P.A. 1980 a. The food and feeding ecology of blue petrel Halobaena caerulea and dove prion Pachyptila desolata. Journal of Zoology, 190, 59-76.

PRINCE, P.A. 1980 b. The food and feeding ecology of grey-headed albatross Diomedea chrysostoma and black-browed albatross Diomedea melanophrys. Ibis, 122, 476-488.

PRINCE, P.A. (in press). Ecological and trophodynamic aspects of the relationships between black-browed and grey-headed albatrosses and the Southern Ocean marine system. Proceedings of the Fourth SCAR Symposium on Antarctic Biology.

PRINCE, P.A. and CROXALL, J.P. 1983. Birds of South Georgia: New records and re-evaluation of status. British Antarctic Survey Bulletin, 58.

PRINCE, P.A. and FRANCIS, M. (in press). Activity budgets of foraging gray-headed albatrosses. Condor.

PRINCE, P.A. and RICKETTS, C. 1981. Relationships between food supply and growth in albatrosses: an interspecies chick-fostering experiment. Ornis Scandinavica, 12, 207-210.

PRINCE, P.A., RICKETTS, C. and THOMAS, G. 1981. Weight loss in incubating albatrosses and its implications for their energy and food requirements. Condor, 83, 238-242.

RAHN, H. and HAMMEL, H.T. 1982. Incubation water loss, shell conductance and pore dimensions in Adélie penguin eggs. Polar Biology, 1, 91-97.

RANDALL, R.M., RANDALL, B.M. and KLINGELHOEFFER, E.W. 1981. Species diversity and size ranges of cephalopods in the diet of jackass penguins from Algoa Bay, South Africa. South African Journal of Zoology, 16, 163-166.

REECE, A.W. 1945. Natural History notes. Operation Tabarin, report 212 (Unpublished).

REID, B. 1965. The Adélie penguin Pygoscelis adeliae egg. New Zealand Journal of Science, 8, 503-514.

REILLY, P.N. and BALMFORD, P. 1975. A breeding study of the little penguin Eudyptula minor in Australia. (In STONEHOUSE, B., ed., The biology of penguins, London, MacMillan, 161-187.)

REILLY, P.N. and CULLEN, J.M. 1979. The little penguin Eudyptula minor in Victoria. I: Mortality of adults. Emu, 79, 97-102.

REILLY, P.N. and CULLEN, J.M. 1981. The little penguin Eudyptula minor in Victoria. II: Breeding. Emu, 81, 1-19.

RICHARDS, P.A. 1960. Ornithological report, Signy Island. Falkland Islands Dependencies Scientific Bureau, 135/59 (Unpublished).

RICHDALE, L.E. 1940. Random notes on the genus Eudyptula on the Otago Peninsula, New Zealand. Emu, 40, 180-217.

RICHDALE, L.E. 1949. A study of penguins of known age. Biological Monographs, 1, 1-88.

RICHDALE, L.E. 1950. Further notes on the erect-crested penguin. Emu, 49, 153-166.

RICHDALE, L.E. 1951. Sexual behaviour in penguins. Kansas, University of Kansas Press.

RICHDALE, L.E. 1957. A population study of penguins. Oxford, Clarendon Press, 195 pp.

RICKETTS, C. and PRINCE, P.A. 1981. Comparison of growth of albatrosses. Ornis Scandinavica, 12, 120-124.

RICKLEFS, R.E. 1965. Brood reduction in the curve-billed thrasher. Condor, 47, 45-62.

RICKLEFS, R.E. 1968 a. Patterns of growth in birds. Ibis, 110, 419-451.

RICKLEFS, R.E. 1968 b. Weight recession in nestling birds. Auk, 85, 30-35.

RICKLEFS, R.E. 1968 c. On the limitation of brood size in passerine birds by the ability of birds to nourish their young. Proceedings of the National Academy of Sciences of the United States of America, 61, 847-851.

RICKLEFS, R.E. 1969. Preliminary models for growth rates of altricial birds. Ecology, 50, 1031-1039.

RICKLEFS, R.E. 1973. Patterns of growth in birds. II, Growth and mode of development. Ibis, 115, 177-201.

RICKLEFS, R.E. 1974. Energetics of reproduction in birds. (In PAYNTER, R.A. Jr., ed., Avian energetics. Publications of the Nuttall Ornithological Club, 15, 152-297.)

RICKLEFS, R.E. 1976. Growth rates of birds in the humid new world tropics. Ibis, 118, 179-207.

RICKLEFS, R.E. 1979 a. Patterns of growth in birds. V, A comparative study of development in the starling, common tern and Japanese quail. Auk, 96, 10-30.

RICKLEFS, R.E. 1979 b. Adaptation, constraint and compromise in avian postnatal development. Biological Reviews of the Cambridge Philosophical Society, 54, 269-290.

RICKLEFS, R.E. (in press). The optimization of growth rate in altricial birds. Ecology.

ROBERTS, B. 1940. The breeding behaviour of penguins with special reference to Pygoscelis papua (Forster). British Grahamland Expedition 1934-37, Scientific Report, 1, 195-254.

ROBERTSON, C.J.R. and BELL, B.D. (in press). Seabird status and conservation in the New Zealand region. (In: CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, W.R., eds., The status and conservation of seabirds. ICBP, Croom Helm.)

ROOTES, D.M. 1978. Ornithological report, Signy Island. British Antarctic Survey report Q1/78/H (Unpublished).

ROSS, G.J.S., HAWKINS, D., JONES, R.D., KEMPTON, R.A., LAUCKNER, F.B., PAYNE, R.W. and WHITE, R.P. 1980. MLP: Maximum Likelihood Program. Rothamstead Experimental Station, U.K.

ROUNSEVELL, D.E. and BROTHERS, N.P. (in press). The status and conservation of seabirds at Macquarie Island. (In: CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, W.R., eds., The status and conservation of seabirds. ICBP, Croom Helm.)

ROWAN, M.K. 1965. Regulation of seabird numbers. Ibis, 107, 54-59.

SAPIN-JALOUSTRE, J. 1960. Ecologie du manchot Adélie. Paris, Herman, 211 pp.

SAPIN-JALOUSTRE, J. and BOURLIERE, F. 1951. Incubation et developpement du poussin chez le manchot Adélie Pygoscelis adeliae. Rêvue internationale d'Ornithologie, 19, 65-83.

SCHALLER, G. 1964. Breeding behaviour of the white pelican at Yellowstone Lake, Wyoming. Condor, 66, 3-23.

SCHLATTER, R. (in press). The status and conservation of seabirds in Chile. (In: CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, W.R., eds., The status and conservation of seabirds. ICBP, Croom Helm.)

SCOLARO, J.A., HALL, M., XIMENEZ, I.M. and KOVACS, O. 1980. El pingüino de magallanes (Spheniscus magellanicus). II: Biología y desarrollo de la incubación en la colonia de Punta Tombo, Chubut, Argentina. Revista del Museo Argentino de Ciencias Naturales "Bernadino Rivadávia", Ecología, 2, 103-110.

SCOTLAND, C.D. 1958. Ornithological report-Signy Island, 1957-58. Falkland Islands Dependencies Survey No. 99/58 (Unpublished) 9 pp.

SEALY, S.G. 1972. Adaptive differences in breeding biology in the marine bird family Alcidae. Unpublished Ph.D.thesis, University of Michigan.

SHARMAN, A. 1959. Bird report, Signy Island. Falkland Islands Dependencies Scientific Bureau, No. 38/59 (Unpublished).

SHEVTSOV, V.V. and MAKAROV, R.R. 1969. On the biology of the Antarctic krill. Trudy VNIRO, 66, 177-206.

SLADEN, W.J.L. 1953. The Adélie penguin. Nature, 171, 952-955.

SLADEN, W.J.L. 1954. The biology of the pygoscelid penguins. D.Phil. Thesis, University of Oxford.

SLADEN, W.J.L. 1955. Some aspects of the behaviour of Adélie and chinstrap penguins. Acta XI Congressus Internationalis Ornithologici. Basel, 229-30.

SLADEN, W.J.L. 1958. The pygoscelid penguins: I. Methods of study; II. The Adélie penguin Pygoscelis adeliae (Hombron & Jacquinot). Falkland Islands Dependencies Survey Scientific Reports, No.17, 97 pp.

SLADEN, W.J.L. 1964. The distribution of the Adélie and chinstrap penguins. (In CARRICK, R., HOLDGATE, M. and PREVOST, J., eds., Biologie Antarctique. Paris, Hermann, 359-365.)

SLADEN, W.J.L. 1978. Sexing penguins by cloacascope. International Zoo Yearbook, 18, 77-80.

SLADEN, W.J.L. and LERESCHE, R.E. 1970. New and developing techniques in Antarctic ornithology. (In HOLDGATE, M.W., ed., Antarctic Ecology, Vol.1. New York, Academic Press, 585-604.)

SLADEN, W.J.L. and PENNEY, R.L. 1960. Penguin flipper-bands used by the USARP bird-banding program 1958-1960. Bird-banding, 31, 79-81.

SPELLERBERG, I.F. 1975. The predators of penguins. (In STONEHOUSE, B., ed., The biology of penguins. London, Macmillan, 413-434.)

SPURR, E.B. 1972. Social organization of the Adélie penguin Pygoscelis adeliae. Ph.D. Thesis. University of Canterbury, Christchurch, New Zealand.

SPURR, E.B. 1974. Individual differences in aggressiveness of Adélie penguins. Animal Behaviour, 22, 611-616.

SPURR, E.B. 1975 a. The breeding of the Adélie penguin Pygoscelis adeliae at Cape Bird. Ibis, 117, 324-338.

SPURR, E.B. 1975 b. Communication in the Adélie penguin. (In STONEHOUSE, B., ed., The biology of penguins, London, MacMillan, 449-501.)

SPURR, E.B. 1977. Adaptive significance of the re-occupation period of the Adélie penguin. (In LLANO, G.A., ed., Adaptations within Antarctic ecosystems. Washington D.C., Smithsonian Institute.)

STEMPNIEWICZ, L. 1981. Breeding biology of the little auk Plautus alle in the Hornsund region, Spitsbergen. Acta Ornithologica, 18, 141-165.

STEPNIK, R. 1982. All-year populational studies of Euphausiacea (Crustacea) in the Admiralty Bay (King George Island, South Shetland Islands, Antarctica). Polish Polar Research, 3, 49-68.

STONEHOUSE, B. 1953. The emperor penguin Aptenodytes forsteri. I, Breeding behaviour and development. Falkland Islands Dependencies Survey Scientific Report, 6, 1-33.

STONEHOUSE, B. 1960. The king penguin Aptenodytes patagonicus of South Georgia. I, Breeding behaviour and development. Falkland Islands Dependencies Survey Scientific Report, 23, 1-81.

STONEHOUSE, B. 1963. Observations on Adélie penguins Pygoscelis adeliae at Cape Royds, Antarctica. XIII International Ornithological Congress, Proceedings, 766-779.

STONEHOUSE, B. 1970. Adaptation in polar and sub-polar penguins (Spheniscidae). (In HOLDGATE, M.W., eds., Antarctic Ecology, Vol.1. London, Academic Press, 526-541.)

STONEHOUSE, B. 1975. Introduction: The Spheniscidae. (In STONEHOUSE, B., ed., The biology of penguins, London, MacMillan, 1-15.)

TAYLOR, R.H. 1962. The Adélie penguin Pygoscelis adeliae at Cape Royds. Ibis, 104, 176-204.

TAYLOR, R.H. and ROBERTS, H.S. 1962. Growth of Adélie penguin Pygoscelis adeliae (Hombron & Jacquinot) chicks. New Zealand Journal of Science, 5, 191-97.

TENAZA, R. 1971. Behaviour and nesting success relative to nest location in Adélie penguins Pygoscelis adeliae. Condor, 73, 81-92.

THOMAS, G. 1982. The food and feeding ecology of the light-mantled sooty albatross at South Georgia. Emu, 82, 92-100.

THOMAS, G., CROXALL, J.P. and PRINCE, P.A. 1983. Breeding biology of the light-mantled sooty albatross Phoebetria palpebrata at South Georgia. Journal of Zoology, 199, 123-135.

THOMPSON, D.H. 1981. Feeding chases in the Adélie penguin. Antarctic Research Series, 30, 105-122.

THOMPSON, D.H. and EMLEN, J.J. 1968. Parent-chick individual recognition in the Adélie penguin. Antarctic Journal of the United States, 3, 132.

TICKELL, W.L.N. 1956. Bird report, Signy Island. Falkland Islands Scientific Bureau, Q61/1956/H (Unpublished).

TICKELL, W.L.N. and PINDER, R. 1975. Breeding biology of the black-browed albatross Diomedea melanophris and grey-headed albatross D.chrystoma at Bird Island, South Georgia. Ibis, 117, 433-451.

TINBERGEN, N. 1951. The study of instinct. London, Oxford University Press.

TOLLU, B. 1978. Contributions à l'étude des Spheniscides du genre Eudyptes dans les Iles australes Francaises (Amsterdam, St. Paul, Crozet, Kerguelen). Unpublished Thèse de doctorat es-sciences biologique. Université Paris VII.

TOPLIFFE, F. 1963. Ornithological report, Signy Island. Falkland Islands Scientific Bureau, Q/1962/H (Unpublished).

TRIVELPIECE, W.Z. 1981. Ecological studies of pygoscelid penguins and Antarctic skuas. Unpublished Ph.D.Thesis, State University of New York.

TRIVELPIECE, W.Z. and VOLKMAN, N.J. 1979. Nest site competition between Adélie and chinstrap penguins: an ecological interpretation. Auk, 96, 675-681.

VOLKMAN, N.J. and TRIVELPIECE, W.Z. 1980. Growth in pygoscelid penguin chicks. Journal of Zoology, 191, 521-530.

VOLKMAN, N.J. and TRIVELPIECE, W.Z. 1981. Nest-site selection among Adélie, chinstrap and gentoo penguins in mixed species rookeries. Wilson Bulletin, 93, 243-248.

VOLKMAN, N.J., PRESLER, P. and TRIVELPIECE, W.Z. 1980. Diets of pygoscelid penguins at King George Island, Antarctica. Condor, 82, 373-378.

WARHAM, J. 1963. The rockhopper penguin Eudyptes chrysocome at Macquarie Island. Auk, 80, 229-256.

WARHAM, J. 1971. Aspects of breeding in the royal penguin Eudyptes chrysollophus schlegeli. Notornis, 18, 91-115.

WARHAM, J. 1974 a. Breeding biology and behaviour of the Snares crested penguin. Journal of the Royal Society of New Zealand, 4, 63-108.

WARHAM, J. 1974 b. The Fiordland crested penguin Eudyptes pachyrhynchus. Ibis, 116, 1-27.

WATSON, G.E. 1975. Birds of the Antarctic and Sub-Antarctic. Washington, American Geophysical Union, 350 pp.

WHITE, P.O. 1958. Report on observations of bird life. Deception Island. Falkland Islands Dependencies Scientific Bureau, No.53/58 (Unpublished).

WHITE, M.G. and CONROY, J.W.H. 1975. Aspects of competition between pygoscelid penguins at Signy Island, South Orkney Islands. Ibis, 117, 371-373.

WIENS, J.A. and SCOTT, J.M. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor, 77, 439-452.

