ECOLOGICAL ENERGETICS OF *EUDYPTES* PENGUINS AT MARION ISLAND

by

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To my wife Susan and daughter Robynne who stayed at home.

TABLE OF CONTENTS

ABSTRACT

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Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*) breed sympatrically at Marion Island in the sub-Antarctic, where they account for a substantial proportion of the avian biomass breeding at the island. This thesis documents the energy requirements of the two species during their respective breeding and moulting cycles at the island.

Resting metabolic rates, calculated from lowest, stable rates of oxygen consumption over 24 h, averaged 25 % greater than basal metabolic rates predicted from allometric equations. Body temperatures of the penguins and the relationships between metabolic rates and temperature were investigated over a range of -10°C to 25°C. Lower critical temperature of Rockhopper Penguins was between 0°C and 5°C, but that of Macaroni Penguins could not be clearly ascertained. Measured metabolic rates of other species of penguins are reviewed and intra- and inter-specific differences in metabolic rates are discussed. In contrast to most penguins measured, individuals maintained in zoos or held in captivity for long periods had metabolic rates lower than predicted basal levels.

Macaroni and Rockhopper Penguins undergo periods of fasting during incubation. Energy expenditures during

incubation were estimated from rates of oxygen consumption. Incubating metabolic rates were similar to resting levels in both species, but mass-specific metabolic rates were significantly lower and were close to predicted values for basal metabolic rates. Results are also compared to estimates based on rates of loss of body mass.

Penguins undergo a rapid moult lasting, in Macaroni and Rockhopper Penguins, about four weeks, during which the birds remain ashore fasting. Energy expenditures during moult were estimated from rates of oxygen consumption at three to four-day intervals during moult. Changes in mass-specific energy expenditures are discussed in terms of new feather synthesis and reduction of insulation during old feather loss. Peak energy expenditure of moulting birds was 1.26 and 1.10 times that of resting, non-moulting birds in Macaroni and Rockhopper Penguins, respectively, or about 1.81 and 1.50 times greater, respectively, than that of incubating birds. Energy expenditures measured are compared to those estimated from daily rates of loss of body mass. The development of the new feathers and the duration of moult were also investigated. New feathers began developing under the skin before the birds return ashore to moult. Total moult lasted between 25 and 35 days.

Eudyptes penguins lay two eggs which are markedly dimorphic in size, the first laid A-egg being smaller than the second laid B-egg. Although laid three to four-days before the B-egg, when retained, the A-egg always hatches

last. Although A-eggs incubated alone or in different positions in a two-egg clutch had slightly different temperatures and rates of embryonic oxygen consumption, differences were insufficient to explain their longer incubation periods. Furthermore, A-eggs of Macaroni Penguins, which are the same size as B-eggs of Rockhopper Penguins, also had lower rates of metabolism and longer incubation periods than the latter, suggesting that the embryos of A-eggs have inherently slower rates of development.

Energy requirements for growth and maintenance of Macaroni and Rockhopper Penguin chicks were estimated from rates of oxygen consumption during growth and from body composition analysis. Daily energy requirements increased from 417 and 211 kJ day^{-1} for Macaroni and Rockhopper Penguins, respectively, to peaks of 1 540 and 1 170 kJ day^{-1} about halfway through the growth period before decreasing until independence. An energy budget is presented for chicks from hatching to fledging and food requirements, calculated from the energy budget, are compared with data from the literature, based on meal sizes fed to chicks and the feeding frequency.

The diets of Macaroni and Rockhopper Penguins were investigated quantitatively over two successive chick-rearing seasons. The diets were broadly similar, both species feeding predominantly on crustaceans with fish and cephalopods being of lesser importance. However, there were

notable differences in prey-species composition in some instances. Seasonal changes in diet were evident, with pelagic fish and cephalopods comprising a greater proportion of food taken later in chick-rearing when the adults foraged farther from their colonies. Prey species are compared to those known from net hauls to occur in the vicinity of Marion Island, and the diets of the two species of penguins at other localities are briefly reviewed. Dietary segregation of the two species at Marion Island is commented upon.

Travelling speed and foraging ranges of Macaroni and Rockhopper Penguins were measured using autoradiographic devices. Both species travel at about 7.5 km h^{-1} but spend only 30 % to 40 % of their time at sea swimming at speed. Mean maximum foraging ranges of Rockhopper Penguins feeding small chicks were between 4 and 160 km and those of Macaroni Penguins feeding large chicks between 60 and 300 km. Measured foraging ranges are discussed in relation to diet.

Data on energy expenditures of adults and chicks and the diets of the two species were combined with information on population size and activity budgets from the literature to construct a model of the energy requirements and food consumption of Macaroni and Rockhopper Penguins at Marion Island and neighbouring Prince Edward Island. Total food requirements of the two species during their six to seven-month breeding and moulting cycle at Marion and Prince

Edward Islands amounted to 145 000 tonnes, of which Macaroni Penguins consumed 87 %. Food consumption estimates are compared with available information on potential primary production in the vicinity of the Prince Edward Islands.

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Penguins are widely distributed throughout the southern hemisphere and are especially prominent in cool Antarctic and sub-Antarctic regions, where they sometimes form colonies of millions of individuals (Stonehouse 1967). Most abundant in the sub-Antarctic are Macaroni Penguins (*Eudyptes chrysolophus*) with an estimated world population, including the closely related Royal Penguin (*E. c. schlegeli*), in excess of 8 X 10^6 breeding pairs (Wilson 1983). Consequently, Macaroni Penguins account for an appreciable avian biomass and are major consumers of marine resources in the region. Indeed, Croxall (1984) suggests that 80 % of the avian biomass in the sub-Antarctic can be considered to be penguins, of which 50 % are Macaroni Penguins. Almost as numerous as the Macaroni Penguin in the sub-Antarctic is the congeneric Rockhopper Penguin (*E. chrysocome*) with an estimated world population of about 6.5 X 10^6 breeding pairs (Wilson 1983).

Macaroni and Rockhopper Penguins are, respectively, the largest and the smallest of the crested penguins which comprise the genus *Eudyptes* (Warham 1975). Macaroni Penguins are distributed between 46^{o} and 62^{o}S and Rockhopper Penguins between 37^{o} and 54^{o}S (Wilson 1983), and the two species breed sympatrically throughout much of their ranges (Fig. 1).

Penguins are flightless seabirds which are highly adapted for an aquatic lifestyle, but which nevertheless must return ashore to breed. The contrasting properties of air and water pose special problems for the birds' thermoregulation (Stonehouse 1967). Consequently, considerable interest has been shown in their morphological and physiological adaptations. For example, much effort has been devoted to understanding the thermoregulation and energy requirements of Emperor Penguins (*Aptenodytes forsteri*), which not only undergo lengthy periods of fasting during their winter breeding cycle in the Antarctic, when temperatures may fall as low as -40^{o}C, but which also travel long distances over the ice between their breeding colonies and the sea (Pinshow *et al.* 1976, Le Maho *et al.* 1978, Pinshow and Welch 1980, Le Maho and Dewasmes 1985). In addition, presumably because of their accessibility, some attention has been given to aspects of the metabolism and thermoregulation of more temperate species, in particular the Jackass Penguin (*Spheniscus demersus*), the Humboldt Penguin (*S. humboldti*) and the Little Penguin (*Eudyptula minor*) (e.g. Drent and Stonehouse 1971, Erasmus and Smith 1974, Erasmus and Wessels 1985, Stahel and Nicol 1982, Baudinette *et al.* 1986).

In contrast to the above species, relatively little work has been done on Macaroni and Rockhopper Penguins. Warham (1963) and Strange (1982) described the breeding biology of

Rockhopper Penguins at Macquarie Island (54°40'S, 158°55'E) and the Falkland Islands (52°00'S, 60°00'W), and Warham (1971) and Carrick (1972) investigated the breeding biology of Royal Penguins at Macquarie Island. Williams (1980) documented aspects of the breeding biology of both Macaroni and Rockhopper Penguins at Marion Island (46°52'S, 37°51'E). Similarly, the diets of the two species have been studied quantitatively at only a few localities (e.g. Croxall and Furse 1980, Croxall and Prince 1980, Croxall *et al.* 1985, Horne 1985, Jablonski 1985). However, much of the available information on diet is of an anecdotal nature. Few physiological studies have been carried out on *Eudyptes* penguins to date. Although measurements of basal metabolic rates of Macaroni and Rockhopper Penguins are available, these are limited to estimates from captive individuals away from their natural habitats (Gavrilov 1977).