WILLIAMS, A.J. 1980 a. Aspects of the breeding biology of the gentoo penguin Pygoscelis papua. Le Gerfaut, 70, 283-295.

WILLIAMS, A.J. 1980 b. Offspring reduction in rockhopper and macaroni penguins. Auk, 97, 754-759.

WILLIAMS, A.J. 1981 a. Why do penguins have long laying intervals? Ibis, 123, 202-204.

WILLIAMS, A.J. 1981 b. The laying interval and incubation period of rockhopper and macaroni penguins. Ostrich, 52, 226-229.

WILLIAMS, A.J. 1982. Chick feeding rates of macaroni and rockhopper penguins at Marion Island. Ostrich, 53, 129-134.

WILLIAMS, A.J. (in press). Breeding distribution, numbers and conservation of seabirds on islands in the African sector of the Southern Ocean. (In: CROXALL, J.P., EVANS, P.G.H. and SCHREIBER, W.R., eds., The status and conservation of seabirds. ICBP, Croom Helm.)

WILLIAMS, A.J. and LAYCOCK, P.A. 1981. Euphausiids in the diet of some Subantarctic Eudyptes penguins. South African Journal of Antarctic Research, 10/11, 27-28.

WILLIAMS, A.J., SIEGFRIED, W.R., BURGER, A.E. and BERRUTI, A. 1979. The Prince Edward Is: A sanctuary for seabirds in the Southern Ocean. Biological Conservation, 15, 59-71.

WILSON, E.A. 1907. Aves. British National Antarctic Expedition Reports, 1901-1904. Natural History, 2, 1-121.

WILSON, G.J. 1983. Distribution and abundance of Antarctic and Subantarctic penguins: A synthesis of current knowledge. BIOMASS Scientific Series, No. 4, 46 pp.

WILSON, R.P. (in press). An improved stomach pump for penguins and other seabirds. Journal of Field Ornithology.

YEATES, G.W. 1968. Studies on the Adélie penguin at Cape Royds 1964-65 and 1965-66. New Zealand Journal of Marine and Freshwater research, 2, 472-496.

YEATES, G.W. 1975. Microclimate, climate and breeding success in Antarctic penguins. (In STONEHOUSE, B., ed., The biology of penguins. London, Macmillan, 397-409.)

# APPENDICES

Appendix 1.1. The variation of the ice conditions around Signy I during the summer months of 1980/81.

| Month | Day | Ice amount (tenths) | Areas of open water | Major areas of leads in the ice |
|---|---|---|---|---|
| October | 09 | 5-10 | West horizon | |
| | 16 | 10 | West Normanna Strait | |
| | 23 | 10 | West horizon | Robertson Is |
| | | | West Normanna Strait | |
| | 26 | 10 | 10 km south | Robertson Is, Moe Is, |
| | | | 9 km west | Fyr Channel, Gourlay |
| | | | | Peninsula |
| | 30 | 6-9 | 10 km south | Normanna Strait |
| | | | 9 km west | Gourlay Peninsula |
| | | | 30 km east | |
| November | 06 | 5-9 | 10 km west | Moe I east to Gourlay |
| | | | 9 km south | Peninsula, Normanna |
| | | | | Strait |
| | | | 30 km east | |
| | 13 | " | " | " |
| | 21 | 6-8 | All horizons | All coasts Signy I |
| | 26 | 7 | | |
| December | 04 | 5-8 | Open, loose pack | All coasts except east |
| | | | | Signy I and Robertson |
| | | | | Is |
| | 11 | 5 | Loose pack west | |
| | | 7-8 | South to northeast | |

Appendix 1.1. (continued)

| Month | Day | Ice amount (tenths) | Areas of open water | Major areas of leads in the ice |
|---|---|---|---|---|
| December | 18 | 4-6 | Loose pack, open only to southeast | |
| January | 03 | 7-10 | None | North Point and south coast of Signy I |
| | 04 | 10 | None | |
| | 06 | | | East and south coast of Signy I |
| | 08 | 4-8 | North and west horizons | Generally loose |
| | 09 | 8 | Normanna Strait | |
| | | | Orwell Bight | |
| | 12 | 10 | Coasts of Signy I | |
| | | | Orwell Bight | |
| | 16 | 9 | None | None |
| | 17 | 9 | None | Loose on coasts of Signy I |
| | 18 | 9 | None | None |
| | 19 | 10 | None | None |
| | 22 | 7-10 | West and south horizons | Robertson Is |
| | 23 | | To horizon, beyond coastal ice | Gourlay Peninsula, Orwell Bight |
| | 29 | 8-10 | Southwest | Normanna Strait, Moe I |
| February | 05 | 5 | Southeast | Coasts of Signy I |
| | 11 | Ice completely left the vicinity of the South Orkney Is | | |

| Study colony | Breeding[3] pairs | Area[5] ($m^2$) | Max[5] length | Max[5] width | Basic shape | Height a.s.l. (m) | Distance[6] to sea (m) | Slope Angle | Slope Faces | Drainage % Wet[7] | Drainage % Inter-[8] mediate | Drainage % Dry[9] | Terrain % Large[10] rocks | Terrain % Small[11] rocks | Terrain % Flat areas | Colony border % Irreg-ular | Colony border % Undulat-ing | Colony border % Regular | Adjacent colonies | % edge covered |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Adélie | | | | | | | | | | | | | | | | | | | | |
| A26[1] | 207 | 208 | 18 | 11 | Oval | 20 | 46 | Flat | - | 40 | 30 | 30 | 5 | 20 | 75 | 0 | 20 | 80 | C66 | 75 |
| A40[1] | 491 | 220 | 24 | 11 | Oval | 23 | 91 | Flat | - | 60 | 20 | 20 | 5 | 15 | 80 | 0 | 20 | 80 | C78 | 60 |
| A41[1,2] | 378 | 284 | 22 | 18 | Oval | 26 | 91 | Flat | - | 25 | 50 | 25 | 0 | 10 | 90 | 0 | 20 | 80 | C82 | 5 |
| A42[1] | 153 | 49 | 14 | 6 | Oval | 10 | 27 | 5° | East | 0 | 5 | 95 | 0 | 20 | 80 | 0 | 0 | 100 | C83 | 60 |
| A47[1], | 1957 | 827 | 44 | 21 | Oval | 10 | 35 | 5° | West | 60 | 35 | 5 | 0 | 30 | 70 | 0 | 50 | 50 | C100 | 80 |
| Chinstrap | | | | | | | | | | | | | | | | | | | | |
| C76[1,2] | 1597 | 2289 | 71 | 48 | Rect. | 8-12 | 9 | 20° | North | 10 | 45 | 45 | 20 | 50 | 30 | 40 | 60 | 0 | C77 | 20 |
| C77[2] | 1365 | 266[4] | 20[4] | 15[4] | Rect. | 20-25 | 69 | 35° | North | 10 | 45 | 45 | 20 | 40 | 40 | 40 | 60 | 0 | C76 | 10 |
| C78[2] | 1442 | 173[4] | 40[4] | 16[4] | Oval | 8-12 | 15 | 30° | East | 5 | 80 | 15 | 30 | 60 | 10 | 40 | 60 | 0 | A39,A40 | 10 |
| C79[1] | 185 | 241 | 24 | 13 | Rect. | 6 | 15 | 40° | North | 0 | 50 | 50 | 30 | 40 | 30 | 50 | 50 | 0 | None | None |
| C80[1,2] | 853 | 1171 | 58 | 9-34 | Tria. | 8-12 | 23 | 10-50° | North | 10 | 40 | 50 | 5 | 60 | 35 | 50 | 50 | 0 | None | None |
| C91[1] | 119 | 165 | 18 | 13 | Rect. | 3 | 9 | Flat | - | 60 | 20 | 20 | 20 | 20 | 60 | 30 | 50 | 20 | None | None |
| C94[1] | 411 | 431 | 42 | 13 | Oval | 10 | 18 | 25° | North | 0 | 50 | 50 | 40 | 20 | 40 | 0 | 100 | 0 | None | None |
| C100[2] | 1240 | 77 | 20 | 6 | Oval | 10 | 15 | 40° | South | 20 | 40 | 40 | 25 | 50 | 25 | 0 | 50 | 50 | A47 | 50 |

Notes:
1. used for study in 1980/81. 2. used for study in 1981/82. 3. from Croxall and others (1981). 4. measurements of parts where study nests were located - separated by natural barrier from rest of colony. 5. from field measurements and from maps used by Croxall and others (1981). 6. shortest feasible walking route for penguins. 7. perpetually wet during breeding season. 8. waterlogged after heavy rain. 9. well drained - dry after rain. 10. > $1m^3$. 11. < 1 $m^3$. 12. increased colony edge irregularity increases number of peripherally nesting birds.

Appendix 2.1. Dimensions and descriptions of all the colonies used for this study.

Appendix 2.2. The dates of first arrival at breeding sites.

| Locality | Latitude °S | Year | Arrival date | Reference |
|---|---|---|---|---|
| Adélie | | | | |
| Signy I | 61° | 1903 | 07/10 | Clarke (1906) |
| " | " | 1904 | 08/10 | " |
| " | " | 1947 | 04/10 | Ewer and Anderson (1948) |
| " | " | 1948 | 02/10 | Laws (1949) |
| " | " | 1950 | 08/10 | Sladen (1953) |
| " | " | 1953 | 04/10 | " |
| " | " | 1955 | 03/10 | Tickell (1956) |
| " | " | 1957 | 29/09 | Scotland (1958) |
| " | " | 1958 | 01/10 | Sharman (1959) |
| " | " | 1960 | 03/10 | Pinder (1961) |
| " | " | 1961 | 01/10 | Jones and Pinder (1962) |
| " | " | 1962 | 25/09 | Topliffe (1963) |
| " | " | 1979 | 30/09 | This study |
| " | " | 1980 | 21/09 | " |
| " | " | 1981 | 28/09 | " |
| King George I | 62° | 1977 | 20/10 | Trivelpiece and Volkman (1979) |
| Hope Bay | 63° | 1945 | 07/10 | Sladen (1958) |
| " | " | 1946 | 21/09 | " |
| " | " | 1947 | 04/10 | " |
| " | " | 1948 | 30/09 | " |
| " | " | 1952 | 20/09 | " |
| Paulet I | 64° | 1903 | 12/10 | Menegaux (1907) |
| Booth I | 65° | 1904 | 15/10 | " |
| Peterman I | 65° | 1909 | 12/10 | Gain (1913) |
| Point Martin | 66° | 1950 | 20/10 | Sapin-Jaloustre (1960) |
| Pointe-Géologie | 66° | 1950 | 21/10 | " |
| " | " | 1952 | 18/10 | Mougin (1968) |
| " | " | 1956 | 21/10 | " |
| " | " | 1961 | 13/10 | " |
| " | " | 1962 | 18/10 | " |
| " | " | 1963 | 16/10 | " |
| " | " | 1964 | 08/10 | " |
| Cape Denison | 67° | 1912 | 12/10 | Falla (1937) |
| " | " | 1913 | 17/10 | " |
| Avian I | 67° | 1978 | 10/10 | Poncet (unpublished) |
| Cape Adare | 71° | 1899 | 14/10 | Bernacchi (1901) |
| " | " | 1911 | 13/10 | Levick (1915) |
| Cape Crozier | 77° | 1902 | 20/10 | Wilson (1907) |
| " | " | 1968 | 19/10 | Ainley and LeResche (1973) |
| " | " | 1969 | 22/10 | " |
| Cape Royds | 77° | 1959 | 23/10 | Taylor (1962) |
| " | " | 1961 | 21/10 | Stonehouse (1963) |
| Cape Bird | 77° | 1968 | 25/10 | Spurr (1975a) |

Appendix 2.2 (continued)

| Locality | Latitude °S | Year | Arrival date | Reference |
|---|---|---|---|---|
| Chinstrap | | | | |
| Signy I | 61° | 1947 | 31/10 | Ewer and Anderson (1948) |
| " | " | 1957 | 12/11 | Scotland (1955) |
| " | " | 1958 | 28/10 | Sharman (1959) |
| " | " | 1960 | 28/10 | Pinder (1961) |
| " | " | 1961 | 01/11 | Jones and Pinder (1962) |
| " | " | 1962 | 16/10 | Topliffe (1963) |
| " | " | 1970 | 01/11 | Conroy and others (1975a) |
| " | " | 1979 | 30/10 | This study |
| " | " | 1980 | 08/11 | " |
| " | " | 1981 | 05/11 | " |
| King George I | 62° | 1977 | 02/11 | Trivelpiece and Volkman (1979) |
| Deception I | 63° | 1944 | 05/11 | Flett (1944) |
| " | " | 1945 | 25/10 | Reece (1945) |
| " | " | 1956 | 26/10 | White (1957) |
| " | " | 1960 | 26/10 | Hodges and Ferrar (1961) |
| " | " | 1961 | 21/10 | Kyte (1962) |
| " | " | 1962 | 28/10 | Ashworth (1963) |
| Waterboat Point | 64° | 1921 | 02/11 | Bagshawe (1938) |

Appendix 2.3.
Laying dates and intervals from Adélie and chinstrap breeding sites.

| Locality | Latitude °S | Year | First egg | First egg mean | Second egg | Laying interval (d) | Single egg | Reference |
|---|---|---|---|---|---|---|---|---|
| Adélie | | | | | | | | |
| Signy I | 61° | 1903 | 29/10 | | | | | Clarke (1906) |
| " | " | 1904 | 02/11 | | | | | " |
| " | " | 1950 | 29/10 | | | 3.0 | | Sladen (1958) |
| " | " | 1953 | 27/10 | 08/11 | 11/11 | 3.0 | | " |
| " | " | 1957 | 26/10 | | | | | Scotland (1958) |
| " | " | 1959 | 28/10 | | | | | Richards (1960) |
| " | " | 1960 | 25/10 | | | | | Pinder (1961) |
| " | " | 1961 | 24/10 | | | | | Jones and Pinder (1961) |
| " | " | 1962 | 22/10 | | | | | Topliffe (1963) |
| " | " | 1979 | 29/10 | | | | | This study |
| " | " | 1980 | 27/10 | 03/11 | 06/11 | 3.1 | 07/11 | " |
| " | " | 1981 | 27/10 | 03/11 | 06/11 | 3.0 | 04/11 | " |
| King George I | 62° | 1977 | 29/10 | | | | | Trivelpiece and Volkman (1979) |
| Hope Bay | 63° | 1946 | 06/11 | | | | | Sladen (1958) |
| " | " | 1947 | 02/11 | | | | | " |
| " | " | 1948 | 01/11 | 13/11 | 16/11 | 3.7 | | " |
| " | " | 1952 | 04/11 | | | | | " |
| Booth I | 65° | 1904 | 03/11 | | | | | Menegaux (1907) |
| Peterman I | 65° | 1909 | 09/11 | | | | | Gain (1913) |
| Pointe-Géologie | 66° | 1952 | 10/11 | | | 2.8 | | Mougin (1968) |
| " | " | 1956 | 13/11 | | | | | " |
| " | " | 1961 | 09/11 | | | | | " |
| " | " | 1962 | 09/11 | | | | | " |
| " | " | 1963 | 08/11 | | | | | " |
| " | " | 1964 | 09/11 | | | | | " |
| Point Martin | 66° | 1950 | 10/11 | | | | | Sapin-Jaloustre (1960) |
| Avian I | 67° | 1978 | 11/11 | | | 3.0 | | Poncet (unpubl.) |
| Cape Denison | 67° | 1912 | 03/11 | | | | | Falla (1937) |
| " | " | 1913 | 09/11 | | | | | " |
| Cape Adare | 71° | 1899 | 02/11 | | | | | Bernacchi (1901) |
| " | " | 1911 | 03/11 | 12/11 | 15/11 | 3.5 | | Levick (1915) |
| Cape Bird | 77° | 1967 | | | 16/11 | 3.0 | 20/11 | Spurr (1975a) |
| " | " | 1968 | | 13/11 | 16/11 | | 19/11 | " |
| " | " | 1969 | | 11/11 | 14/11 | | 17/11 | " |
| " | " | 1970 | | | 15/11 | | 18/11 | " |
| Cape Crozier | 77° | 1963 | | 20/11 (3 years old) | | | | Ainley and others (1983) |
| | | ↓ | | ↓ | | | | |
| | | 1975 | | 17/11 (12-14 years old) | | | | |
| Cape Royds | 77° | 1959 | 04/11 | 15/11 | | 3.1 | 18/11 | Taylor (1962) |
| " | " | 1961 | 07/11 | | | | | Stonehouse (1963) |

Appendix 2.3 (continued)

| Locality | Latitude °S | Year | First egg | First egg mean | Second egg | Laying interval (d) | Single egg | Reference |
|---|---|---|---|---|---|---|---|---|
| Chinstrap | | | | | | | | |
| Signy I | 61° | 1947 | 03/12 | | | | | Ewer and Anderson (1948) |
| " | " | 1959 | 27/11 | | | | | Richards (1960) |
| " | " | 1960 | 19/11 | | | | | Pinder (1961) |
| " | " | 1975 | 20/11 | 25/11 | | 2-4 | | Conroy and others (1975 a) |
| " | " | 1978 | 26/11 | | | | | Rootes (1978) |
| " | " | 1979 | 22/11 | | | | | This study |
| " | " | 1980 | 26/11 | 08/12 | 12/12 | 3.4 | 10/12 | " |
| " | " | 1981 | 27/11 | 04/12 | 07/12 | 3.2 | 06/12 | " |
| King George I | 62° | 1977 | 18/11 | | | | | Trivelpiece and Volkman (1979) |
| Deception I | 63° | 1956 | 15/11 | | | | | White (1957) |
| " | " | 1962 | 10/11 | | | | | Ashworth (1963) |
| Elephant I | 63° | 1970 | 08/11 | 14/11 | | | | Conroy and others (1975 b) |
| Waterboat Point | 64° | 1921 | 25/11 | | | | | Bagshawe (1938) |

Appendix 2.4.
Hatching dates from Adélie and chinstrap breeding sites.

| Locality | Latitude °S | Year | Hatch date | Interval | Reference |
|---|---|---|---|---|---|
| Adélie | | | | | |
| Signy I | 61° | 1903 | 04/12 | | Clarke (1906) |
| " | " | 1904 | 12/12 | | " |
| " | " | 1947 | 03/12 | | Ewer and Anderson (1948) |
| " | " | 1950 | 04/12 | | Sladen (1958) |
| " | " | 1957 | 05/12 | | Scotland (1958) |
| " | " | 1960 | 04/12 | | Pinder (1961) |
| " | " | 1961 | 01/12 | | Jones and Pinder (1962) |
| " | " | 1980 | 01/12 | 0.98 | This study |
| " | " | 1981 | 02/12 | 1.86 | " |
| Point Martin | 66° | 1950 | 13/12 | | Sapin-Jaloustre (1960) |
| Pointe-Géologie | 66° | 1952 | 16/12 | | Mougin (1958) |
| " | " | 1961 | 14/12 | | " |
| " | " | 1963 | 14/12 | | " |
| " | " | 1964 | 12/12 | | " |
| Cape Denison | 67° | 1913 | 17/12 | | Falla (1937) |
| Avian I | 67° | 1978 | | 1.20 | Poncet (unpublished) |
| Cape Royds | 77° | 1959 | 10/12 | | Taylor (1962) |
| Cape Bird | 77° | 1968 | | 1.43 | Spurr (1975a) |
| Chinstrap | | | | | |
| Signy I | 61° | 1904 | 07/01 | | Clarke (1906) |
| " | " | 1947 | 30/12 | | Ewer and Anderson (1948) |
| " | " | 1958 | 03/01 | | Scotland (1958) |
| " | " | 1960 | 01/01 | | Richards (1960) |
| " | " | 1960 | 27/12 | | Pinder (1961) |
| " | " | 1970 | 26/12 | 1.00 | Conroy and others (1975a) |
| " | " | 1980 | 05/01 | 0.65-1.35 | This study |
| " | " | 1981 | 02/01 | 1.28 | " |

Adélie

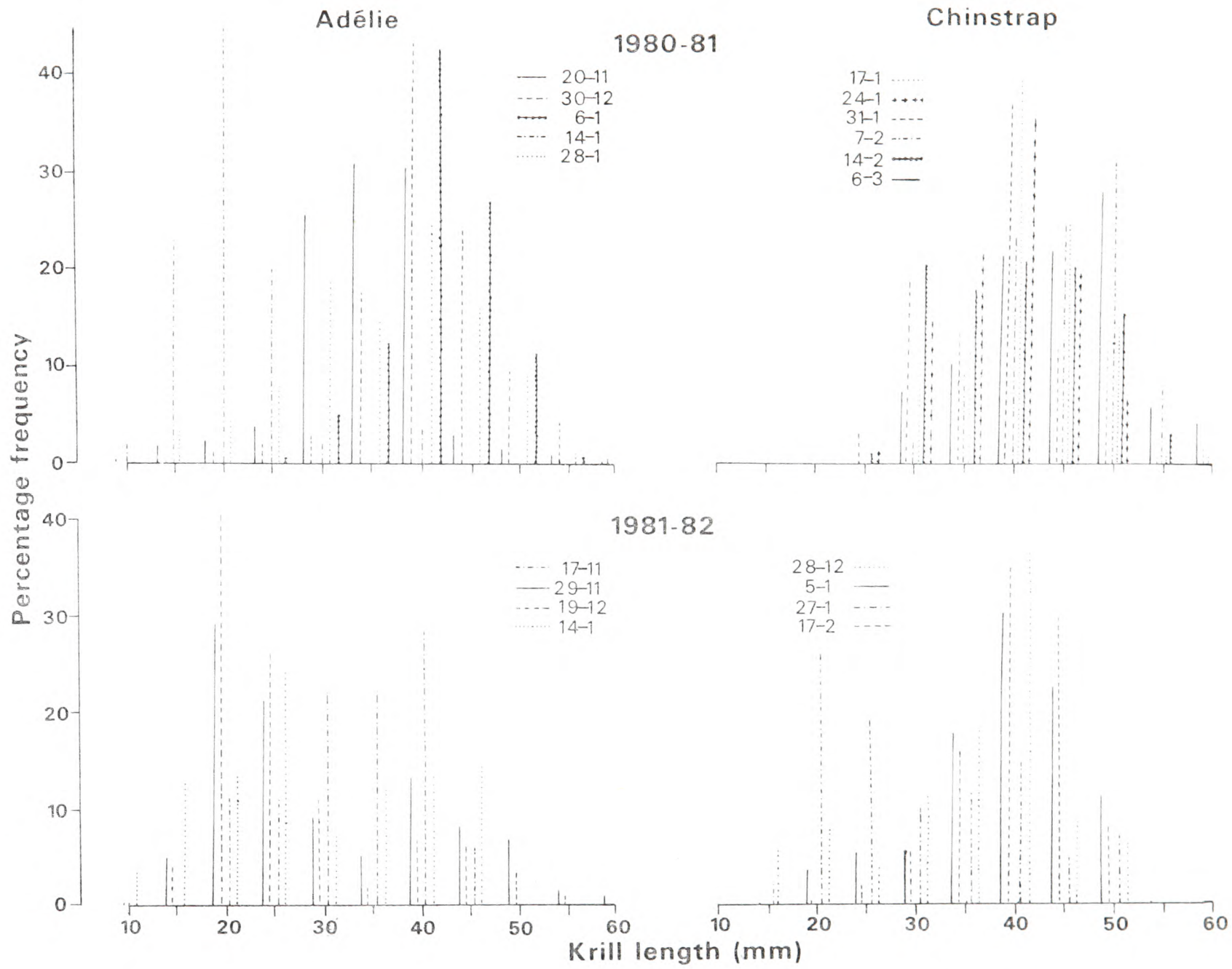
| Location/latitude °S | Cape Bird 77° | | | | Cape Royds 77° | | | | King George I 62° | Signy I 61° | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Reference | Spurr 1975 | | | | Taylor 1962; Yeates 1968 | | | | Trivelpiece 1981 | This study | | | |
| Year | 1967/68 | 1968/69 | 1969/70 | 1970/71 | 1959/60 | 1964/65[1] | 1965/66[1] | 1965/66[2] | 1977/78 | 1980/81[1] | 1980/81[2] | 1981/82[1] | 1981/82[2] |
| No pairs | 201 | 198 | 186 | 179 | 122 | 1051 | 1186 | 138 | 12 | 394 | 60 | 456 | 27 |
| No eggs | 373 | 318 | 350 | 327 | 225 | 2172 | 2440 | 257 | 22 | 788 | 120 | 754 | 49 |
| No chicks | 297 | 180 | 253 | 260 | 150 | | | 145 | 14 | 647 | 98 | 612 | 35 |
| % eggs hatched | 79.6 | 56.6 | 72.3 | 79.5 | 66.7 | | | 56.4 | 63.6 | 82 | 82 | 81 | 71 |
| Chicks hatched/pair | 1.5 | 0.9 | 1.4 | 1.4 | 1.2 | | | 1.0 | 1.2 | 1.6 | 1.6 | 1.3 | 1.3 |
| No chicks fledged | 247[3] | 136[3] | 192 | 208 | 113 | 1467 | 1390 | 122 | 12 | 303 | 9 | 578 | 11 |
| % chicks fledged | 83.2 | 75.6 | 75.9 | 80.0 | 75.3 | | | 84.1 | 82.0[5] | 46.8 | 9.2 | 94.4 | 31.4 |
| Chicks fledged/pair | 1.23 | 0.68 | 1.03 | 1.16 | 0.92 | 1.39 | 1.17 | 0.88 | 0.98[5] | 0.77 | 0.15 | 1.27 | 0.41 |
| Overall mortality (%) (eggs → fledging) | 33.8 | 57.2 ICE[4] | 45.1 | 36.4 | 49.8 | 32.5 | 43.0 | 52.5 | 54.5 | 61.5 ICE[4] | 92.5 ICE[4] | 23.3 | 77.6 |

Chinstrap

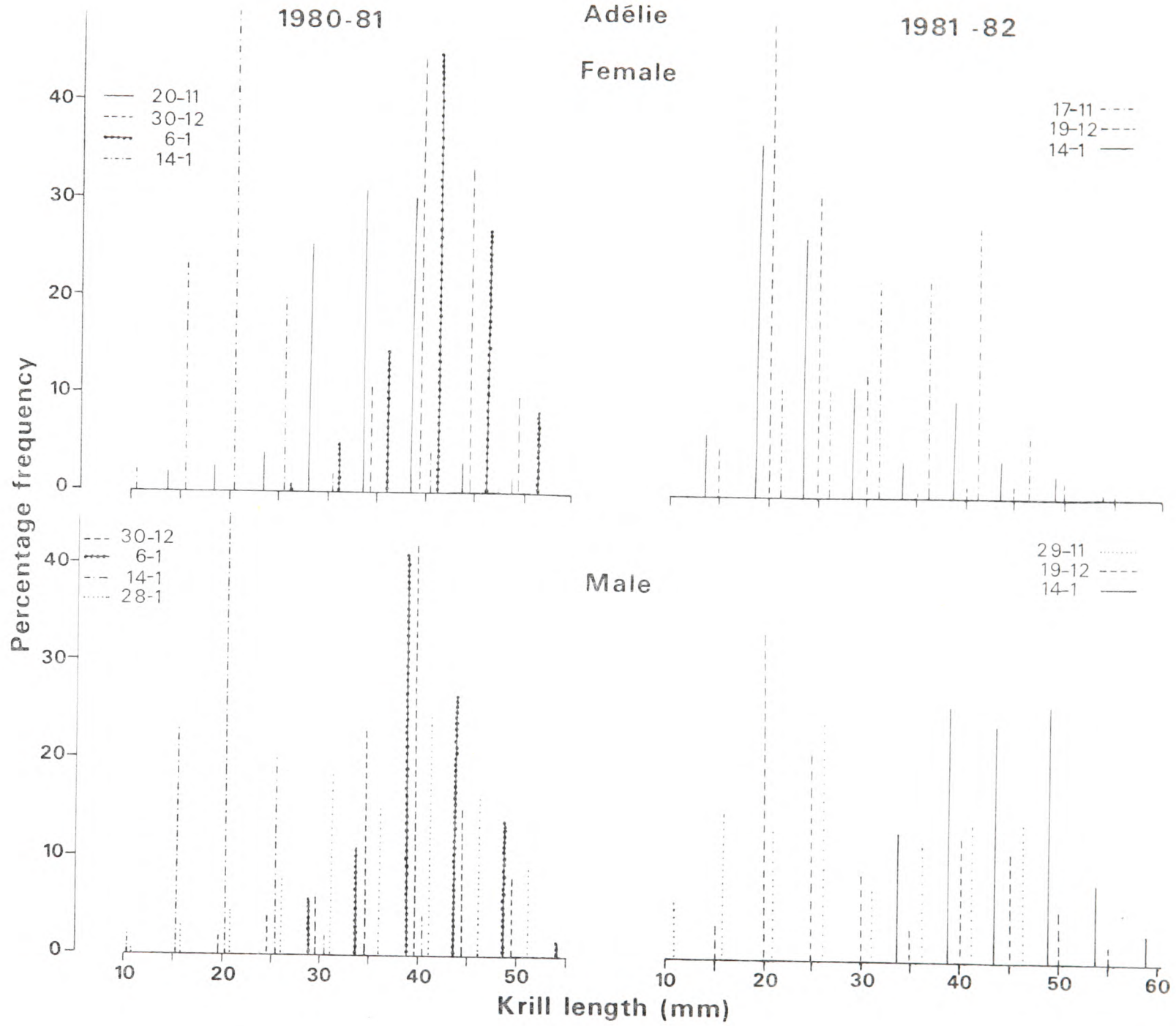
| Location/latitude °S | King George I 62° | Signy I 61° | | | | | |
|---|---|---|---|---|---|---|---|
| Reference | Trivelpiece 1981 | Conroy et al. 1975a, this study | | | | | |
| Year | 1977/78 | 1969/70 | 1970/71 | 1980/81[1] | 1980/81[2] | 1981/82[1] | 1981/82[2] |
| No pairs | 12 | | | 294 | 60 | 343 | 64 |
| No eggs | 22 | | | 543 | 105 | 642 | 123 |
| No chicks | 13 | | 386 | 106 | 39 | 431 | 55 |
| % eggs hatched | 59.1 | | | 20 | 37 | 67 | 45 |
| Chicks hatched/pair | 1.1 | | | 0.5 | 0.6 | 1.3 | 0.9 |
| No chicks fledged | 13 | | 326 | 13 | 1 | 262 | 23 |
| % chicks fledged | 95.0[5] | 8.4[6] | 84.0 | 15.1 | 2.6 | 60.8 | 41.8 |
| Chicks fledged/pair | 1.06 | | 1.83 | 0.04 | 0.016 | 0.76 | 0.36 |
| Overall mortality (%) (eggs → fledging) | 59.1 | ICE[4] | 24.6 | 97.6 ICE[4] | 99.0 ICE[4] | 59.2 | 81.3 |

Notes:
1. data from whole colony counts. 2. data obtained from a sample within a colony. 3. no. of chicks present in mid-February.
4. unusually heavy ice conditions during breeding. 5. data are chicks crēched/pair and % chicks surviving to crēche age.
6. "Much lower survival rate ... 1/10 of 1970/71".