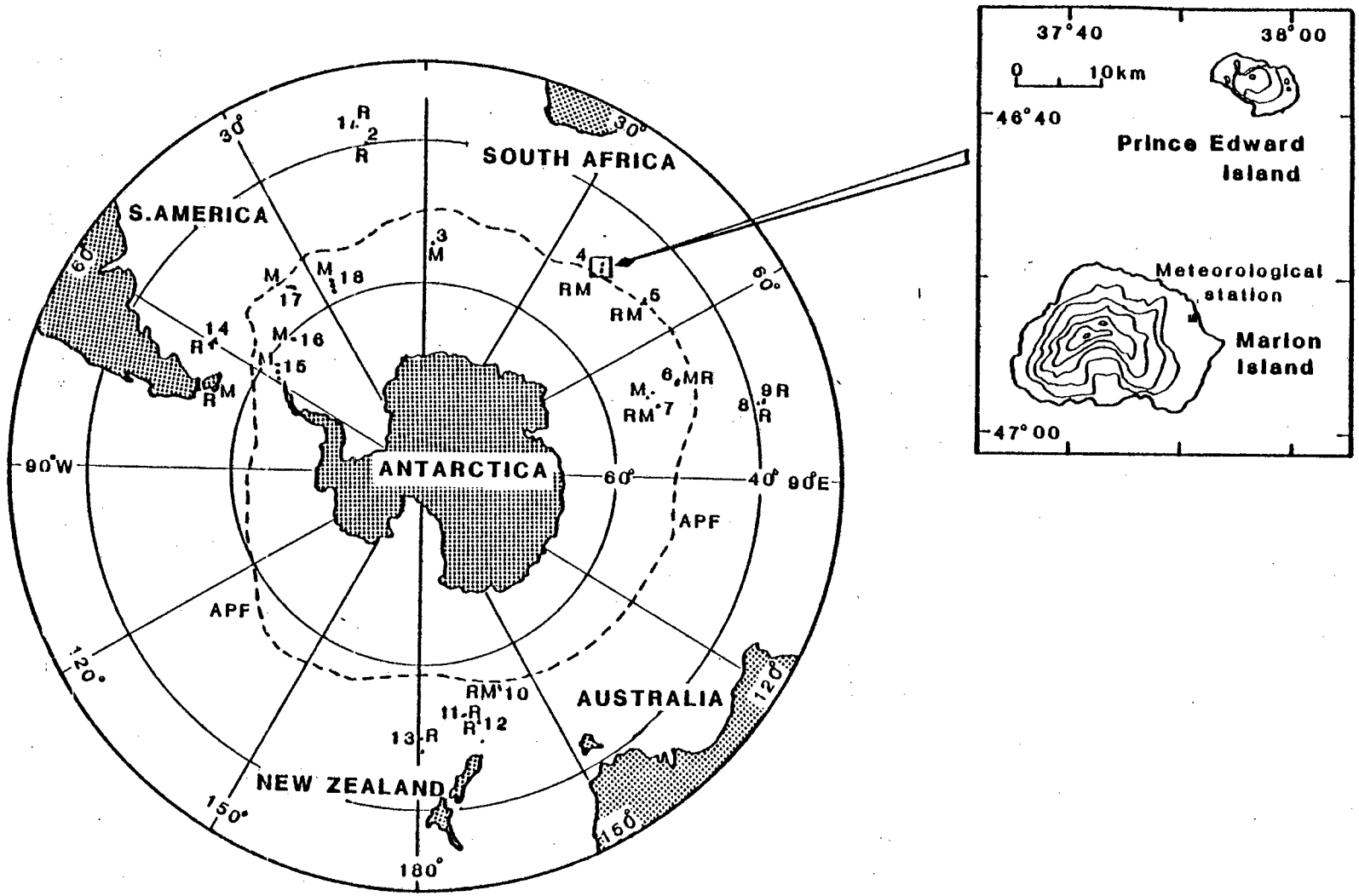
The increase in commercial fishing in the Antarctic and sub-Antarctic, especially for Antarctic Krill (*Euphausia superba*), in the past decade has stimulated interest in the roles of seabirds as predators of marine resources in these regions. Potential seabird-fisheries interactions have further highlighted the need for estimates of the food requirements of seabirds. For example, intense fishing activity around the Falkland Islands has been implicated in an unusually high mortality of adult Rockhopper Penguins during the 1985/86 breeding season (Lyster 1986). Because of their importance in terms of biomass, Macaroni Penguins have

been the focus of much of the research in recent years. As a result primarily of work carried out by researchers of the British Antarctic Survey at Bird Island, South Georgia (54°00'S, 37°00'W), estimates of energy expenditures during the incubation and moult fasts of Macaroni Penguins, based on rates of loss of body mass, are available (see review by Croxall 1982). In addition, radio-isotopes have been used to estimate energy expenditures of Macaroni Penguins at sea (Davis *et al.* 1983). These data, combined with allometric equations, have been used to estimate the energy requirements and food consumption of Macaroni Penguins at South Georgia , where they were estimated to account for 51 % of the food consumed by all seabirds breeding there (Croxall *et al.* 1984).

Despite their large numbers, Rockhopper Penguins in the sub-Antarctic have been relatively little studied, estimates of energy expenditure being limited to adults during moult and the food requirements of chicks. These were estimated from body composition and rates of loss of body mass, and from sizes and frequency of meals fed to chicks, respectively (Williams *et al.* 1977, Williams 1982).

Both Macaroni and Rockhopper Penguins breed at sub-Antarctic Marion Island (46°52'S, 37°51'E), the larger of two islands which make up the Prince Edward islands group (see Fig. 1). The smaller Prince Edward Island lies 19 km to the northeast of Marion Island. The islands are volcanic in

Figure 1. Distribution of Macaroni (M) and Rockhopper (R) Penguins in the Antarctic and sub-Antarctic: 1 Tristan da Cunha Is., 2 Gough I., 3 Bouvetoya, 4 Prince Edward Is., 5 Iles Crozet, 6 Iles Kerguelen, 7 Heard I., 8 Ile St. Paul, 9 Ile Amsterdam, 10 Macquarie I., 11 Campbell I., 12 Aukland Is., 13 Antipodes Is., 14 Falkland Is. 15 South Shetland Is., 16 South Orkney Is. 17 South Georgia, 18 South Sandwich Is. Inset shows Prince Edward Island in relation to Marion Island.


SOUTH AFRICA
S.AMERICA
ANTARCTICA
AUSTRALIA
NEW ZEALAND
APF
APF
30°
60°
90°W
120°
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180°
60°
40°
90°E
120°
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1 R
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10 RM
11 R
12 R
13 R
14 R
15 M
16 M
17 M
18 M
37°40
38°00
0 10km
46°40
Prince Edward Island
Meteorological station
Marion Island
47°00

origin and the coastlines are precipitous with few suitable landing beaches for penguins. The implications of this for the distribution of penguins at Marion Island have been discussed by Williams (1978), particularly with reference to Macaroni Penguins. Nevertheless, an estimated 405 000 pairs of Macaroni Penguins breed at 33 colonies around Marion Island (Watkins, in press); 90 % of these breed at two very large colonies. Approximately 93 300 pairs of Rockhopper Penguins breed in scattered colonies along most of the coastline (Siegfried *et al.* 1978). A further 17 000 and 35 000 pairs of Macaroni and Rockhopper Penguins, respectively, breed at Prince Edward Island (Williams *et al.* 1979).

Marion and Prince Edward islands lie about 200-250 km to the north of the Antarctic Polar Front (Lutjeharms and Valentine 1984), and the climate is typically oceanic, with little diel and seasonal variation. Annual rainfall averages 2 500 mm and air temperatures range from extremes of -6.8°C to 22.3°C with an annual mean of 5.1°C. Sea surface temperatures average 5.0°C, with a range of 2.1 - 8.0°C. Winds are predominantly from the west and frequently are gale force (Schulze 1971).

This thesis aims to investigate aspects of the energy requirements of adult Macaroni and Rockhopper Penguins and their chicks at Marion Island. Specific objectives were:

1) To measure the energy expenditures of adult Macaroni and Rockhopper Penguins during resting, non-fasting activites ashore and during their incubation and moult fasts, using indirect calorimetry.

2) To measure the energy requirements for growth and maintenance of Macaroni and Rockhopper Penguin chicks by means of indirect calorimetry and body composition analysis.

3) To ascertain the diets and foraging ranges of Macaroni and Rockhopper Penguins.

4) To use the preceding information to estimate the energy requirements and food consumption of Macaroni and Rockhopper Penguins during their respective breeding seasons.

The thesis is divided broadly into four parts, each comprising one or more chapters. Part 1 investigates the energy expenditures of adult Macaroni and Rockhopper Penguins during rest, incubation and moult, and includes some aspects of feather growth (Chapters 1-4). Part 2 comprises two chapters on aspects of embryonic metabolism in relation to egg-size dimorphism and energy requirements of chicks for growth and maintenance (Chapters 5 and 6). Part 3 investigates the diets and foraging ranges of adult Macaroni and Rockhopper Penguins during the chick-rearing period (Chapters 7 and 8), and Part 4 comprises a single chapter (Chapter 9) in which information from the preceding chapters

is used to construct a model of the energy requirements and food consumptions of the breeding populations of Macaroni and Rockhopper Penguins at Marion and Prince Edward Islands.

With the exception of the final chapter, all chapters have been published, are in press, or have been submitted for publication in refereed journals. This facilitates rapid dissemination of the work but inevitably results in some repetition. Chapters 1 and 2 were originally published as a single paper, but additional data have resulted in their being separated in the thesis. N.T. Klages was a junior co-author of Chapter 8. For convenience, the chapters are in the format of the journals to which they have been submitted.

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CHAPTER 1

RESTING METABOLIC RATES OF MACARONI AND ROCKHOPPER PENGUINS

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ABSRACT

1. Oxygen consumption of resting Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*) was measured at sub-Antarctic Marion Island.

2. Resting metabolic rates, calculated from lowest, stable periods measured over 24 h, averaged 1 161 kJ day^{-1} for Macaroni Penguins of mean mass 3.78 kg, and 863 kJ day^{-1} for Rockhopper Penguins of mean mass 2.51 kg.

3. Metabolic rates of Macaroni Penguins increased between temperatures of 25°C and -10°C, and lower critical temperature could not be ascertained. Metabolic rates of Rockhopper Penguins were relatively constant between 25°C and 5°C but increased below 5°C. The lower critical temperature of this species was estimated to be between 0°C and 5°C.

4. Mean body temperature of resting Macaroni Penguins was 38.5 ± 0.6°C and that of Rockhopper Penguins was 39.0 ± 0.2°C.

5. The relationship between body mass and metabolic rate for 12 species of penguins is described by the equation $M_{(kJ\ day\text{-}1)} = 1.82\ W_{(g)}^{0.76}$.

INTRODUCTION

Penguins are distributed from the Antarctic to the tropics. Their semi-aquatic lifestyles, reported low body temperatures and long fasts during breeding and moulting have resulted in considerable interest in their thermoregulation in air and water (Kooyman *et al.*, 1976; Stahel and Nicol, 1982), as well as during prolonged fasts (Le Maho *et al.*, 1976; Le Maho and Despin, 1976; Pinshow *et al.*, 1976). Estimates of metabolic rate, based on oxygen consumption measurements, are available for several species: in particular, basal metabolic rate (BMR) and standard metabolic rate (SMR) have been measured for Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*) (Gavrilov, 1977), although these measurements were made on captive birds away from their natural habitat.