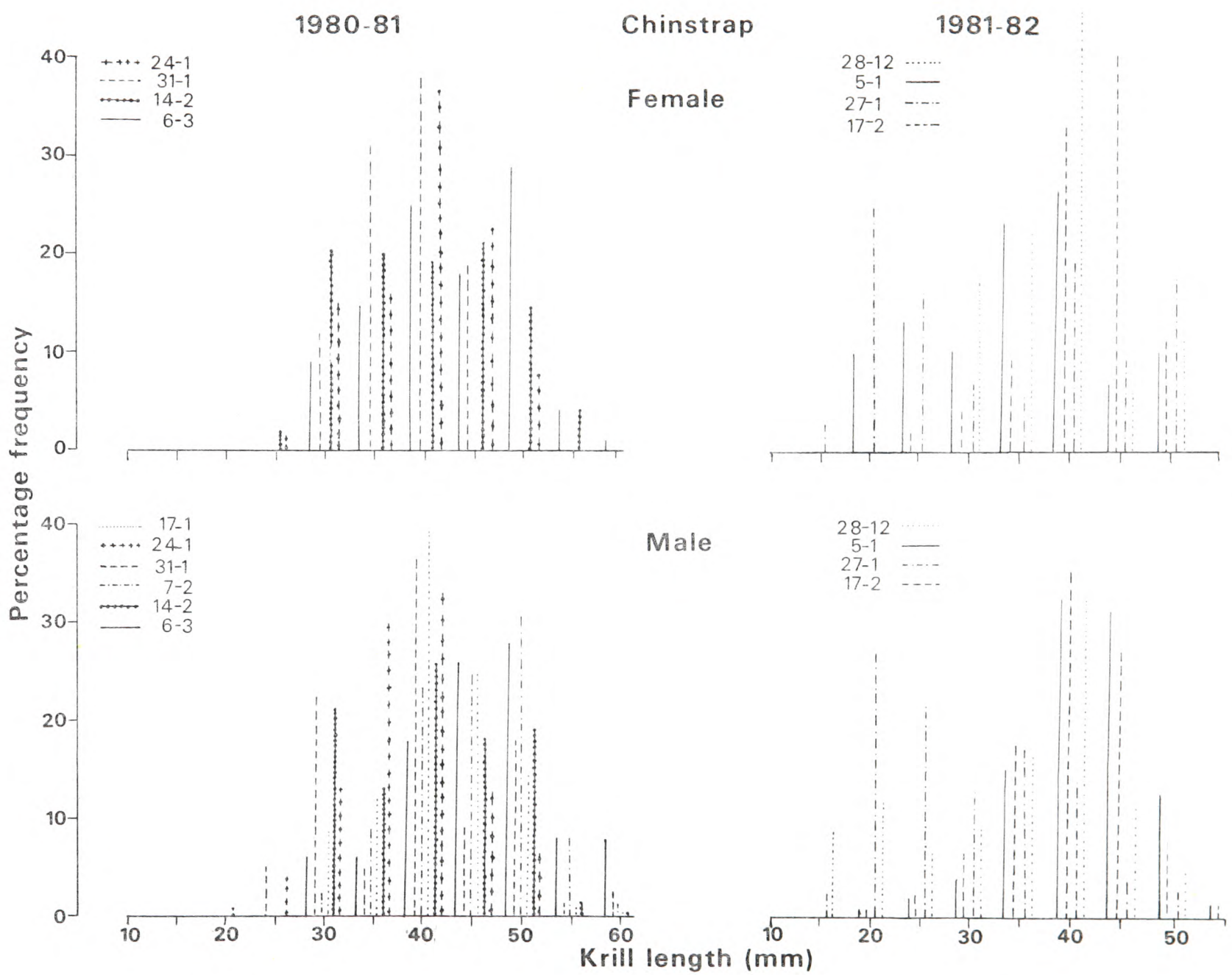
Appendix 2.5. Breeding success of Adélie and chinstrap penguins from main studies.



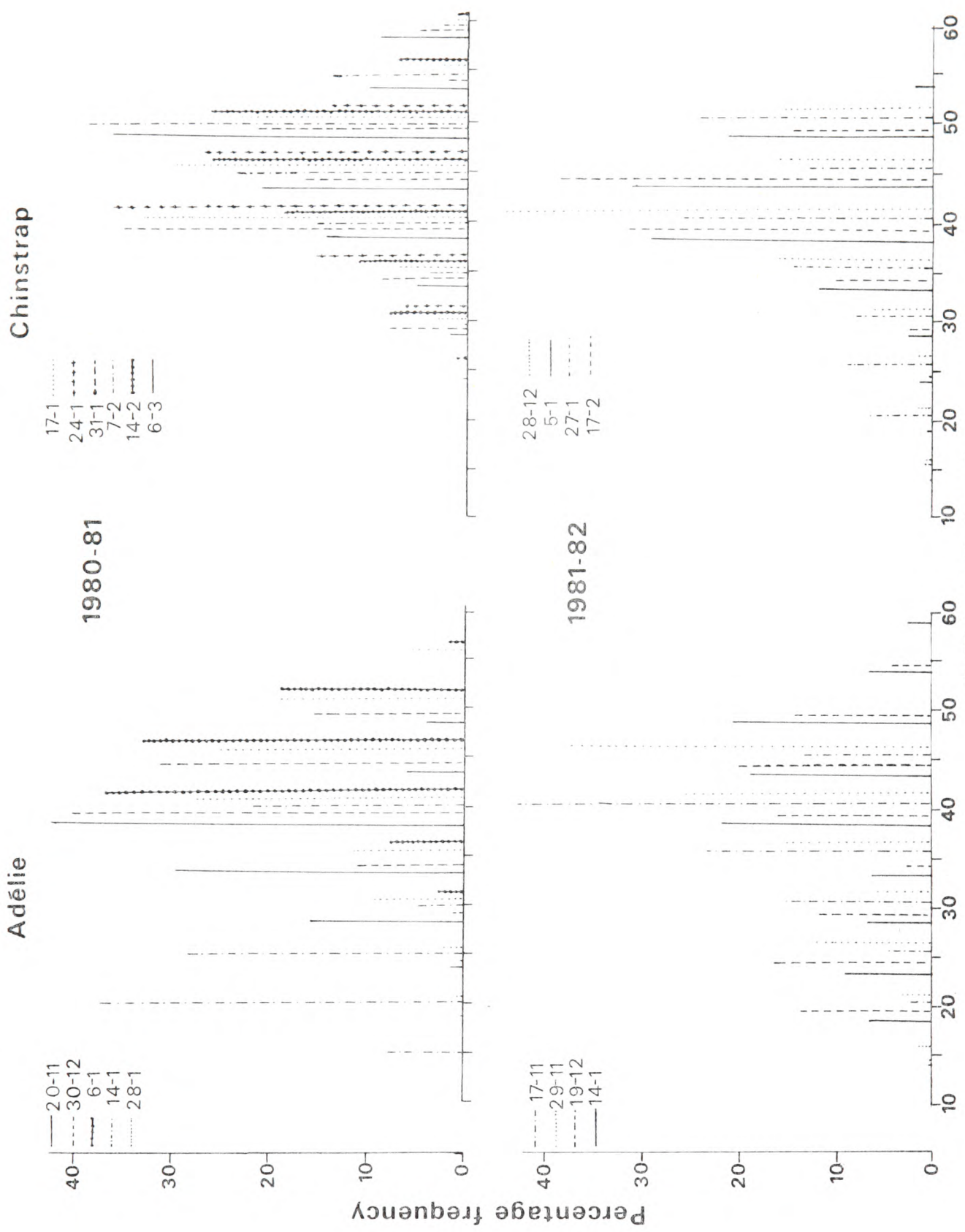

Appendix 3.1. Length-frequency distribution of the number of krill from each length class found in each sample.




Appendix 3.2. Length-frequency distribution of the number of krill from each length class found in stomachs of each sex from each sample.




Appendix 3.2 (continued).




Appendix 3.3. The length-frequency distribution of the weight of krill in each length class found in each sample.

Adélie 1980/81

| Date | Krill length (mm) | 10 | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 50 | 55 | 60 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 20/11 | Number | | 2.00 | 2.50 | 4.00 | 25.50 | 31.00 | 30.50 | 3.00 | 1.50 | | |
| | Weight | | 0.18 | 0.49 | 1.46 | 15.84 | 29.82 | 47.43 | 5.89 | 3.89 | | |
| 30/12 | Number | | | 1.00 | 2.00 | 3.00 | 17.50 | 43.50 | 24.00 | 9.00 | | |
| | Weight | | | 0.13 | 0.49 | 1.23 | 11.18 | 40.18 | 31.31 | 15.48 | | |
| 06/01 | Number | | | | 0.20 | 5.60 | 12.40 | 42.40 | 27.00 | 11.60 | 0.80 | |
| | Weight | | | | 0.05 | 2.17 | 7.44 | 36.80 | 33.10 | 18.74 | 1.70 | |
| 14/01 | Number | 2.00 | 23.00 | 49.00 | 20.00 | 2.00 | | 4.00 | | | | |
| | Weight | 0.20 | 7.89 | 37.24 | 28.32 | 4.81 | | 21.54 | | | | |
| 28/01 | Number | 0.30 | 3.00 | 4.30 | 7.70 | 18.70 | 14.70 | 24.30 | 16.00 | 9.00 | 2.00 | |
| | Weight | 0.01 | 0.21 | 0.67 | 2.25 | 9.28 | 11.31 | 27.03 | 25.14 | 18.64 | 5.46 | |

Adélie 1981/82

| Date | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 17/11 | Number | | | 11.00 | 11.00 | 22.00 | 22.00 | 28.00 | 6.00 | | | |
| | Weight | | | 2.35 | 4.39 | 14.89 | 23.07 | 42.45 | 12.85 | | | |
| 29/11 | Number | 3.57 | 12.82 | 13.00 | 24.14 | 6.79 | 11.64 | 13.75 | 14.29 | | | |
| | Weight | 0.12 | 1.51 | 3.39 | 11.74 | 5.60 | 14.90 | 25.42 | 37.32 | | | |
| 19/12 | Number | | 4.06 | 40.75 | 26.00 | 10.90 | 1.70 | 6.70 | 5.95 | 3.20 | 0.74 | |
| | Weight | | 0.62 | 13.75 | 16.35 | 11.64 | 2.80 | 16.03 | 20.10 | 14.36 | 4.34 | |
| 14/01 | Number | 0.07 | 5.10 | 29.08 | 21.18 | 9.09 | 5.36 | 13.24 | 8.01 | 6.74 | 1.61 | 0.52 |
| | Weight | 0.01 | 0.54 | 6.79 | 9.22 | 6.72 | 6.13 | 21.90 | 18.72 | 20.77 | 6.54 | 2.66 |

Chinstrap 1980/81

| Date | Krill length (mm) | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 50 | 55 | 60 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 17/01 | Number | | | | 8.50 | 11.50 | 39.00 | 25.00 | 14.50 | 1.00 | 0.50 |
| | Weight | | | | 3.24 | 6.79 | 33.32 | 30.17 | 23.06 | 2.10 | 1.32 |
| 24/01 | Number | | 0.20 | 2.80 | 14.40 | 21.40 | 35.20 | 18.80 | 7.20 | | |
| | Weight | | 0.03 | 0.76 | 6.62 | 15.23 | 36.23 | 27.33 | 13.80 | | |
| 31/01 | Number | | | 3.30 | 19.00 | 13.70 | 37.00 | 12.30 | 12.00 | 1.00 | 1.70 |
| | Weight | | | 0.84 | 8.22 | 9.18 | 35.83 | 16.83 | 21.64 | 2.38 | 5.08 |
| 07/02 | Number | | | | 2.20 | 9.00 | 23.40 | 24.80 | 31.00 | 8.40 | 1.20 |
| | Weight | | | | 0.67 | 4.21 | 15.84 | 23.72 | 39.09 | 13.96 | 2.51 |
| 14/02 | Number | | | 1.00 | 20.50 | 18.00 | 20.70 | 20.50 | 15.70 | 3.30 | 0.25 |
| | Weight | | | 0.24 | 8.35 | 11.36 | 18.88 | 26.42 | 26.67 | 7.38 | 0.70 |
| 06/03 | Number | | | | 7.5 | 10.5 | 21.5 | 22.0 | 28.25 | 6.0 | 4.25 |
| | Weight | | | | 2.33 | 5.05 | 14.97 | 21.64 | 36.62 | 10.25 | 9.14 |

Chinstrap 1981/82

| Date | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 28/12 | Number | 5.95 | 8.00 | 4.16 | 11.60 | 18.30 | 36.13 | 9.16 | 6.70 | |
| | Weight | 0.46 | 1.38 | 1.33 | 6.32 | 15.44 | 44.07 | 15.78 | 15.22 | |
| 05/01 | Number | 0.30 | 4.00 | 5.75 | 6.00 | 18.00 | 30.50 | 22.90 | 11.75 | 0.80 |
| | Weight | 0.02 | 0.54 | 1.45 | 2.58 | 11.98 | 29.35 | 31.13 | 21.06 | 1.89 |
| 27/01 | Number | 2.35 | 26.35 | 9.60 | 10.45 | 12.00 | 15.00 | 5.25 | 7.50 | |
| | Weight | 0.25 | 6.56 | 8.83 | 7.99 | 14.21 | 25.54 | 12.70 | 23.92 | |
| 17/02 | Number | | 0.64 | 2.48 | 6.25 | 16.30 | 34.90 | 30.00 | 8.58 | 0.84 |
| | Weight | | 0.08 | 0.59 | 2.54 | 10.24 | 31.69 | 38.48 | 14.51 | 1.87 |

Appendix 3.4. A comparison of the percentage distributions of the number and weight of krill from each length class found in each sample.

Adélie 1980/81

| Date | Adult wt.(g) Overall | Female | Male | Stomach content wt. (g) Overall | Female | Male | Stomach contents Proportion (%) Overall | Female | Male |
|---|---|---|---|---|---|---|---|---|---|
| 24/10 Mean | 4912 | 4100 | 5325 | 32.2 | 8.5 | 55.8 | 0.6 | 0.2 | 1.0 |
| sd. | 866 | - | - | 33.5 | - | - | 0.4 | - | - |
| No | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| 20/11 Mean | 4162 | 4162 | | 103.9 | 103.9 | | 2.6 | 2.6 | |
| sd. | 512 | 512 | | 51.9 | 51.9 | | 1.1 | 1.1 | |
| No | 2 | 2 | | 2 | 2 | | 2 | 2 | |
| 30/12 Mean | 3983 | 3750 | 4450 | 374.3 | 353.5 | 415.9 | 9.4 | 9.4 | 9.3 |
| sd. | 407 | 71 | - | 71.7 | 87.7 | - | 1.3 | 1.5 | - |
| No | 3 | 2 | 1 | 3 | 2 | 1 | 3 | 2 | 1 |
| 06/01 Mean | 4275 | 3900 | 4525 | 502.8 | 397.7 | 572.9 | 11.7 | 10.2 | 12.6 |
| sd. | 414 | 141 | 313 | 123.8 | 87.8 | 91.6 | 1.8 | 1.9 | 0.9 |
| No | 5 | 2 | 3 | 5 | 2 | 3 | 5 | 2 | 3 |
| 14/01 Mean | 4295 | 3987 | 4500 | 398.1 | 488.4 | 452.9 | 9.0 | 8.0 | 9.7 |
| sd. | 478 | 512 | 409 | 211.9 | 267.8 | 280.0 | 3.7 | 1.2 | 4.5 |
| No | 5 | 2 | 3 | 5 | 2 | 3 | 5 | 2 | 3 |
| 21/01 Mean | 4012 | | 4012 | 354.9 | | 354.9 | 8.9 | | 8.9 |
| sd. | 512 | | 512 | 1.4 | | 1.4 | 0.8 | | 0.8 |
| No | 2 | | 2 | 2 | | 2 | 2 | | 2 |
| 28/01 Mean | 4435 | | 4435 | 454.9 | | 454.9 | 10.2 | | 10.2 |
| sd. | 322 | | 322 | 159.1 | | 159.1 | 2.7 | | 2.7 |
| No | 5 | | 5 | 5 | | 5 | 5 | | 5 |

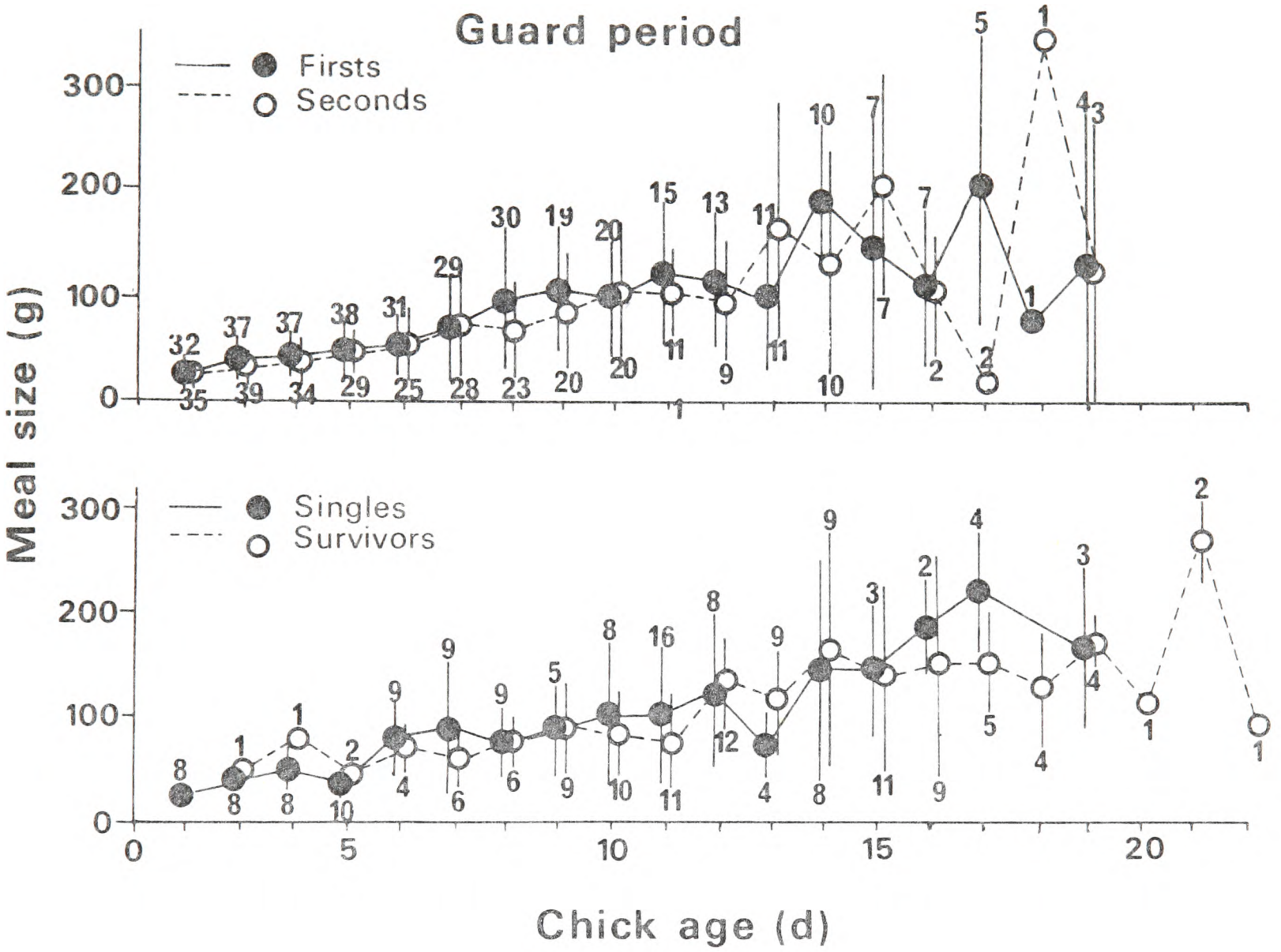
Chinstrap 1980/81

| Date | Adult wt. (g) Overall | Female | Male | Stomach content wt. (g) Overall | Female | Male | Stomach contents proportion (%) Overall | Female | Male |
|---|---|---|---|---|---|---|---|---|---|
| 21/11 Mean | 4139 | | 4139 | 10.7 | | 10.7 | 0.25 | | 0.25 |
| sd. | - | | - | - | | - | - | | - |
| No | 1 | | 1 | 1 | | 1 | 1 | | 1 |
| 24/12 Mean | 4347 | | 4347 | 2.6 | | 2.6 | 0.06 | | 0.06 |
| sd. | - | | - | - | | - | - | | - |
| No | 1 | | 1 | 1 | | 1 | 1 | | 1 |
| 03/01 Mean | 3800 | 3725 | 4025 | 12.6 | 4.6 | 36.4 | 0.68 | 0.61 | 0.90 |
| sd. | 339 | 373 | - | 16.0 | 2.4 | - | 0.64 | 0.72 | - |
| No | 4 | 3 | 1 | 4 | 3 | 1 | 4 | 3 | 1 |
| 10/01 Mean | 3905 | 3768 | 4450 | 8.3 | 9.6 | 2.8 | 0.19 | 0.24 | 0.06 |
| sd. | 359 | 220 | - | 8.3 | 8.9 | - | 0.21 | 0.19 | - |
| No | 5 | 4 | 1 | 5 | 4 | 1 | 5 | 4 | 1 |
| 17/01 Mean | 4475 | | 4475 | 189.6 | | 189.6 | 4.25 | | 4.25 |
| sd. | 177 | | 177 | 53.6 | | 53.6 | 0.97 | | 0.97 |
| No | 2 | | 2 | 2 | | 2 | 2 | | 2 |
| 24/01 Mean | 3685 | 3250 | 4337 | 227.4 | 206.1 | 259.5 | 6.20 | 6.30 | 6.00 |
| sd. | 598 | 50 | 88 | 65.5 | 77.6 | 41.3 | 1.61 | 1.97 | 0.76 |
| No | 5 | 3 | 2 | 5 | 3 | 2 | 5 | 3 | 2 |
| 31/01 Mean | 4025 | 3775 | 4275 | 222.2 | 159.8 | 253.5 | 5.40 | 4.20 | 5.95 |
| sd. | 331 | - | 282 | 56.7 | - | 24.0 | 0.98 | - | 0.67 |
| No | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 |
| 07/02 Mean | 4250 | | 4250 | 390.8 | | 390.8 | 9.10 | | 9.10 |
| sd. | 232 | | 232 | 121.1 | | 121.1 | 2.25 | | 2.25 |
| No | 5 | | 5 | 5 | | 5 | 5 | | 5 |
| 14/02 Mean | 3975 | 3966 | 4000 | 491.9 | 471.3 | 553.6 | 12.40 | 11.90 | 13.80 |
| sd. | 260 | 318 | - | 51.1 | 37.2 | - | 0.96 | 0.52 | - |
| No | 4 | 3 | 1 | 4 | 3 | 1 | 4 | 3 | 1 |
| 06/03 Mean | 4333 | 4150 | 4425 | 554.9 | 700.9 | 482.0 | 12.90 | 16.90 | 10.80 |
| sd. | 161 | - | 35 | 303.6 | - | 370.0 | 5.79 | - | 6.17 |
| No | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 |

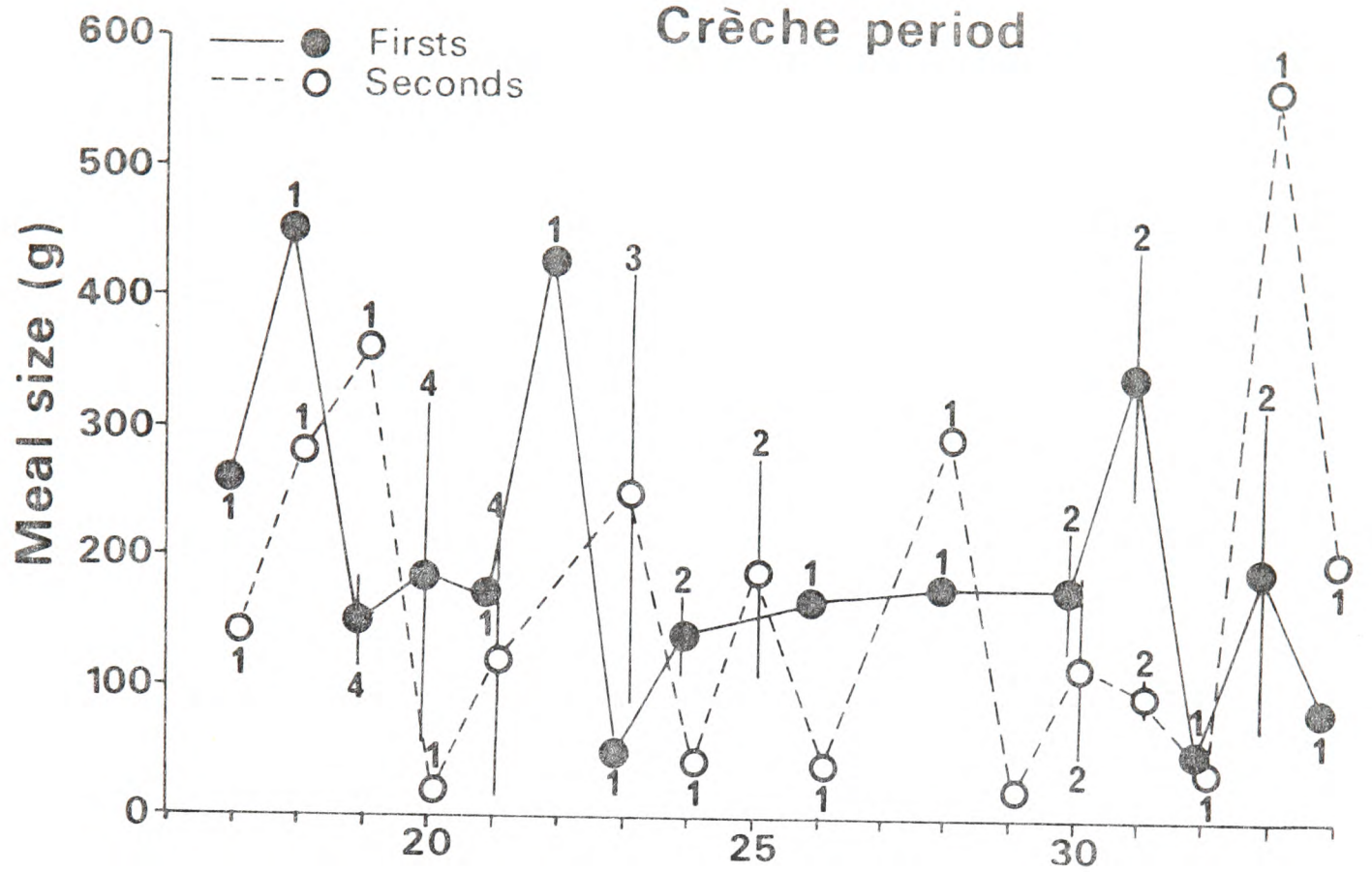
Appendix 3.5. The mean adult weight, krill weight and proportional krill weight of each sample.

| Adélie 1981/82 | | | | | | | | | | Chinstrap 1981/82 | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Adult wt.(g) | | | Stomach content wt. (g) | | | Stomach contents Proportion (%) | | | | Adult wt. (g) | | | Stomach content wt. (g) | | | Stomach contents proportion (%) | | |
| Date | | Overall | Female | Male | Overall | Female | Male | Overall | Female | Male | Date | Overall | Female | Male | Overall | Female | Male | Overall | Female | Male |
| 17/11 | Mean | 4651 | 4651 | | 27.1 | 27.1 | | 0.5 | 0.5 | | 28/12 Mean | 4350 | 4200 | 4425 | 92.4 | 98.0 | 76.0 | 2.3 | 2.5 | 1.95 |
| | sd. | 310 | 310 | | 26.2 | 26.2 | | 0.4 | 0.4 | | sd. | 350 | - | 459 | 12.5 | - | 2.0 | 0.4 | - | 0.15 |
| | No | 4 | 4 | | 4 | 4 | | 4 | 4 | | No | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 |
| 29/11 | Mean | 4675 | | 4675 | 122.6 | | 122.6 | 2.6 | | 2.6 | 05/01 Mean | 4466 | 4400 | 4500 | 166.3 | 559.0 | 207.0 | 3.7 | 1.5 | 4.85 |
| | sd. | 175 | | 175 | 40.2 | | 40.2 | 0.6 | | 0.6 | sd. | 208 | - | 283 | 89.0 | - | 18.5 | 1.6 | - | 0.55 |
| | No | 3 | | 3 | 3 | | 3 | 3 | | 3 | No | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 |
| 19/12 | Mean | 4210 | 4240 | 4350 | 440.8 | 366.4 | 520.0 | 10.2 | 8.8 | 12.4 | 27/01 Mean | 3960 | 3700 | 4133 | 456.6 | 510.0 | 380.0 | 11.6 | 14.2 | 9.93 |
| | sd. | 566 | 576 | 71 | 160.9 | 176.6 | 87.5 | 2.8 | 2.5 | 1.7 | sd. | 319 | 0 | 301 | 66.9 | 9.0 | 1.7 | 2.1 | 0.1 | 0.20 |
| | No | 5 | 3 | 2 | 5 | 3 | 2 | 5 | 3 | 2 | No | 5 | 2 | 3 | 5 | 2 | 3 | 5 | 2 | 3 |
| 14/01 | Mean | 4150 | 4037 | 4600 | 539.8 | 495.3 | 624.3 | 12.8 | 12.6 | 13.6 | 17/02 Mean | 4280 | 3850 | 4387 | 563.0 | 336.7 | 601.0 | 12.9 | 9.1 | 13.95 |
| | sd. | 393 | 350 | - | 150.7 | 162.0 | - | 2.5 | 2.8 | - | sd. | 305 | - | 217 | 203.0 | - | 194.0 | 3.5 | - | 3.21 |
| | No | 5 | 4 | 1 | 5 | 4 | 1 | 5 | 4 | 1 | No | 5 | 1 | 4 | 5 | 1 | 4 | 5 | 1 | 4 |