The purpose of this study was to measure metabolic rate in Macaroni and Rockhopper Penguins to provide a basis for comparison with energy expenditures during breeding activities, and to compare their metabolic rates with those of other penguins.

MATERIALS AND METHODS

The study was carried out at sub-Antarctic Marion Island ($46^{o}52'S$, $37^{o}51'E$) between December 1981 and April 1982 and between December 1984 and March 1985.

Resting metabolic rate

Resting metabolic rates (RMR) were initially measured on five Macaroni Penguins (three males and two females) and on four Rockhopper Penguins (two males and two females). All birds used for these measurements were rearing small chicks and so were not undergoing lengthy, natural fasts.

Oxygen consumption ($\dot{V}O_2$) was measured in the laboratory in a translucent, airtight metabolic chamber (400 mm diam. X 750 mm high) using an open, flow-through system. Air, drawn from outside the laboratory, was pumped through a regulating flow meter before entering the chamber. Air exiting the chamber was passed through a carbosorb/silica gel tube before entering a Taylor-Servomex OA 570 paramagnetic oxygen analyzer. Flow rate was set to between 2 500 and 3 500 ml min^{-1}. This was sufficient to produce a drop in oxygen content in the expired air of between 1 and 2 % below that of ambient air. The oxygen analyzer was calibrated with nitrogen before the experiment and the oxygen content of ambient air was checked at regular intervals throughout the run. A thermocouple, inserted into the chamber through a rubber bung, measured chamber temperature. An initial period of at least 1 h was allowed for the birds to settle and the chamber air to equilibrate before the first reading was taken. Thereafter, readings of chamber temperature, flow rate and the percentage of oxygen in the expired air were recorded at 30-min intervals over 24 h at normal photoperiod. Chamber temperature during RMR measurements ranged from 11.6 to 15.9°C (mean = 13.4°C).

VO_2 (STPD) for RMR was calculated from the lowest, stable period during the 24-h runs, using the equation of Hill (1972). Stable periods ranged from 1-9 h. VO_2 was converted to an energy equivalent using 1 l O_2 = 20.083 kJ.

Metabolic rates were subsequently measured on a further three Macaroni Penguins (two males and one female) and two Rockhopper Penguins (males) which had failed in their breeding attempt. Metabolic rates of these birds were measured and calculated over a period of 5-8 h during daylight as described above.

In order to investigate the affect of temperature on metabolic rate, oxygen consumption was measured on four birds of each species at approximately 5°C intervals between -10°C and 25°C. Chamber temperature was regulated by placing the chamber in a chest-type deep freeze (-10°C - 0°C) or in a large water bath (5°C - 25°C). Temperature control using this system was relatively imprecise, but could generally be maintained within 2°C of that desired. Birds were left for a period of at least 1 h at each temperature before oxygen consumption was recorded. Thereafter, oxygen consumption was measured as already described over a further period of 1 h at 15-min intervals before chamber temperature was increased. Error estimates quoted are $\pm$ 1 SD.

Body temperatures

Body temperatures of resting birds were made during measurements of thermal relations. Birds were force-fed a

Table 1.1. Resting metabolic rate (RMR) and average daily metabolic rates during rest (ADMR) of Macaroni and Rockhopper Penguins, with values for predicted BMR for comparison.

	Mean mass (kg)	N	RMR ($kJ\ day^{-1}$)	RMR ($kJ\ kg^{-1}\ day^{-1}$)	ADMR ($kJ\ day^{-1}$)	BMR[a] ($kJ\ day^{-1}$)	RMR/BMR
Macaroni Penguins	3.78	5	1 161 ± 149	307 ± 39	1 320 ± 197	929	1.25
Rockhopper Penguin	2.51	4	863 ± 163	344 ± 65	1 001 ± 173	687	1.26

[a] Predicted from Kendeigh *et al.* (1977).

previously calibrated minimitter (Minimitter Co., Indianapolis) before being placed in the chamber. A thin strand of thread attached to the transmitter was looped around the birds' lower mandible to facilitate easy recovery of the transmitter after the experiment.

RESULTS

Resting metabolic rates

There were no consistent, well-defined phases of rest and activity in metabolic rates of Macaroni and Rockhopper Penguins. Although four Macaroni Penguins exhibited lowest, stable periods of metabolic rate during the night, one bird was least active between late morning and late afternoon. Two Rockhopper Penguins exhibited lowest levels of metabolism in the morning, one in the afternoon and one at night.

There was no significant difference in metabolic rates of males and females of either species when compared on a mass-specific basis (Macaroni Penguins t = 0.292, P > 0.50; Rockhopper Penguins t = 1.12, P > 0.20) so all results were pooled. Resting metabolic rates of Macaroni Penguins, calculated from lowest, stable periods, averaged 1 161 kJ day^{-1} and those of Rockhopper Penguins 863 kJ day^{-1}, 25 % and 26 % greater, respectively, than predicted basal metabolic rates for birds of equivalent masses (Table 1.1).

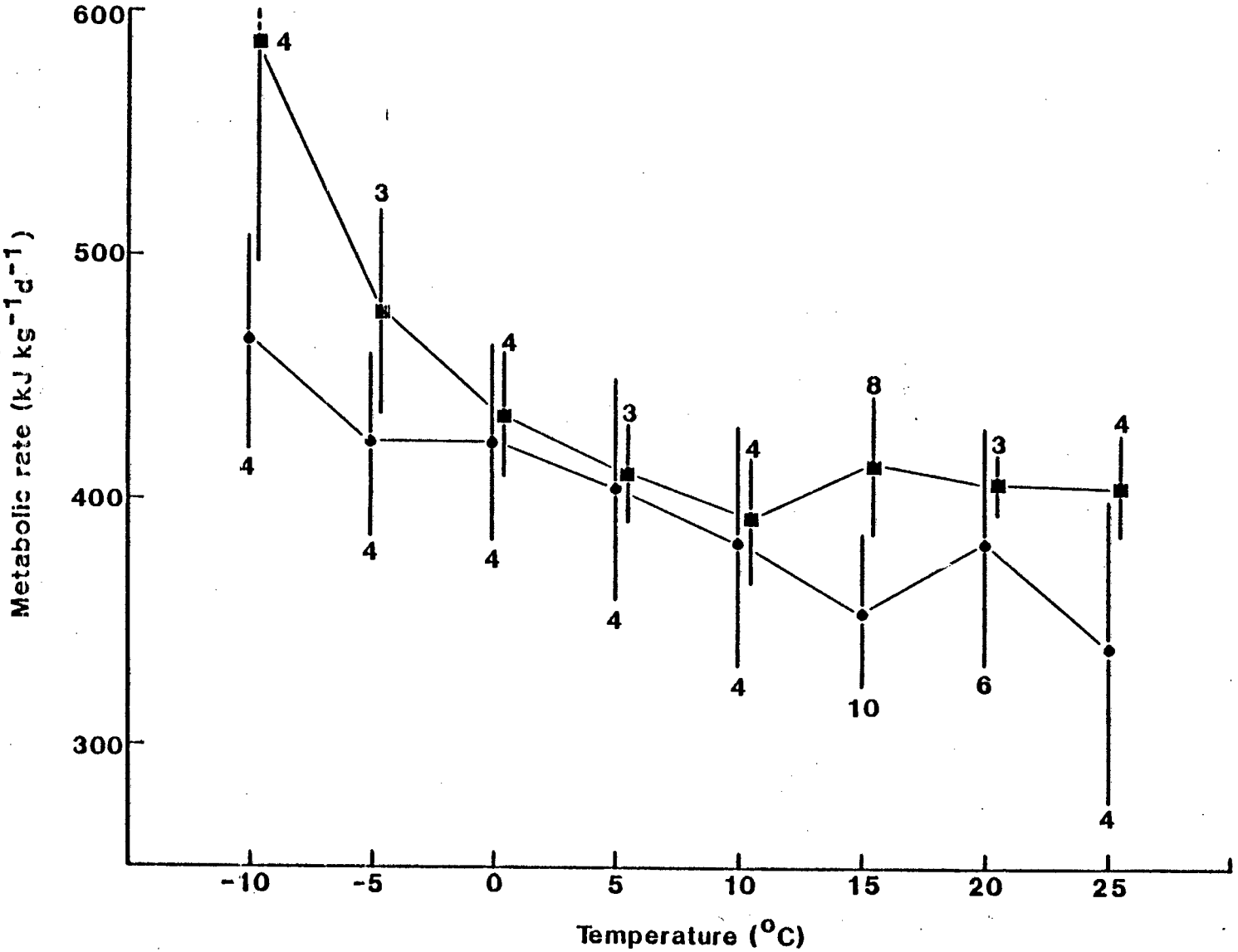
Mean metabolic rates over 24 h, here referred to as the average daily metabolic rate (ADMR) were between 10 % and 20 % greater than RMR calculated from stable periods.

Metabolic rates of failed breeders, measured over 5-8 h, were higher than those calculated from the lowest stable periods of active breeders over 24 h, averaging 1 311 ± 124 kJ day^{-1} for Macaroni Penguins of mean mass 3.87 kg and 1 257 ± 276 kJ day^{-1} for Rockhopper Penguins of mean mass 2.58 kg. These values are, however, similar to measured ADMR's.

Macaroni Penguins exhibited a general increase in metabolic rate from 339 kJ $kg^{-1}day^{-1}$ at 25°C to 465 kJ $kg^{-1}day^{-1}$ at -10°C (Fig. 1.1), and no clear lower critical temperature could be ascertained. In contrast, metabolic rates of Rockhopper Penguins were relatively constant between 25°C and 5°C, averaging 407 kJ $kg^{-1}day^{-1}$ over this range (Fig. 1.1). Below 5°C, metabolic rate increased markedly, reaching 586 kJ $kg^{-1}day^{-1}$ at -10°C. Lower critical temperature for this species therefore probably lies between 0°C and 5°C.

During temperature runs, neither Macaroni nor Rockhopper Penguins attained metabolic rates as low as those calculated from lowest stable periods over 24 h, lowest levels recorded averaging 15 % and 20 % above RMR, respectively. Metabolic rates measured at temperatures similar to those recorded during the 24-h runs were, however, similar to ADMR's measured over the entire 24-h period, differing by only 1 % in Macaroni Penguins and 4 % in Rockhopper Penguins.

Fig. 1.1. Metabolic rates of Macaroni and Rockhopper Penguins in relation to temperature. Points are means ± 1 standard deviation and numbers are sample sizes.


600
500
400
300
Metabolic rate (kJ kg^{-1}d^{-1})
-10
-5
0
5
10
15
20
25
Temperature (°C)
4
3
4
4
4
3
4
4
8
4
3
4
4
10
6
4

Body temperatures

Body temperatures of resting birds did not alter significantly between temperatures of -10°C and 25°C, averaging 38.5 ± 0.6°C (range 37.5°C - 39.8°C, *n* = 4 individuals) overall in Macaroni Penguins and 39.0 ± 0.2°C (range 38.7°C - 39.4°C, *n* = 4 individuals) in Rockhopper Penguins.

DISCUSSION

BMR is regarded as the lowest level of metabolism of an organism during normal existence, upon which the energy cost of all activities is superimposed (Kendeigh *et al.*, 1977). As defined by Kendeigh *et al.* (1977), it is measured on an organism which is in a resting, postabsorbtive state within its thermoneutral zone.

Birds used in this study were caught when returning to sea after feeding chicks and were considered to be postabsorbtive. Chamber temperatures during measurements of RMR were slightly higher than average ambient temperatures at this time, but were within the range that the birds might normally experience at Marion Island during summer (Schulze, 1971). Gavrilov (1977) calculated lower critical temperatures of Macaroni, Rockhopper and King (*Aptenodytes patagonicus*) Penguins to be 12, 16 and 3°C respectively, but Le Maho (1983) reports a lower critical temperature of -5°C for the King Penguin, some 8°C lower than that measured by Gavrilov (1977). Since Macaroni, Rockhopper and King

Penguins are found sympatrically throughout much of their respective ranges, it is likely that their lower critical temperatures are also lower than those measured by Gavrilov (1977). This is supported by the observation for Rockhopper Penguins which suggests a lower critical temperature for this species of 0-5^{o}C, 10 - 16^{o}C below that estimated by Gavrilov (1977). The lower critical temperature of Macaroni Penguins is likely to be similar to that of Rockhopper Penguins, the lack of a clearly defined lower critical temperature in the present study possibly resulting from the stepwise alteration of chamber temperatures or too short a time at each temperature. Metabolic rates of incubating birds, however, were lower than those of non-incubating birds measured under the same conditions (see Chapter 2). Consequently, although conditions comply with the definition of BMR *sensu* Kendeigh *et al.* (1977), the metabolic rate measured cannot be regarded as a measure of BMR in the traditional sense. For this reason, for the purpose of this study, measured metabolic rate of non-incubating penguins resting in a postabsorbtive state within their thermoneutral zones, is referred to as RMR.

The question arises as to how many other measurements of metabolic rate, referred to as BMR, are in fact true estimates of BMR. The need for workers to describe the conditions under which the measurements were made, and to define the terms which they use to describe these measurements, is clearly highlighted. In addition, metabolic rates calculated from lowest stable periods over 24 h were

lower than those measured over shorter periods, demonstrating the need to measure metabolic rates over relatively long periods to obtain true resting levels, particularly in species which demonstrate no clear diurnal or nocturnal patterns of metabolic rate.

Resting metabolic rate

RMRs of Macaroni and Rockhopper Penguins measured in this study were higher than predicted BMR for birds of equivalent masses. Gavrilov (1977) measured BMR and SMR (metabolic rate below the zone of thermoneutrality) on zoo specimens of Macaroni and Rockhopper Penguins. He found BMR of Macaroni Penguins of mean mass 3.87 kg to be 747 kJ day^{-1} and that of Rockhopper Penguins of mean mass 2.33 kg to be 504 kJ day^{-1}. However, the figure presented in the text by Gavrilov (1977) for Macaroni Penguins does not agree with that presented in his tables, the former being 1 035 kJ day^{-1} as opposed to 747 kJ day^{-1}. Data for energy expenditure from Gavrilov quoted in this paper have been taken from the tables. These are 21 and 23 % lower respectively than predicted BMR from the equation of Kendeigh *et al.* (1977), and 46 and 49 % lower, respectively, than RMRs of Macaroni and Rockhopper Penguins measured in this study. SMRs measured by Gavrilov (1977) on the same birds were 1 275 and 764 kJ day^{-1} for Macaroni and Rockhopper Penguins, respectively. Although Gavrilov (1977) does not give the temperatures at which SMR measurements were made, from the data presented in his Fig. 1. it is estimated that temperatures were $0^{o}C$ for Macaroni Penguins and $5^{o}C$ for Rockhopper Penguins.

Gavrilov's figures for SMR are more comparable to the RMRs measured in this study, differing by 7 % and 4 %, respectively.

Estimates of metabolic rates in Macaroni Penguins also have been made by Scholander (quoted in Weathers, 1979). These have been discounted here because they were measured on forcibly submerged, struggling birds, a condition certain to result in elevated metabolic rates.

Available data on metabolic rates in other non-incubating penguins, derived from oxygen consumption measurements, are summarized in Table 1.2. These can be compared with those for RMR of Macaroni and Rockhopper Penguins using the ratio of the measured metabolic rate to predicted BMR for birds of equivalent mass. RMRs of both Macaroni and Rockhopper Penguins are comparable with metabolic rates of other species although it is evident that there is considerable variation in measured metabolic rates, both between and within species. Some of this variation may be accounted for by differences in experimental techniques, the physiological state of the experimental birds and the conditions under which oxygen consumption was measured. It is noteworthy that measurements of metabolic rate on zoo penguins and penguins held in captivity for long periods (Drent and Stonehouse, 1971; Gavrilov, 1977; Erasmus and Wessels, 1985; Baudinette *et al.*, 1986;) are, with the single exception of Little Penguins measured by Stahel and Nicol (1982), the lowest reported and are also lower than predicted BMR. Whether this is due to acclimatization of the birds to

Table 1.2. Metabolic rates of penguins, derived from oxygen consumption measurements (data from the literature).

Species	N	Mean mass (g)	Metabolic rate measured	Metabolic rate (kJ day^{-1})	Predicted BMR[a] (kJ day^{-1})	MR/BMR	Reference
Emperor Penguin	4	31 750	RMR (fasting)	5 791[b]	4 436	1.31	Dewasmes *et al.* (1980)
Aptenodytes forsteri	11	24 800	BMR (fasting)	4 239	3 700	1.15	Le Maho *et al.* (1976)
	5	23 370	SMR (fasting)	3 704	3 542	1.04	Pinshow *et al.* (1976)
	4	20 790	RMR	3 307	3 250	1.02	Pinshow *et al.* (1977)
King Penguin	4	13 270	BMR	2 237	2 337	0.96	N.J. Adams (unpubl. data)
A. patagonicus	3	12 662	RMR (fasting)	2 877[c]	2 258	1.27	Le Maho & Despin (1976)
	8	11 080	BMR	1 888	2 047	0.92	Gavrilov (1977)
			SMR	2 099		1.02	
Gentoo Penguin	4	6 290	RMR	1 605	1 305	1.19	N.J. Adams (Unpubl. data)
Pygoscelis papua							
Yelloweyed Penguin	1	4 800	BMR	996	1 107	0.90	Stonehouse (1968), in Drent & Stonehouse (1971)
Megadyptes antipodes							
Adélie Penguin	-	*c.*4 500[d]	BMR	1 562	1 056	1.48	Le Resche & Boyd (1969)
P. adeliae	14	3 970	RMR	1 057	963	1.10	Kooyman *et al.* (1976)
Peruvian Penguin	3	3 870	BMR	820	945	0.87	Drent & Stonehouse (1971)
Spheniscus humboldti							
Macaroni Penguin	4	3 870	BMR	747	945	0.79	Gavrilov (1977)
Eudyptes chrysolophus			SMR	1 275	945	1.35	
	5	3 780	RMR	1 161	929	1.25	This study
Jackass Penguin	5	2 880	BMR	541	761	0.71	Erasmus & Wessels (1985)
S. demersus							
Fjordland Penguin	4	2 600	BMR	598	703	0.85	Stonehouse (1968), in Drent & Stonehouse (1971)
E. pachyrhynchus							
Rockhopper Penguin	4	2 506	RMR	863	687	1.26	This study
E. chrysocome	2	2 330	BMR	504	651	0.77	Gavrilov (1977)
			SMR	764	651	1.17	
Whiteflippered Penguin	3	1 150	RMR	571	388	1.47	Pinshow *et al.* (1977)
Eudyptula albosignata							
Little Penguin	6	900	BMR	383	324	1.18	Stahel & Nicol (1982)
E. minor	8	1 191	BMR	344	398	0.86	Baudinette *et al.* (1986)

[a] From Kendeigh *et al.* (1977); BMR = 0.5224 $W^{0.7347}$ where BMR is in kcal day^{-1}, converted here to kJ day^{-1}, and W is the body mass in grams.

[b] Using the relationship between body mass and metabolic rate where y = 1.238x + 27.72, where x is the body mass in kg and y is the metabolic rate in Watts, converted to kJ day^{-1}, calculated from text-figure points at the midpoint of the fast.

[c] Using the relationship between body mass and metabolic rate from Croxall (1982) where y = 0.0043x - 21.0; x is the body mass in grams and y is the metabolic rate in Watts, converted to kJ day^{-1}, calculated from text-figure points after day five.

[d] Mass from Croxall (1982).

ambient conditions at their respective locations, familiarization of the birds to handling and disturbance is not certain, although the latter appears the more likely explaination.