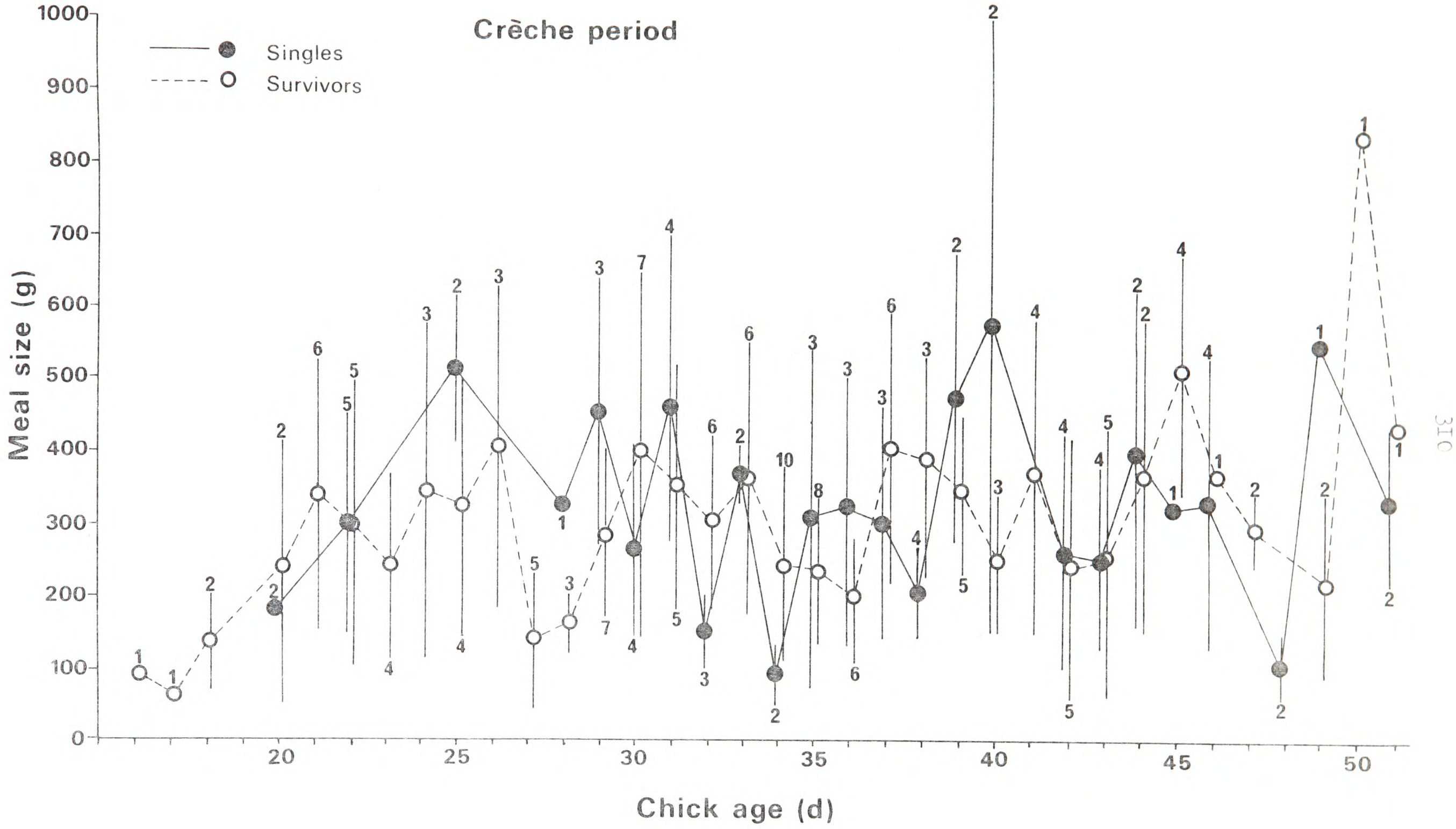
Appendix 3.5. (continued)



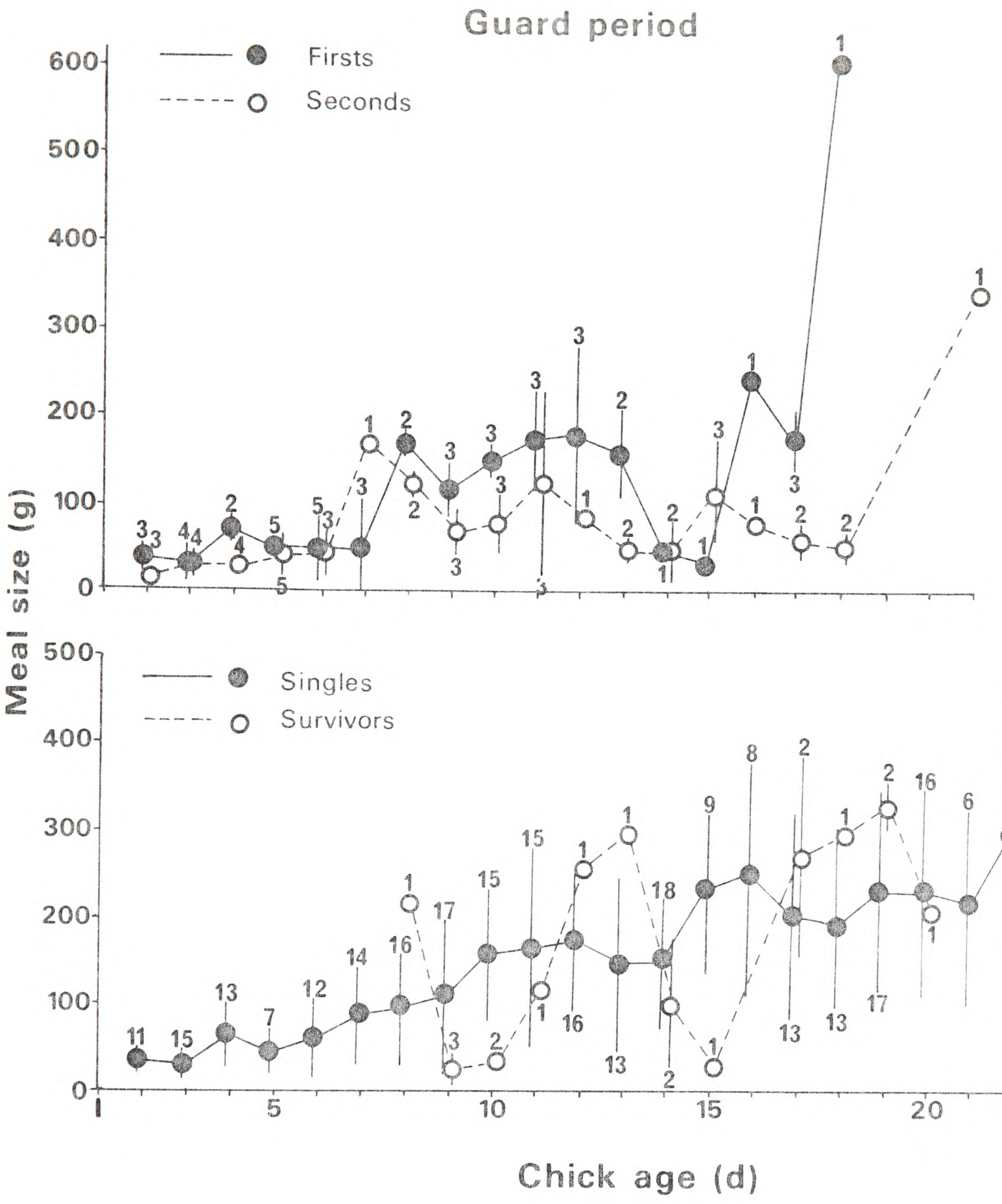

Appendix 4.1. The variation with chick age of the mean meal size (± 1 sd.) given to Adélie chicks in 1980/81.



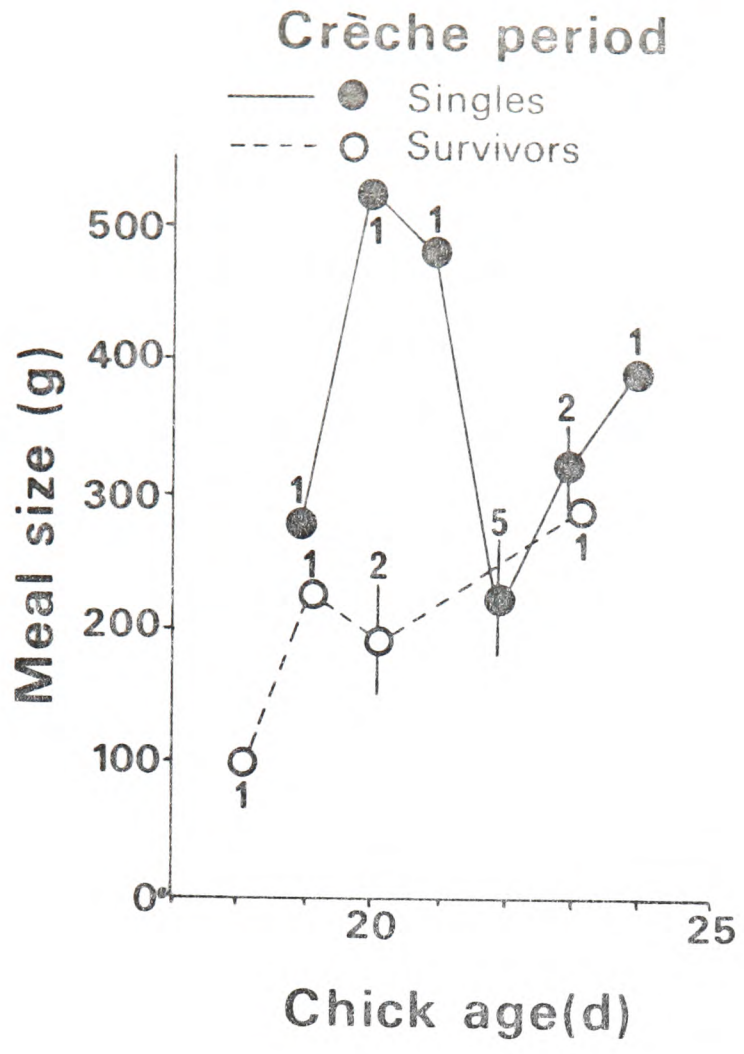

Appendix 4.1 (continued).



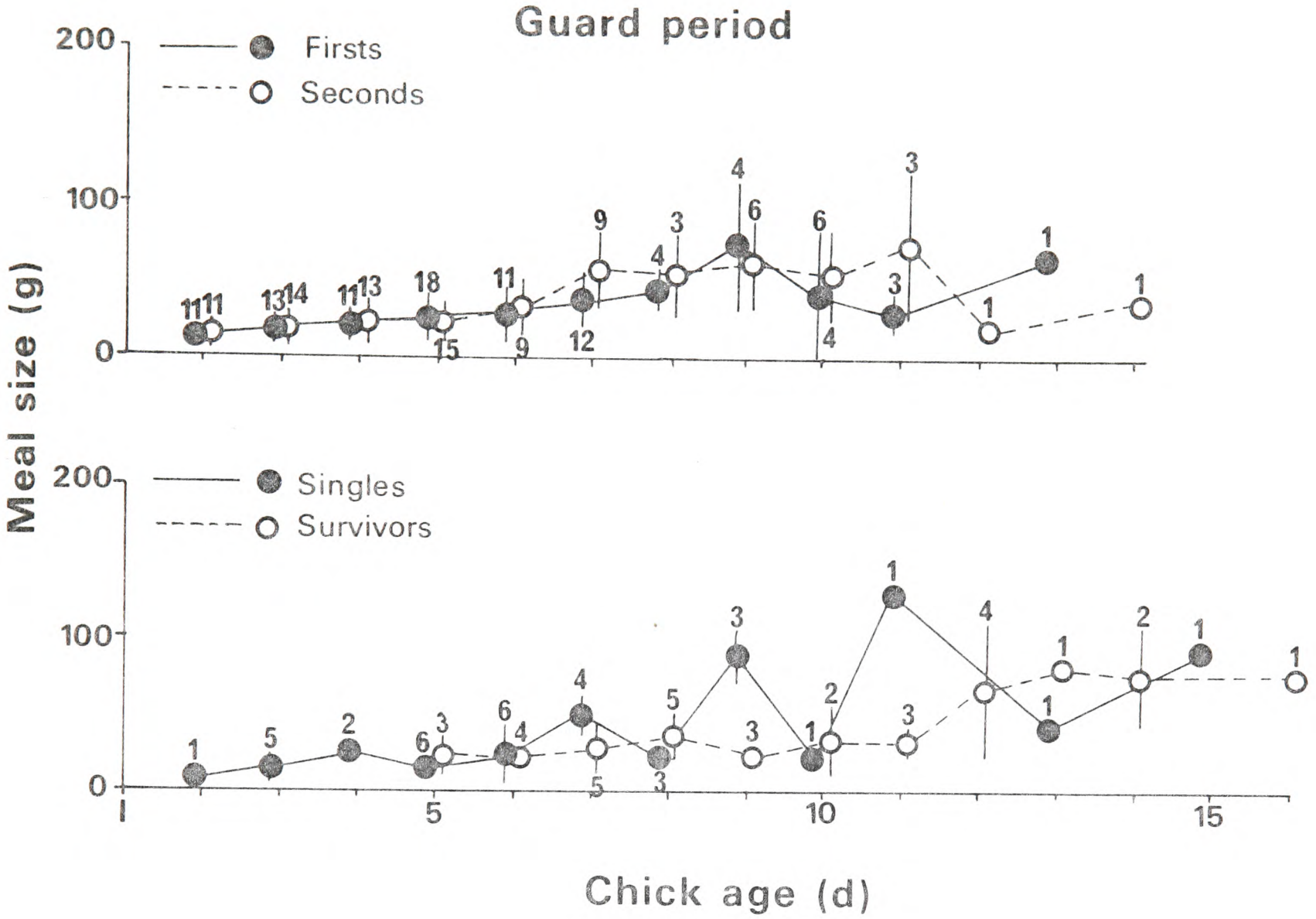

Appendix 4.1 (continued).