Mean body temperature of 81 species of birds averaged 40.8 $\pm$ 0.2°C (McNab 1966). Penguins generally have body temperatures lower than this. Body temperatures of Macaroni and Rockhopper Penguins in the present study (38.5°C and 39.0°C, respectively, were similar to those of at least six other species, which had body temperatures ranging from 37.1°C to 39.9°C (Farner, 1958; Goldsmith and Sladen, 1961; Drent and Stonehouse, 1971; Le Maho *et al.*, 1976; Gavrilov, 1977; Stahel and Nicol, 1982). Warham (1971) has suggested that low body temperatures imply low metabolic rates. This argument is supported if metabolic rates of zoo and long-term captive penguins are regarded as being more representative of BMR than those of wild birds in temporary captivity. However, the mean overall level of metabolism of wild penguins in temporary captivity (excluding SMR measurements of Gavrilov (1977)) is about 20 % greater than predicted. Elevated levels of metabolism have also been observed in aquatic and semi-aquatic mammals (Irving, 1973; Morrison *et al.*, 1974) and have been explained as an adaptation to maintain body temperature in water, which has a higher cooling capacity than that of air. The variation in measured metabolic rates precludes resolution of this hypothesis until further, standardized, information on penguin metabolism becomes available.

The regression of log metabolic rate against log body mass for the data presented in Table 1.2 is illustrated in Fig. 1.2. The regression is described by the equation $M = 1.82\ W^{0.76} \pm 1.64$ ($r = 0.93$, $n = 21$), where M is the metabolic rate in kJ day^{-1} $\pm$ the standard error of the estimate and W is the body mass in grams. The slope of the regression line (0.76) is similar to that obtained by Croxall (1982) for only ten sets of measurements on seven species of penguin and very close to the slope of 0.73 derived by Kendeigh *et al.* (1977) for non-passerines. This supports the suggestion of Croxall (1982) that penguins have similar body-mass/metabolism relationships to other birds. However, if the measured metabolic rates of long-term captive penguins are considered more typical of BMR, then BMR of penguins is best described by the relationship $BMR = 3.01\ W^{0.68} \pm 1.48$ ($r = 0.93$, $n = 9$), and metabolic rates of wild penguins in temporary captivity should, at best, be considered as RMRs. RMR is then best described by the relationship $RMR = 4.94\ W^{0.66} \pm 1.45$ ($r = 0.97$, $n = 12$), where conventions are as given above.

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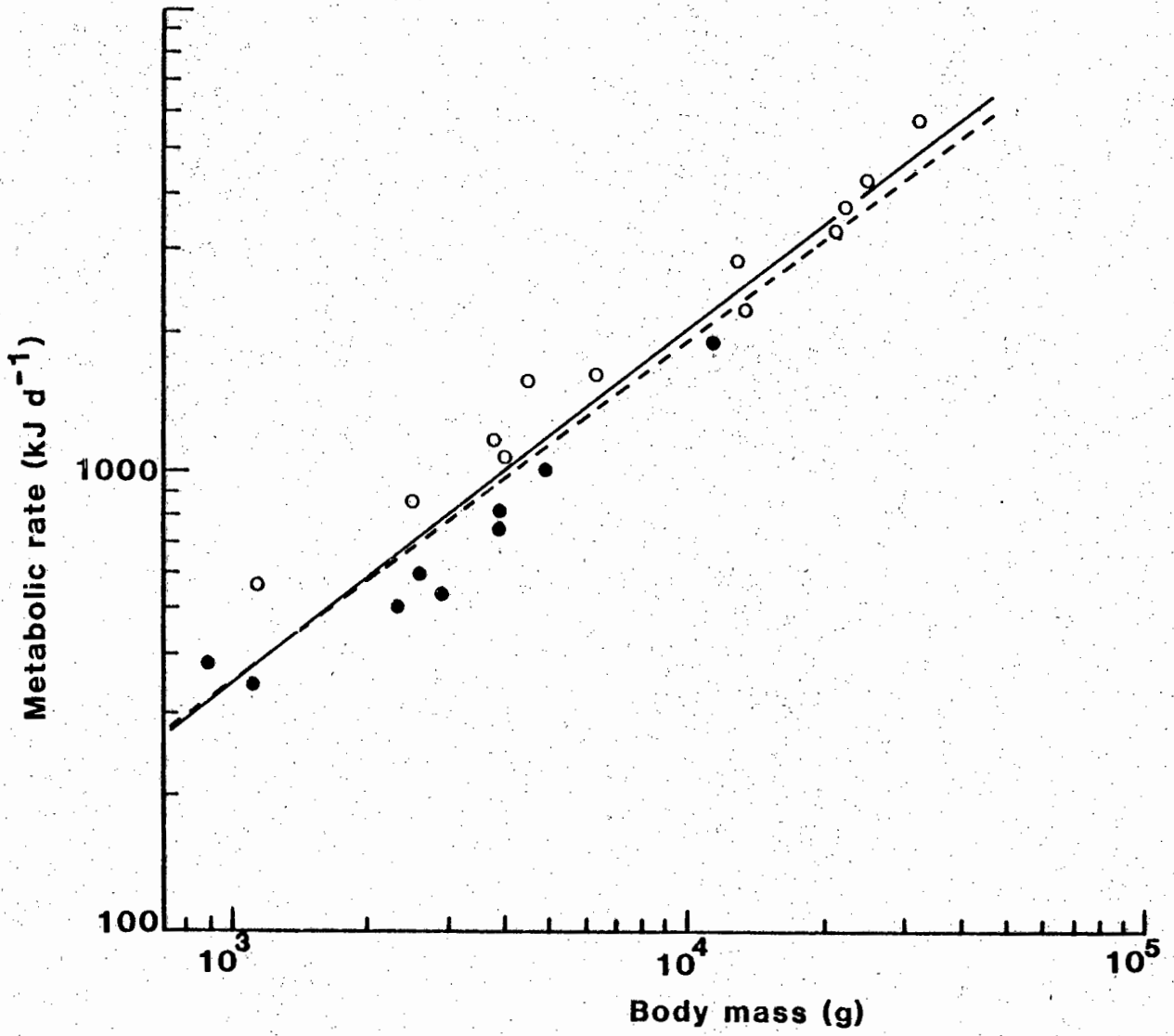
Fig. 1.2. Relationship between log metabolic rate, based on oxygen consumption measurements, and log body mass in penguins, from data presented in Table 1.2. SMR measurements of Gavrilov (1977) are excluded. Dashed line represents values predicted from the equation of Kendeigh *et al.* (1977).


Metabolic rate (kJ d^{-1})
1000
100
10^3
10^4
10^5
Body mass (g)

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CHAPTER 2

ENERGY EXPENDITURE DURING INCUBATION IN MACARONI AND ROCKHOPPER PENGUINS

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ABSTRACT

1. Energy expenditures, from rates of oxygen consumption, of Macaroni and Rockhopper Penguins were measured during incubation at sub-Antarctic Marion Island.

2. Incubating metabolic rates averaged 1 032 kJ day^{-1} for Macaroni Penguins of mean mass 4.84 kg and 701 kJ day^{-1} for Rockhopper Penguins of mean mass 2.77 kg.

3. Mean body temperature of incubating Macaroni Penguins was 38.1 $\pm$ 0.4°C and that of Rockhopper Penguins was 38.2 $\pm$ 0.4°C.

4. Energy expenditure during incubation was similar to or slightly lower than resting metabolic rate in both species but was significantly lower when compared on a mass-specific basis, and was also close to predicted values of basal metabolic rate for birds of equivalent masses.

4. Incubation may not be energetically expensive for small penguins, and their incubating metabolic rate may represent a better indication of basal metabolic rate than does resting metabolic rate.

INTRODUCTION

Incubation in Macaroni (*Eudyptes chrysolophus*) Penguins and Rockhopper (*E. chrysocome*) Penguins is shared between the sexes. Each sex generally undertakes one shift which lasts 10 - 19 d in females, which take the first shift, and 8 - 16 d in males (Warham, 1963; 1971). Incubating birds fast during their individual shifts and their rates of energy expenditure during these periods can be estimated from their loss of body mass, provided that the metabolites that they oxidize during the fasts are known (Croxall, 1982). To date, this method has been used for several species of penguins, including Royal Penguins (*E. chrysolophus schlegeli;* Carrick, 1972; review by Croxall, 1982). An alternative, and probably more accurate method of estimating energy expenditure, is to measure the rate of oxygen consumption of incubating birds. A particular advantage of using oxygen consumption is that it does not require any knowledge of the composition of metabolites oxidized during the fast because the ratio of energy production to oxygen consumption is similar for fat, protein and carbohydrate (Schmidt-Nielsen, 1979). Although oxygen consumption has been used to measure energy expenditure during fasting in penguins (Le Maho *et al.*, 1976; Le Maho and Despin, 1976; Dewasmes *et al.*, 1980) it has not previously been used to measure energy expenditure during incubation. In this study, I measured energy expended by

Macaroni and Rockhopper Penguins during incubation by measuring their rates of oxygen consumption.

MATERIALS AND METHODS

The study was carried out at sub-Antarctic Marion Island (46°52'S, 37°51'E) during November and December 1981. Incubating adult birds and their eggs were removed from the nest and placed in a metabolic chamber in the laboratory. A shallow metal tray filled with stones and gravel prevented the eggs from rolling about in the chamber. Five Macaroni and five Rockhopper Penguins incubated readily in the chamber. A further two birds of each species covered their eggs but did not adopt the normal incubating posture. These were regarded as not incubating and results were not used in later calculation of incubating metabolic rate (IMR). Egg temperatures were not measured.

Oxygen consumption was measured in a translucent, airtight metabolic chamber using an open, flow-through system. A pump drew air from outside the laboratory and passed it through a regulating flowmeter before entering the chamber. Air exiting the chamber was passed through a silica gel tube to absorb water-vapour, a Rotameter flowmeter, and a Carbosorb/silica gel tube before entering a Taylor-Servomex OA 570 paramagnetic oxygen analyzer. Flow rate was between 2 500 and 3 500 ml min^{-1} and resulted in a drop in oxygen content of expired air of 1 - 2 % below that of ambient air. The analyzer was zeroed with nitrogen before the experiment and calibrated with ambient air which was

assumed to have an oxygen content of 20.9 %. A thermocouple, inserted into the chamber through a rubber bung, measured chamber temperature which ranged from 8.7 - 17.5°C (mean = 13.5°C), within the thermoneutral zones of Macaroni and Rockhopper Penguins (see Chapter 1).

An initial period of at least 1 h was allowed for the birds to settle on their eggs and the oxygen content of the chamber air to equilibrate before commencing the experiment. Thereafter, readings of chamber temperature, flow rate and the percentage oxygen in the expired air were recorded at 30-min intervals over a period of 24 h at normal photoperiod. Oxygen consumption was calculated from the equation of Hill (1972) and converted to energy equivalents using 1 l O_2 = 20.083 kJ. Incubating metabolic rates (IMRs) were calculated from the lowest stable periods exhibited by each bird during the 24-h runs and mean metabolic rates over the entire 24-h period are referred to as average daily incubating metabolic rates (ADIMR).

Body temperatures of incubating birds were measured in the field using a thermocouple connected to a Bailey model BAT-12 digital telethermometer with a precision of 0.1°C. The birds were held loosely on their eggs and the thermocouple inserted 7-10 cm into the oesophagus. Body temperature was recorded as soon as temperatures stabilized, which usually occurred within 1-min of insertion.

RESULTS

Examples of VO_2 for a Macaroni and a Rockhopper Penguin over 24 h at normal photoperiod, showing the stable periods from which IMR was calculated, are illustrated in Fig. 2.1. Stable periods ranged from 4 - 12 h in duration and, unlike non-incubating birds, were generally observed at night. Two Macaroni Penguins, however, had stable periods which began in the afternoon and extended into the night and a single Rockhopper Penguin exhibited two stable periods, one in the morning and the second in the afternoon.

Measured metabolic rates during incubation, calculated from the lowest, stable periods, averaged 1 032 kJ day^{-1} for Macaroni Penguins of mean mass 4.84 kg and 701 kJ day^{-1} for Rockhopper Penguins of mean mass 2.77 kg (Table 2.1), close to the predicted BMR for birds of equivalent masses. IMRs were slightly, but not significantly lower than metabolic rates of resting birds (see Chapter 1; Macaroni Penguins $t = 0.472$, $P > 0.05$; Rockhopper Penguins $t = 0.522$, $P > 0.05$). However, when compared on a mass-specific basis, measured IMR was significantly lower in both species than measured RMR (Macaroni Penguins $t = 4.19$, $P < 0.005$; Rockhopper Penguins $t = 2.41$, $P < 0.05$). ADIMR averaged 20 % greater than IMR calculated from the stable periods (Table 2.1).

Mean body temperature of incubating Macaroni Penguins was 38.1 $\pm$ 0.4°C (range 37.5°C - 38.8°C, $n = 30$ individuals), slightly, but not significantly, lower

Fig. 2.1. Oxygen consumption for an incubating Rockhopper and Macaroni Penguin over 24 h at normal photoperiod. Dotted areas indicate hours of darkness and arrows indicate the stable periods from which IMR was calculated.

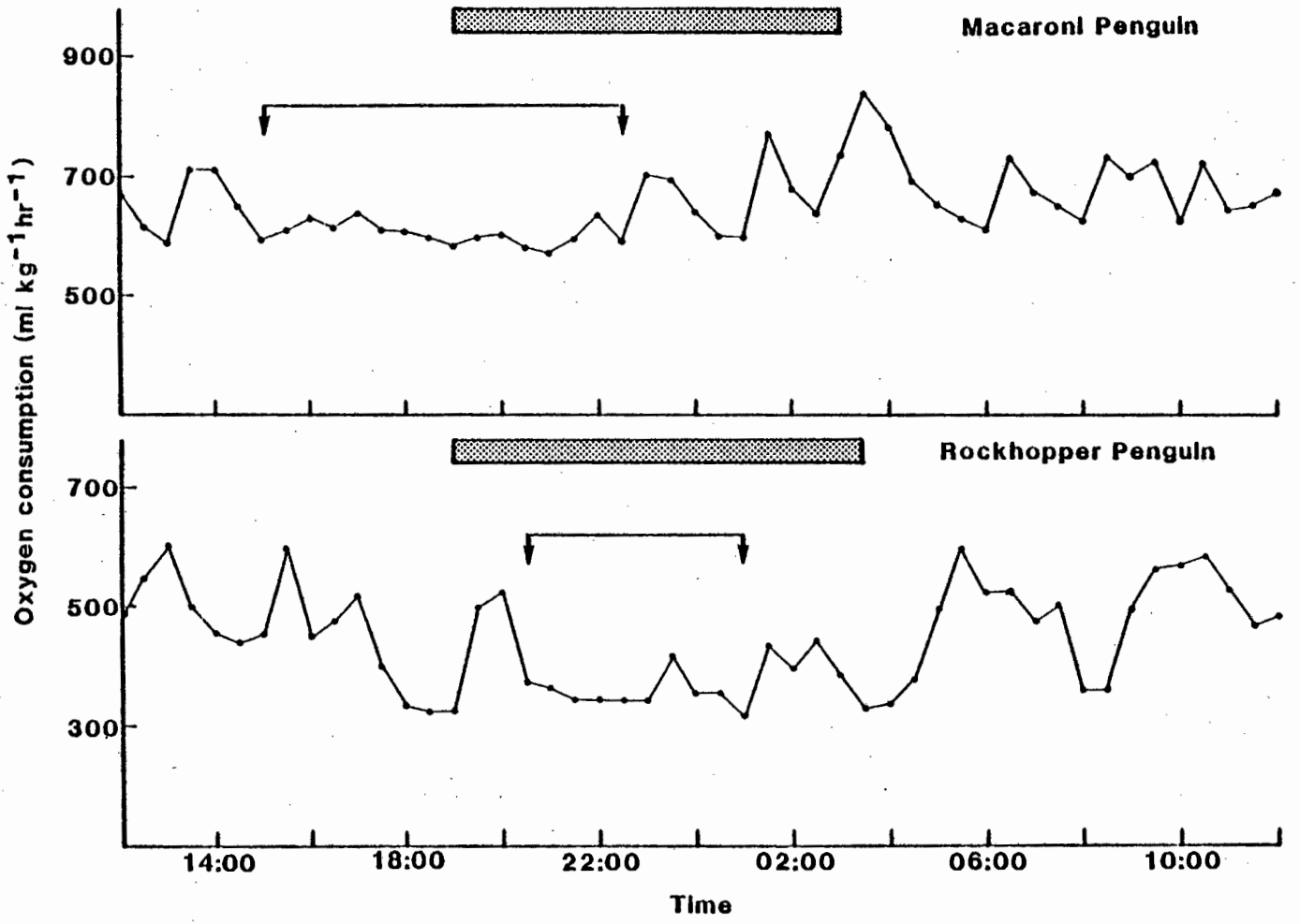
Macaroni Penguin
900
700
500
Rockhopper Penguin
700
500
300
Oxygen consumption (ml kg^{-1}hr^{-1})
14:00
18:00
22:00
02:00
06:00
10:00
Time

Table 2.1. Incubating metabolic rates of Macaroni and Rockhopper Penguins at Marion Island.

	Mean mass (kg)	N	IMR (kJ day^{-1})	IMR (kJ kg^{-1} day^{-1})	ADIMR (kJ day^{-1})	BMR[a] (kJ day^{-1})	IMR/BMR	IMR/RMR[b]
Macaroni Penguin	4.84	5	1 032 ± 251	213 ± 52	1 243 ± 262	1 114	0.93	0.69
Rockhopper Penguin	2.77	5	701 ± 37	253 ± 13	838 ± 211	739	0.95	0.74

[a] Predicted from Kendeigh *et al.* (1977).

[b] RMR from Chapter 1.

than those of resting birds (see Chapter 1; $t = 1.78$, $P > 0.05$). Body temperatures of incubating Rockhopper Penguins, however, averaged 38.2 $\pm$ 0.4°C (range 36.6°C - 38.8°C, $n = 30$ individuals), significantly lower than those of resting birds ($t = 3.90$, $P < 0.001$).

DISCUSSION

Energy expenditures of Macaroni and Rockhopper Penguins during incubation were significantly lower than RMRs of non-incubating birds when compared on a mass-specific basis, but was close to predicted BMR in both species. This result is surprising and suggests that there may be some extrinsic factor resulting in elevated rates of metabolism in non-incubating birds. Incubating birds in the laboratory were noticeably more restful than non-incubating birds, and the stable periods from which IMRs were calculated generally were longer than those used to calculate RMRs, although the difference only approaches significance ($t = 2.14$, $0.1 > P > 0.05$). Comparison of data for King (*Aptenodytes patagonicus*), Gentoo (*Pygoscelis papua*) and Adélie (*P. adeliae*) Penguins led Croxall (1982) to suggest that stress in fasting, non-incubating birds might result in a greater energy expenditure than that required by incubating birds for egg temperature maintenance. It is possible that handling and disturbance during the chick-rearing period might represent a similarly greater stress than that imposed on incubating birds. Although measurements from failed breeders do not support this (see Chapter 1), they were

measured over periods of only 5 - 8 h and birds had evidently not reached basal levels. It is notable that pre-moult Macaroni and Rockhopper Penguins have RMRs similar to those measured in Chapter 1 (see Chapter 3). Consequently, for Macaroni and Rockhopper Penguins, IMR taken from the lowest stable periods might represent a closer estimate of BMR than that measured on non-incubating birds. A further factor which possibly needs to be taken into account when comparing mass-specific IMR and RMR is the greater mass of incubating birds relative to birds feeding chicks (Table 2.1). A large proportion of this mass comprises stored fat which is metabolically relatively inert. This in itself would tend to result in a proportionately lower mass-specific metabolic rate for incubating birds when compared to those feeding chicks. However, a comparison of absolute metabolic rate (kJ day^{-1}) suggests that IMR is close to, or lower than RMR, despite the large difference in mass of incubating and non-incubating birds. Rates of metabolism close to, or lower, than those of resting, non-incubating birds have also been observed during incubation in some species of albatrosses and petrels, which also undergo lengthy individual incubation shifts during which they fast (Grant and Whittow, 1983; C.R. Brown, unpubl. data).