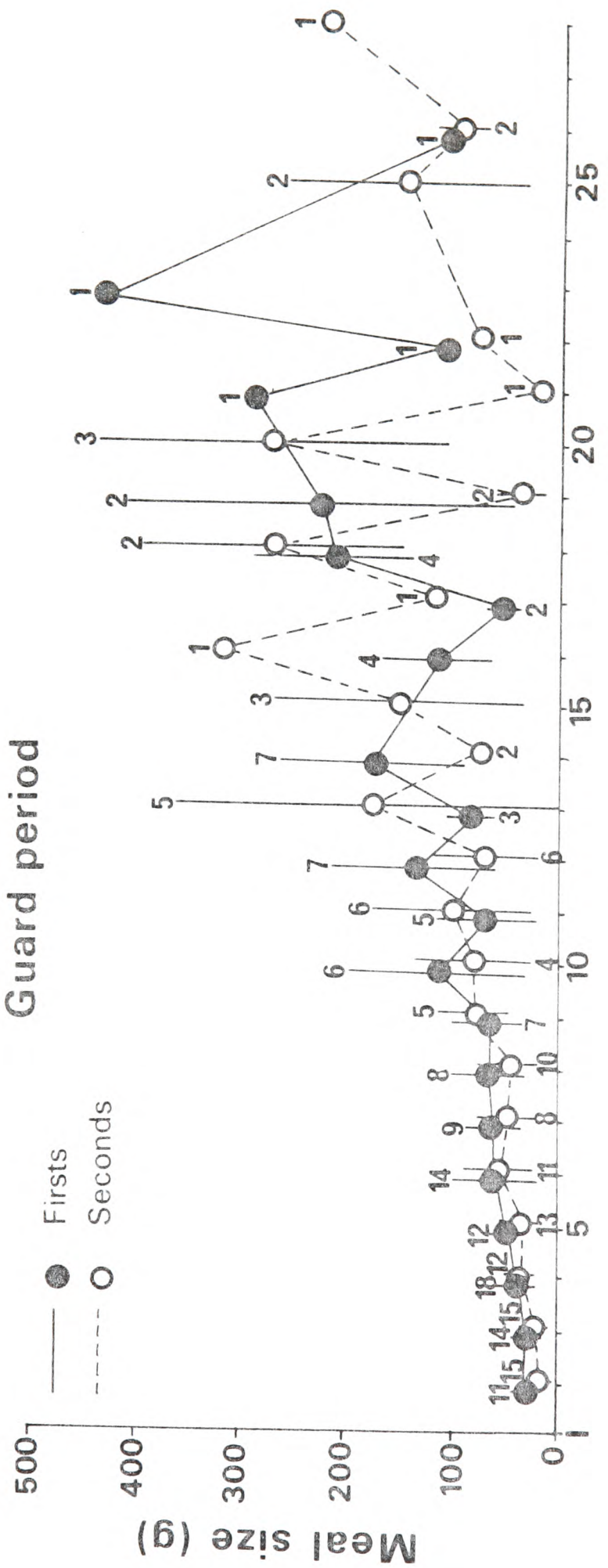

Appendix 4.2. The variation with chick age of the mean meal size (± 1 sd.) given to Adélie chicks in 1981/82.



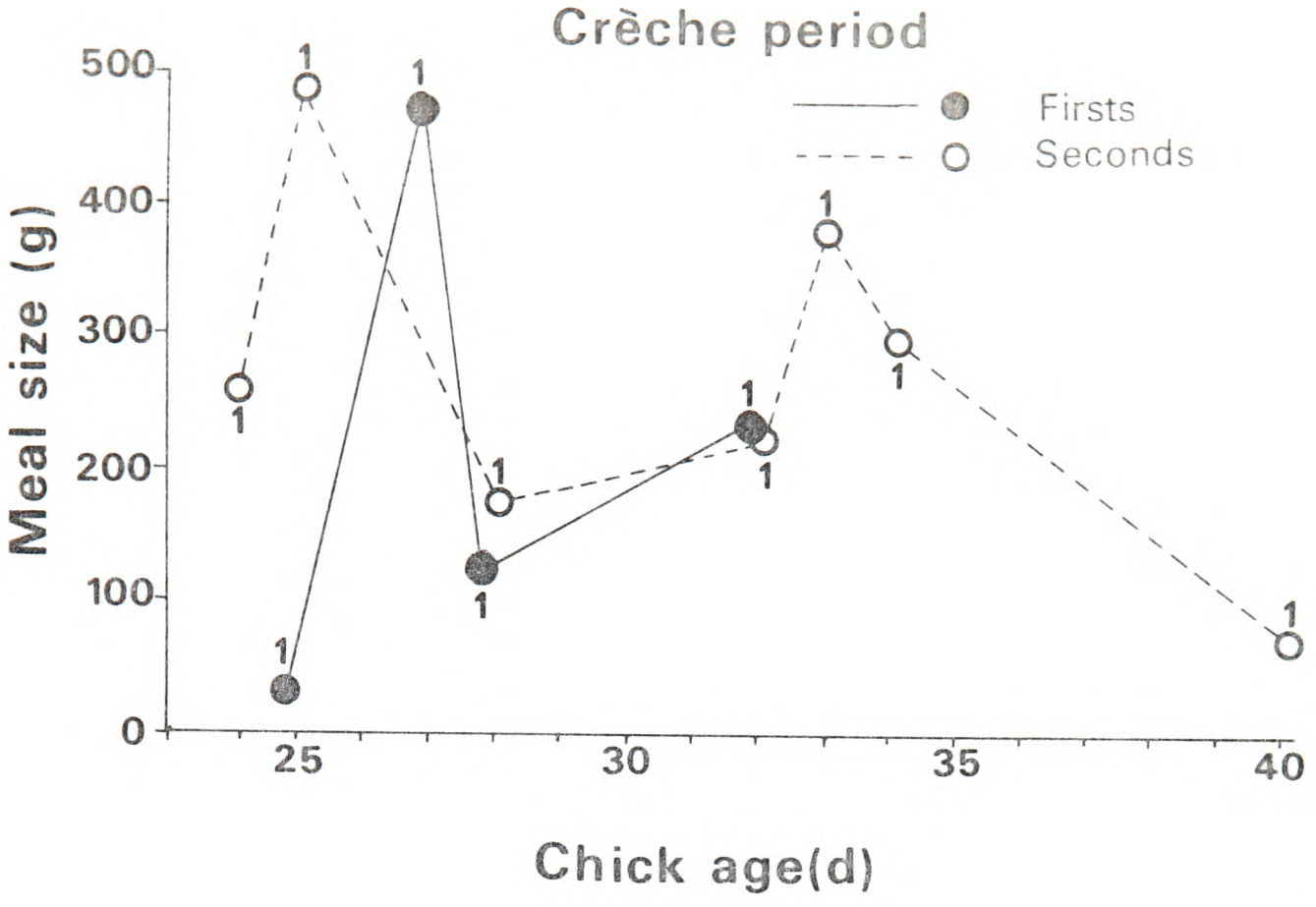

Appendix 4.2 (continued).



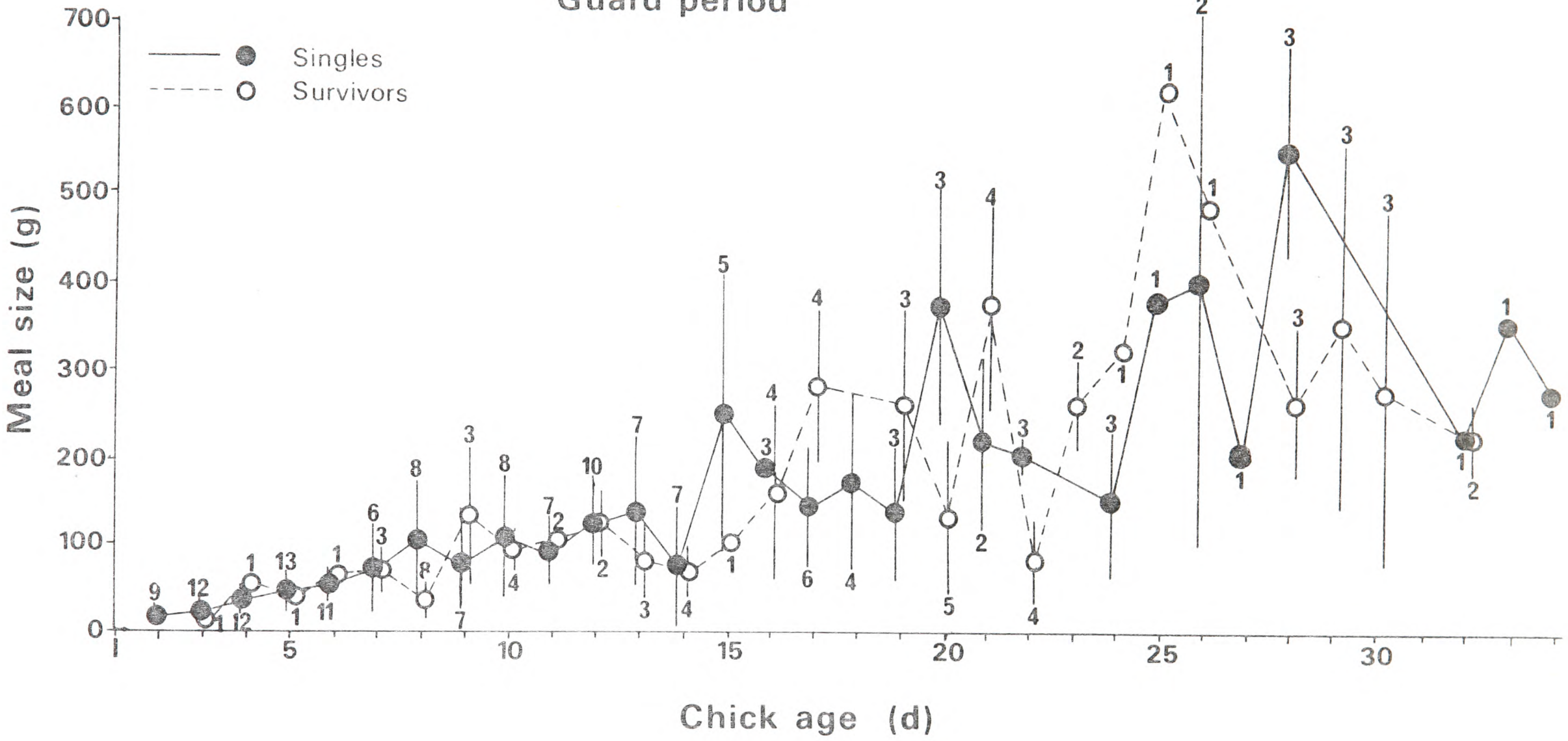

Appendix 4.3. The variation with chick age of the mean meal size (± 1 sd.) given to chinstrap chicks in 1980/81.



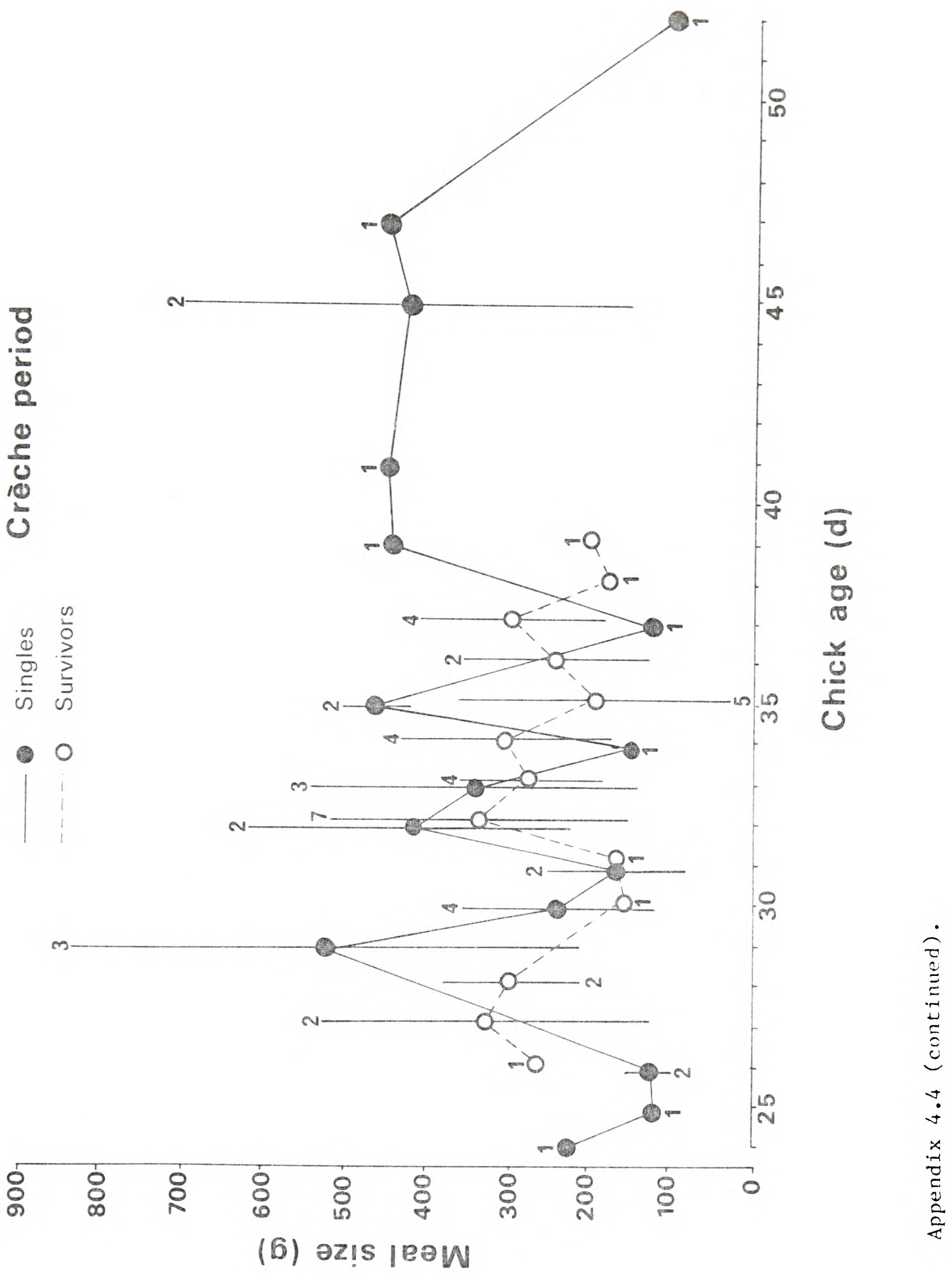

Appendix 4.4. The variation with chick age of the mean meal size (± 1 sd.) given to chinstrap chicks in 1981/82.




Appendix 4.4 (continued).




Appendix 4.4 (continued).




Appendix 4.4 (continued).