Body temperatures of incubating Macaroni and Rockhopper Penguins were lower than those of resting birds, although the difference was only significant for Rockhopper Penguins. In contrast, average body temperatures of

incubating Yellow-eyed Penguins (*Megadyptes antipodes*) (37.7°C) were similar to those of non-incubating birds (37.8°C; Farner, 1958). It is possible that differences in body temperatures observed in the present study result from different sites of measurement (oesophageal versus stomach). Differences in oesophageal and cloacal temperatures in penguins have been previously demonstrated (e.g. Goldsmith and Sladen, 1961; Stahel and Nicol, 1982). It is notable, however, that several species of petrels also have lower body temperatures during incubation than do resting, non-incubating birds (e.g. Farner, 1956; Farner and Serventy, 1959; Mougin, 1970; C.R. Brown, unpubl. data). Lower body temperatures during incubation are consistent with the relatively low levels of metabolism measured for penguins during this period.

No other estimates of energy expenditure during incubation in Rockhopper Penguins are available for comparison with the results of this study, but estimates for Macaroni Penguins, based on rates of mass loss in non-captive, incubating birds, exist (Carrick, 1972; Croxall, 1982). In order to estimate energy expenditure from rates of mass loss, knowledge of the composition of metabolites oxidized during energy production is required. For penguins, figures derived by Groscolas and Clément (1976) from incubating Emperor Penguins (*Aptenodytes forsteri*) are generally used. They found mass loss to comprise 55.5 % fat, 9.2 % protein and 35.5 % water. Since estimates based on rates of mass loss represent average daily metabolic rates, they are compared here with the metabolic rate of

incubating birds measured over 24 h in the chamber (ADIMR) rather than with IMR calculated from the lowest stable period. Mean ADIMR of Macaroni Penguins, measured in the present study, was 1.12 times predicted BMR. This is considerably lower than estimates of 1.50 and 1.91 times predicted BMR obtained from mass-loss data of Carrick (1972) for two birds, but compares well with those of Croxall (1982), who obtained figures between 1.17 and 1.25 times predicted BMR for three individuals. The similarity in the estimates of Croxall (1982) with those of this study, suggests that the composition of metabolites oxidized, derived by Groscolas and Clèments (1976), are realistic for penguins.

The mean daily energy cost of incubation in penguins, estimated by Croxall (1982), is 1.39 times predicted BMR (range 1.02 - 1.57). ADIMR of both Macaroni and Rockhopper Penguins are within this range and daily incubation costs of penguins 10 - 30 % greater than BMR appear reasonable.

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CHAPTER 3

ENERGETIC COST OF MOULT IN MACARONI AND ROCKHOPPER PENGUINS

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SUMMARY

1. Energy expenditure of moulting Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*) was measured using oxygen consumption as an index of metabolic rate.

2. Total energy expenditure decreased throughout moult from 1 952 to 1 102 kJ day^{-1} for Macaroni Penguins, and from 1 390 to 772 kJ day^{-1} for Rockhopper Penguins, during which time the body mass of the fasting birds also decreased by 46 and 43% respectively.

3. During feather loss mass specific energy expenditure peaked at 386 kJ $kg^{-1}day^{-1}$ in Macaroni Penguins and 379 kJ kg^{-1} day^{-1} in Rockhopper Penguins.

4. Energy expenditure estimated from mass loss was 32 and 27 % higher for Macaroni and Rockhopper Penguins respectively than that estimated from oxygen consumption. Possible reasons for this are discussed.

Introduction

Most penguins undergo an annual moult during which they renew their entire plumage. Groscolas (1978) distinguished three moult phases in the Emperor Penguin (*Aptenodytes forsteri*); an initial phase of feather synthesis below the skin, a phase of feather loss as the newly emerging feathers push out the old feathers, and a phase of reduced feather synthesis but continuing emergence of the new feathers to their final external length. Penguin moult is intense, lasting between two and five weeks, and during this time the birds do not feed but remain ashore subsisting on fat and protein reserves accumulated during a pre-moult foraging period (Stonehouse 1967). High rates of mass loss during the fast are indicative of a high energy utilization during moult (Groscolas 1978), and may be used to estimate energy expenditure provided the composition of metabolites oxidized is known (Croxall 1982). Williams *et al.* (1977) estimated, from body composition analysis, the proportions of fat and protein oxidized during moult in Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*). Estimates of energy expenditure during moult based on these data and rates of mass loss have been made for 13 species of penguins (see review by Croxall 1982).

An alternative technique for estimating energy expenditure is to measure the oxygen consumption of moulting birds. Measurements of oxygen consumption are

potentially more accurate than mass loss, and require no knowledge of the composition of metabolites oxidized since the ratio of energy production to oxygen consumption is similar for fat and protein (Schmidt-Nielsen 1979). Despite these apparent advantages, this technique has not previously been used for moulting penguins.

The aims of the present study were to measure the energetic cost of moult in Macaroni and Rockhopper Penguins, using oxygen consumption as a measure of metabolic rate, and to compare the results with those obtained from rates of mass loss and with the metabolic rates of resting non-moulting birds.

Materials and methods

The study was carried out at sub-Antarctic Marion Island ($46^{o}52'$ S, $37^{o}51'$ E) during March and April 1982. Four adult Macaroni and four adult Rockhopper Penguins were caught soon after they came ashore to moult and were kept in wooden crates (750 mm X 500 mm X 400 mm) with grid floors about 50 mm above the bottoms of the boxes. The birds were housed in the laboratory for the duration of the experiment.

Oxygen consumption. Oxygen consumption ($\dot{V}O_2$) was measured in a plastic, translucent, airtight metabolic chamber (400 mm diameter X 750 mm high) using an open, flow-through system. Air, drawn from outside the laboratory, was pumped through a regulating flowmeter before entering the chamber. Air leaving the chamber passed through a Silica gel drying

tube, a Rotameter flowmeter and a Silica gel/Carbosorb tube before entering a Taylor-Servomex OA 570 paramagnetic oxygen analyzer. Flow rate through the chamber was set to between 2 500 and 4 000 ml min^{-1} and produced a drop in oxygen content of 1 - 2 % below that of ambient air. The oxygen analyzer was zeroed with nitrogen and calibrated with ambient air before the experiment. Ambient air was assumed to have an oxygen content of 20.9 % and was checked at regular intervals throughout the experiment. A thermocouple, inserted into the chamber through a rubber bung, measured chamber temperature.

Moult in penguins probably begins before the birds return ashore from their pre-moult foraging trip (Groscolas 1978). Measurements of $\dot{V}O_2$ in this study commenced after the birds had been ashore for several days, but 3 - 4 days before first feather loss in any of the Macaroni, and in one of the Rockhopper Penguins; the other Rockhoppers began shedding feathers within two days of capture. Thereafter, $\dot{V}O_2$ was measured at 3 - 7 day intervals until the end of moult when the birds were released. Previous measurements of $\dot{V}O_2$ for Macaroni and Rockhopper Penguins over 24 hours (Chapter 1) revealed no systematic daily pattern of rest and activity, so all measurements in this study were carried out during daylight or with the laboratory lights on. An initial period of at least one hour was allowed for the birds to settle and the chamber air to equilibrate before the first readings were recorded. Thereafter, readings of chamber

temperature, flow rate and percentage oxygen in the expired air were recorded at 30 minute intervals over a period of 4 - 6 hours. Chamber temperatures during measurements of $\dot{V}O_2$ ranged from 11.8 - 18.0°C for Macaroni Penguins and from 10.9 - 20.2°C for Rockhopper Penguins, almost certainly within the thermoneutral zones of these birds (see Chapter 1).

$\dot{V}O_2$ (STPD) was calculated using the equation of Hill (1972) for dry, CO_2-free air and converted to an energy equivalent using 1 l. O_2 = 20.084 kJ. Error estimates quoted are $\pm$ one Standard Error.

Mass loss. The mass of the penguins was recorded at the same time each day by placing the birds in a canvas bag of known mass and weighing on a Pesola spring balance accurate to $\pm$ 20 g. Feathers shed each day were collected on preweighed plastic sheets which lined the bottom and sides of the crates in which the birds were kept. Loose feathers were removed and weighed to the nearest 1 g while those stuck to the faeces were washed and air dried before weighing. The mean body mass loss day^{-1} (mass lost as feathers subtracted from the total mass lost per day) was calculated. This was converted to an energy cost for moult using a composition of mass loss of 36.4 % fat and 4.9 % non-feather protein for Macaroni Penguins and 40.2 % fat and 7.2 % non-feather protein for Rockhopper Penguins (Williams *et al.* 1977). Energetic values for fat and protein used

were 39.7 and 16.7 kJ g^{-1} respectively (Petrusewicz and Macfadyen 1970).

Results

Energy expenditure from oxygen consumption.

Energy expenditure and mass specific energy expenditure of Macaroni and Rockhopper Penguins through moult are illustrated in Figures 3.1 and 3.2. Mean energy expenditure of Macaroni Penguins decreased from 1 951 to 1 102 kJ day^{-1} while that of Rockhopper Penguins decreased from 1 390 to 772 kJ day^{-1} (Figs. 3.1a and 3.2a). Mean energy expenditures over the period during which metabolism was measured (estimated from graphical integration of Figs. 3.1a and 3.2a) were 1 519 and 1 056 kJ day^{-1} for Macaroni and Rockhopper Penguins respectively.

Mean mass specific energy expenditure (kJ $kg^{-1}day^{-1}$) varied through moult. In the Macaroni Penguin, three phases could be distinguished (Fig. 3.1b): a significant increase from 305 kJ $kg^{-1}day^{-1}$ to a plateau at 356 kJ kg^{-1} day^{-1} (t = 3.66, $P < 0.001$) during initial feather loss; a further significant increase to a peak of 386 kJ kg^{-1} day^{-1} during late feather loss (t = 2.03, $P < 0.05$) and a significant decrease during final feather loss and the post-moult stage (t = 8.21, $P < 0.001$). Mass specific metabolic rate of Rockhopper Penguins showed a general increase during feather loss from 338 kJ $kg^{-1}day^{-1}$ to a significant peak at 378 kJ kg^{-1} day^{-1} during late feather loss (t = 3.66, $P < 0.001$), followed by a significant

Fig. 3.1a Energy expenditure of macaroni penguins throughout moult. Each point represents the mean ± SE and numbers below indicate the number of birds on which VO_2 was measured.

b Mass-specific energy expenditure (± SE) of macaroni penguins throughout moult. The horizontal axis is the time in days with day 0 representing the day on which the first feathers were lost.