Appendix 4.5. The mean meal size and frequency of feeds to chicks, during the guard and crēche periods. Estimates were obtained by weighing chicks either daily, three-hourly or before and after a feed; numbers in parentheses are sample sizes.

| Species/ Year | Period | Chick status | Period length (d) | Meal size (g) | | | Feeding frequency (feeds/day) | |
|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 1 | 2 |
| Adēlie 1980/81 | Guard | First | 16.7 | 98.7(346) | - | - | 0.61 | 0.58 |
| | | Second | 15.8 | 100.4(309) | - | - | | |
| | | Single | 19.0 | 91.5(123) | - | - | 0.62 | 0.52 |
| | | Survivor | | 113.3(117) | | | | |
| | Crēche | First | 39.2 | 201.9 (25) | 240.0 (9) | - | 0.58 | 0.42 |
| | | Second | 40.1 | 173.1 (24) | 350.0 (5) | - | | |
| | | Single | 36.9 | 313.9 (65) | 267.0(11) | | 0.44 | 0.63 |
| | | Survivor | | 300.8(139) | 292.0(16) | 333.0(5) | | |
| Adēlie 1981/82 | Guard | First | 18.0 | 136.6 (45) | - | - | 0.59 | - |
| | | Second | 18.3 | 84.4 (43) | - | - | | |
| | | Single | 21.0 | 152.4(297) | - | - | 0.55 | - |
| | | Survivor | | 163.9 (18) | - | - | | |
| | Crēche | First | 42.6 | - | - | - | - | - |
| | | Second | 42.3 | - | - | - | | |
| | | Single | 39.6 | - | - | 298.0(8) | - | - |
| | | Survivor | | - | - | 206.0(5) | | |
| Chinstrap 1980/81 | Guard | First | 10[4] | 33.7 (95) | - | - | 0.39 | - |
| | | Second | 12[4] | 38.6 (89) | - | - | | |
| | | Single | 14[4] | 33.9 (34) | - | - | 0.46 | - |
| | | Survivor | | 38.5 (34) | - | - | | |
| Chinstrap 1981/82 | Guard | First | 23.0 | 119.6(137) | - | - | 0.56 | 0.66 |
| | | Second | 24.0 | 106.6(137) | - | - | | |
| | | Single | 28.7 | 115.8(160) | - | - | 0.68 | 0.66 |
| | | Survivor | | 178.6 (69) | - | - | | |
| | Crēche | First | 30.3 | 302.0 (5) | 329.0 (5) | - | - | 0.67 |
| | | Second | 29.3 | 270.7 (7) | 348.0 (5) | - | | |
| | | Single | 24.6 | 313.4 (28) | 386.0 (8) | - | 0.79 | 0.83 |
| | | Survivor | | 261.5 (34) | 353.0(22) | - | | |

Notes :

[1] Calculated from the regression of daily weight increase against chick age.
[2] Calculated from positive weight increments recorded by three-hourly weighing.
[3] Mean feed size obtained from weighing chicks before and after a feed.
[4] Not completed - all chicks died.

| Species/ Year | Sex/ Fast | Sample size | Sample period (d) | Weight loss gd$^{-1}$ | range | Weight loss % d$^{-1}$ | range | Energy consumption (kJd$^{-1}$) Calculated Lower | Calculated Upper | Theoretical Basal | Theoretical Existence |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Adēlie | F 1 | 26 | 11 | 64 | 15-121 | 1.62 | 0.35- | 1515 | 2548 | 982 | 1600 |
| 1980/81 | | | | | | | 2.99 | | | | |
| | F 2 | 44 | 10 | 70 | 44-92 | 1.77 | 1.09- | 1665 | 2803 | 965 | 1580 |
| | | | | | | | 2.63 | | | | |
| | M 1 | 37 | 9 | 51 | 15-87 | 1.26 | 0.39- | 1197 | 2017 | 1093 | 1733 |
| | | | | | | | 2.59 | | | | |
| | M 2 | 49 | 12 | 47 | 31-76 | 1.26 | 0.76- | 1105 | 1858 | 969 | 1585 |
| | | | | | | | 1.93 | | | | |
| Chinstrap | F 2 | 42 | 6 | 75 | 15-149 | 2.39 | 0.45- | 1761 | 2966 | 801 | 1376 |
| 1980/81 | | | | | | | 4.04 | | | | |
| | F 3 | 21 | 5 | 71 | 31-137 | 2.11 | 0.97- | 1674 | 2820 | 849 | 1437 |
| | | | | | | | 4.45 | | | | |
| | M 1 | 5 | 4 | 46 | 8-86 | 1.37 | 0.26- | 1092 | 1837 | 917 | 1521 |
| | | | | | | | 2.66 | | | | |
| | M 2 | 17 | 9 | 63 | 35-87 | 1.71 | 0.90- | 1485 | 2502 | 915 | 1519 |
| | | | | | | | 2.21 | | | | |
| | M 3 | 35 | 6 | 91 | 26-151 | 2.39 | 0.70- | 2146 | 3615 | 956 | 1569 |
| | | | | | | | 4.19 | | | | |
| Chinstrap | F 2 | 15 | 4 | 48 | 0-112 | 1.41 | 0.00- | 1134 | 1908 | 854 | 1443 |
| 1981/82 | | | | | | | 3.38 | | | | |
| | F 3 | 36 | 5 | 76 | 25-192 | 1.97 | 0.76- | 1795 | 3021 | 916 | 1519 |
| | | | | | | | 6.07 | | | | |
| | M 2 | 56 | 7 | 78 | 25-150 | 2.16 | 0.73- | 1841 | 3100 | 895 | 1498 |
| | | | | | | | 4.35 | | | | |
| | M 3 | 14 | 5 | 87 | 25-137 | 2.21 | 0.65- | 2054 | 3456 | 954 | 1569 |
| | | | | | | | 3.22 | | | | |

Appendix 6.1. The mean weight loss and energy consumption of adults during pre-laying attendance and incubation (first analysis method: uses weights at or near the beginning and end of fasts).

| Species/ year | Sex/ Fast | Sample size | Sample period (d) | Wt. loss(% $d^{-1}$) range | Wt. loss(% $d^{-1}$) pooled | F | P | Wo(g) ±sd | Wt(g) ±sd | Energy consumption ($kJd^{-1}$) Calculated Lower | Calculated Upper | Theoretical Basal | Theoretical Existence |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Adélie | F 2 | 10 | 15.1 | 1.49- | 2.00 | 0.36 | 0.025 | 4318 | 3231 | 1699 | 2862 | 923 | 1536 |
| 1980/81 | | | | 2.38 | | | | ±347 | ±415 | | | | |
| | M 2 | 10 | 13.6 | 1.00- | 1.09 | 0.05 | 0.025 | 4486 | 3831 | 1138 | 1916 | 996 | 1619 |
| | | | | 1.36 | | | | ±277 | ±253 | | | | |
| Chinstrap | F 2 | 2 | 13.0 | 1.38- | 1.68 | 0.12 | 0.025 | 3336 | 2696 | 1163 | 1958 | 787 | 1360 |
| 1980/81 | | | | 1.98 | | | | ± 39 | ± 45 | | | | |
| | M 2 | 4 | 15.5 | 0.89- | 1.85 | 12.20 | 0.001 | 4052 | 3162 | 1356 | 2280 | 900 | 1498 |
| | | | | 1.98 | | | | ±177 | ±297 | | | | |
| | M 3 | 1 | 14.0 | - | 2.50 | - | - | 4216 | 2969 | 2100 | 3540 | 895 | 1494 |
| Chinstrap | F 3 | 1 | 18.0 | - | 1.90 | - | - | 3851 | 2733 | 1464 | 2469 | 841 | 1423 |
| 1981/82 | | | | | | | | | | | | | |
| | M 2 | 15 | 13.7 | 1.18- | 1.75 | 0.08 | 0.025 | 4019 | 3144 | 1506 | 2540 | 891 | 1490 |
| | | | | 2.27 | | | | ±276 | ±264 | | | | |
| | M 3 | 1 | 17.0 | - | 1.65 | - | - | 4189 | 3165 | 1423 | 2393 | 912 | 1515 |

Appendix 6.2. The mean weight loss and energy consumption of adults during incubation (second analysis method : uses weights of birds for which at least four weights were recorded).

Appendix 6.3. The mean weight loss and energy consumption of adults during pre-layng attendance and incubation (third analysis method: uses all recorded adult weights).

| Species/ Year | Sex/ Fast | Sample size | Sample period (d) | Wt.loss (% $d^{-1}$) | Initial wt.(g) | Final wt.(g) | Energy consumption (kJ $d^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Calculated | | Theoretical | |
| | | | | | | | Lower | Upper | Basal | Existence |
| Adélie | F 1 | 57 | 16 | 1.15 | 4532 | 3835 | 1029 | 1732 | 1000 | 1623 |
| 1980/81 | F 2 | 47 | 13 | 1.64 | 4528 | 3112 | 1452 | 2448 | 937 | 1544 |
| | M 1 | 59 | 22 | 0.83 | 5105 | 4281 | 883 | 1490 | 1088 | 1728 |
| | M 2 | 55 | 16 | 0.87 | 4146 | 3562 | 862 | 1452 | 941 | 1552 |
| Chinstrap | F 2 | 57 | 14 | 1.38 | 3220 | 2662 | 937 | 1582 | 774 | 1339 |
| 1980/81 | F 3 | 48 | 17 | 1.54 | 4024 | 3078 | 1314 | 2213 | 887 | 1485 |
| | M 1 | 43 | 9 | 0.78 | 3463 | 3242 | 582 | 975 | 849 | 1439 |
| | M 2 | 19 | 18 | 1.22 | 4146 | 3318 | 1088 | 1833 | 920 | 1527 |
| | M 3 | 48 | 16 | 1.05 | 4077 | 3395 | 1004 | 1695 | 920 | 1527 |
| Chinstrap | F 2 | 56 | 9 | (+0.66) | (3268) | (3463) | - | - | 854 | 1443 |
| 1981/82 | F 3 | 45 | 21 | 0.24 | 3786 | 3605 | 205 | 343 | 912 | 1519 |
| | M 2 | 58 | 19 | 1.12 | 3913 | 3150 | 950 | 1598 | 883 | 1481 |
| | M 3 | 42 | 18 | 0.39 | 4105 | 3847 | 318 | 569 | 962 | 1577 |

| Genus and species | Adult weight (kg) | Egg wt. (g) 1 | Egg wt. (g) 2 | Incubation (d) | Inc. tasts (d) | Fledge period (d) | Breeding success (chicks/pr.) | Age of first breeding | Annual survival (%) lst yr. | Annual survival (%) Adult | Feeds /day | Diet | Distribution; climate | Breeding population (pairs) | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Aptenodytes forsteri (Emperor) | 30 | 450 | - | 62 | 62 | 160 | 0.64 | 3-6 | 19 | 95 | 0.3 | Fish, squid | Antarctica; extreme | 200,000 | Stonehouse,1953;Prévost,1961;Mougin,1966; LeMaho,1977;Wilson,1983;Ainley & O'Connor; Croxall & others,b;Jouventin & others,in press |
| patagonicus (King) | 12 | 302 | - | 54 | 12-21 | 350 | 0.55 | 4 | ? | 82 | 0.3 | Fish, squid | Subantarctic; moderate | 1 million | Stonehouse,1960;Barrat,1976;Williams & others, 1979;Jouventin & Mougin,1981;Wilson,1983; Croxall & others,e;Jouventin & others,in press |
| Pygoscelis adeliae (Adélie) | 4.5 | 121 | 113 | 35 33 | 13-14 | 56-61 | 0.80-1.27 | 3-7 | 55 | 70 | 0.5 | Krill | Antarctica; harsh | 2 million + | Sladen,1958;Taylor,1962;Reid,1965;Ainley & DeMaster,1980;Ainley & others,1983;Wilson, 1983;Ainley & O'Connor;Croxall & others,b; in press;this study |
| antarctica (Chinstrap) | 4.0 | 114 | 112 | 36 34 | 6-10 | 53 | 0.76-0.86 | 3 | ? | ? | 0.7 | Krill | Subantarctic; moderate | 6 million + | Trivelpiece,1981;Wilson,1983;Croxall & others, in press b;this study |
| papua (Gentoo) | 6.2 | 141 | 134 | 34 37 | c.1 | 70-90 | 1.06 | 2-4 | ? | ? | c.1 | Krill, fish | Subantarctic; moderate | 250,000 | Croxall & Prince,1980a;Trivelpiece,1981;Prince & Croxall,1983;Wilson,1983;Croxall & others,b; Jouventin & others;Williams,in press |
| Eudyptes chrysolophus (Macaroni) | 4.2 | 99 | 157 | 38 36 | 25-25 | 55-70 | c.0.5 | 7-8 | 65 | 56 | 0.5 | Krill | Subantarctic; | 8 million + | Croxall & Prince,1980b;Williams & Laycock, 1981;Wilson,1983;Croxall & others,b;Jouventin & others;Schlatter;Williams,in press |
| chrysocome (Rockhopper) | 2.5 | 76 | 109 | 39 34 | 16 | 70 | ? | ? | ? | ? | 0.4 | Krill, squid | Subantarctic; moderate | 6 million + | Tollu,1978;Williams & Laycock,1981;Wilson, 1983;Croxall & others,e;Jouventin & others; Robertson & Bell;Rounsevell & Brothers; Williams,in press |
| schlegeli (Royal) | 4.3 | 94 | 155 | 35 | 16 | 66 | c.0.5 | 7-8 | 67 | 56 | <1.0 | Krill, squid | Subantarctic; moderate | 1 million + | Carrick,1964;1972;Warham,1971;Rounsevell & Brothers,in press |
| pachyrhynchus (Fiordland) | 3.0 | 100 | 120 | 36 31 | 12 | 75 | ? | ? | ? | ? | <1.0 | ? | New Zealand; mild | 5,000 - 10,000 | Warham,1974b;Robertson & Bell,in press |
| robustus (Snares-crested) | 3.0 | 125 | | 37 31 | 15 | 70 | ? | ? | ? | ? | ? | ? | New Zealand; mild | 10,000 - 50,000 | Warham,1974a;Robertson & Bell,in press |
| sclateri (Erect-crested) | 3.6 | 90 | 134 | 35 | 17 | 70 | ? | ? | ? | ? | ? | ? | New Zealand; mild | 100,000 - 1 million | Richdale,1950;Roberston & Bell,in press |
| Megadyptes antipodes (Yellow-eyed) | 5.0 | 138 | 137 | 43 | c.1 | 106 | 0.59 | 2-3 | 55 | 87 | >1.0 | ? | New Zealand; mild | 1,000 - 5,000 | Richdale,1949;1957;Roberston & Bell,in press |
| Eudytula minor (Little blue) | 1.1 | 52 | ? | 38 | c.1 | 58 | 0.26 | 3-4 | ? | 86 | >1.0 | ? | New Zealand; mild | 25,000 - 50,000 | Richdale,1940;Kinsky,1960;Reilly & Balmford, 1975;Reilly & Cullen,1979;1981;Robertson & Bell,in press |
| Spheniscus demersus (Jackass) | 2.9 | 107 | 104 | 37 | 1.1 | 80 | 0.49 | 2 | ? | ? | >1.0 | Fish, squid | S.Africa; warm | 170,000 | Jackson & others,1976;Cooper,1980;Randall & others,1981;Cooper & others;Williams,in press |
| humboldti (Humboldt) | 4.9 | 129 | 126 | ? | ? | ? | ? | ? | ? | ? | >1.0 | ? | S.America; warm | 4,000 - 6,000 | Boswell & MacIver,1975;Duffy & others; Schlatter,in press |
| magellanicus (Magellanic) | 4.2 | 122 | | 40 | ? | c.70 | 0.94 | ? | ? | ? | >1.0 | ? | S.America; warm | 100,000+ | Grailey-Phipp,1978;Kojima,1978;Scolaro & others,1980;Croxall & others,e;Schlatter, in press |
| mendiculus (Galapagos) | 2.2 | ? | ? | 38 | ? | c.50 | 1.3 | ? | ? | ? | >1.0 | Krill, squid | Galapagos Is; warm | 6,000 - 15,000 | Boersma,1976;1977;1978 |

Appendix 8.1. Synthesis of the available information on the breeding biology, feeding ecology, distribution and demography of the Spheniscidae.