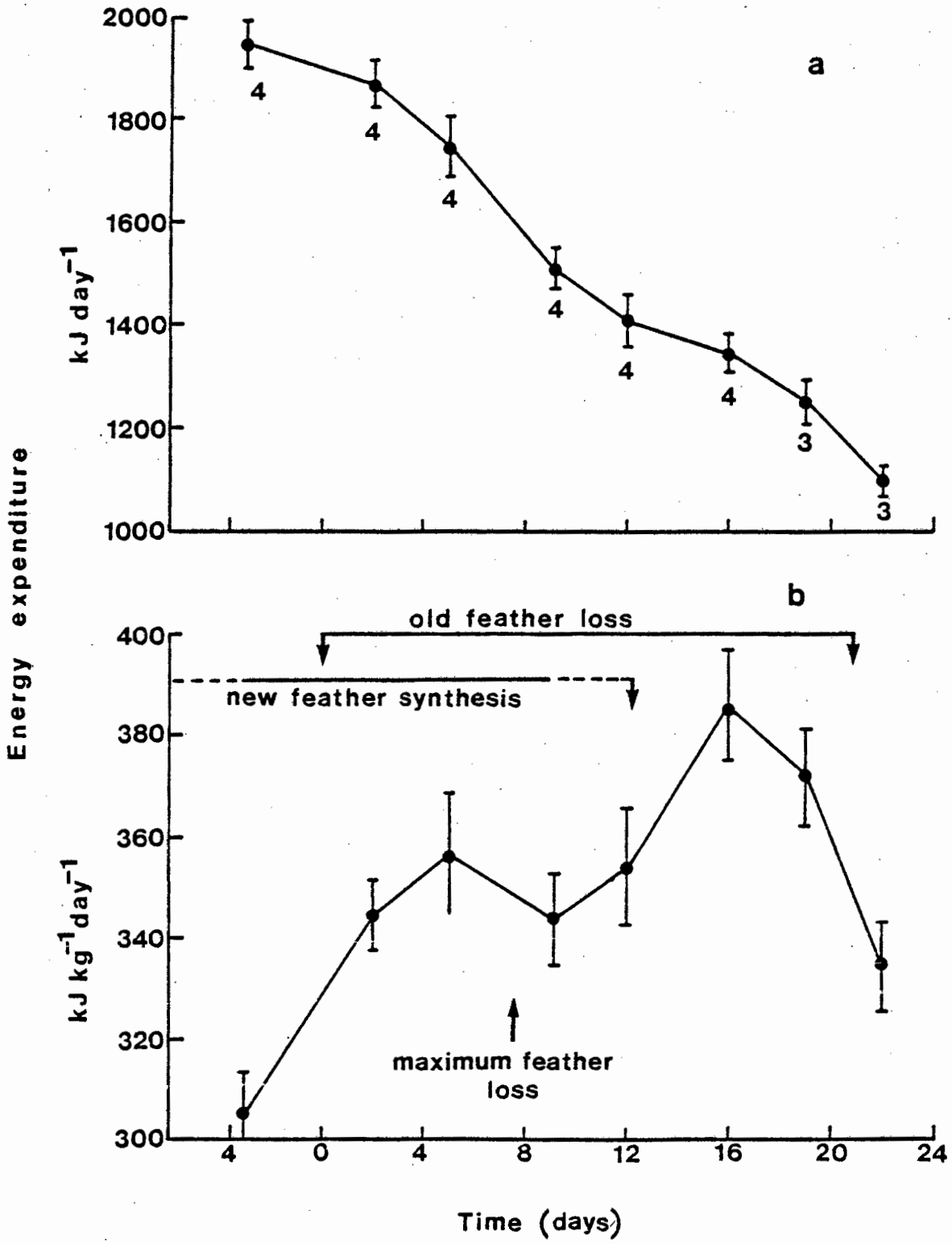
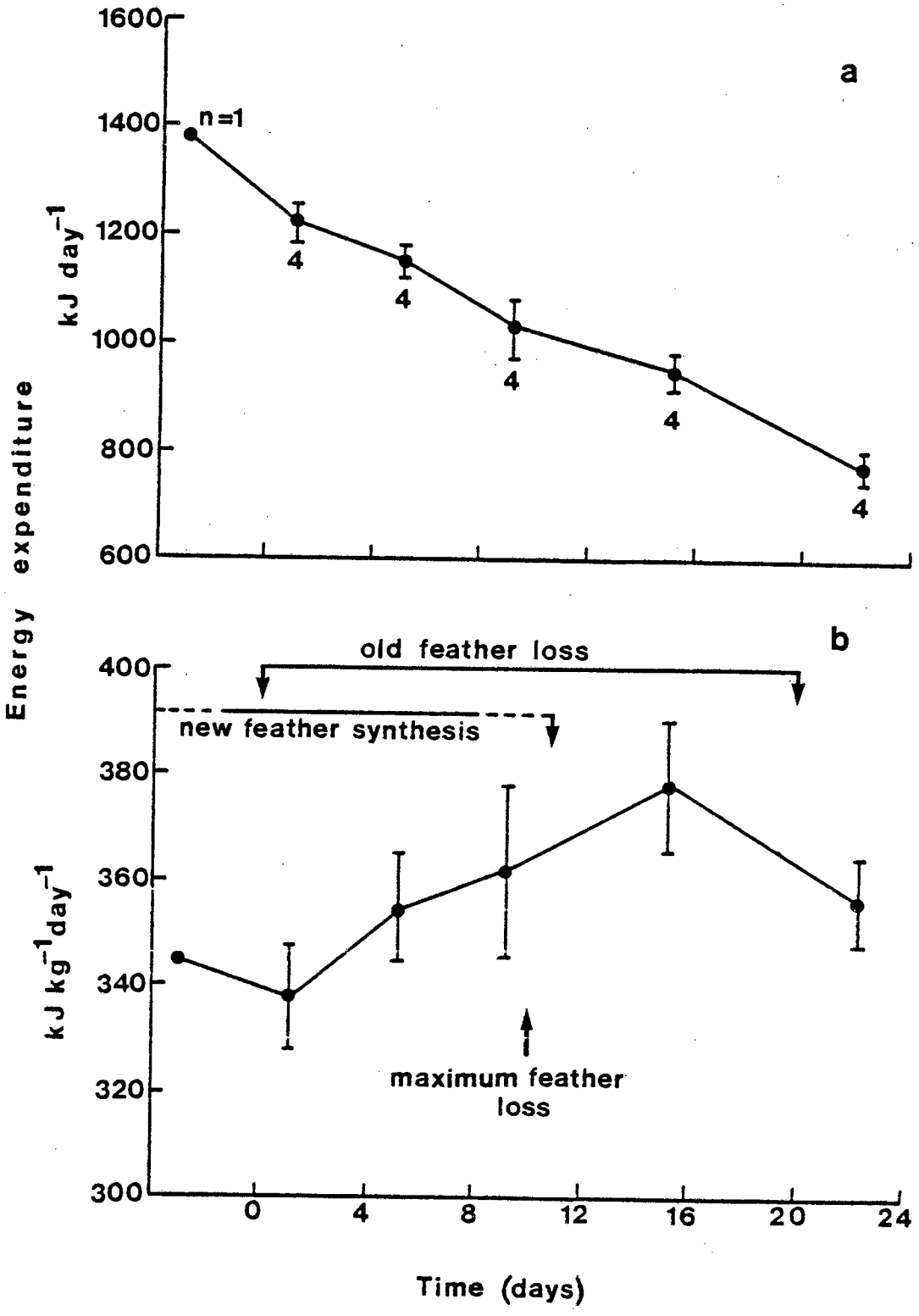

Energy expenditure
kJ day⁻¹
2000
1800
1600
1400
1200
1000
a
4
4
4
4
4
4
3
3
b
old feather loss
new feather synthesis
kJ kg⁻¹day⁻¹
400
380
360
340
320
300
maximum feather loss
4
0
4
8
12
16
20
24
Time (days)

Fig. 3.2a Energy expenditure of rockhopper penguins throughout moult. Each point is the mean ± SE and numbers below indicate the number of birds on which $\dot{V}O_2$ was measured.

b Mass-specific energy expenditure (± SE) of rockhopper penguins throughout moult. The horizontal line is the time in days with day 0 representing the day on which the first feathers were lost.


a
1600
1400
1200
1000
800
600
n=1
4
4
4
4
4
kJ day^{-1}
Energy expenditure
b
old feather loss
new feather synthesis
400
380
360
340
320
300
kJ kg^{-1}day^{-1}
maximum feather loss
0
4
8
12
16
20
24
Time (days)

decrease during final feather loss and the post-moult phase (t = 3.60, P < 0.001). At the time of their release, mass specific metabolism of Rockhopper Penguins was not significantly higher than at the beginning of moult (t = 1.37, P > 0.1) but that of Macaroni Penguins had not yet returned to pre-moult levels (t = 3.05, P < 0.005).

Energy expenditure from mass loss

Mass loss and estimated energy expenditure of Macaroni and Rockhopper Penguins during moult are summarized in Table 3.1. Old feathers and new feather sheaths contributed 225 g of the total mass loss in Macaroni Penguins and 135 g in Rockhopper Penguins, representing 7.2 and 7.6 % of the daily mass loss respectively. Maximum feather loss in Macaroni Penguins occurred between the fifth and ninth day after feather loss had begun, and between the ninth and eleventh day in Rockhopper Penguins.

When mass lost as feathers was subtracted from the total mass loss, Macaroni Penguins lost 2 920 g at a mean rate of 132 g day^{-1} and Rockhopper Penguins lost 1 652 g at a mean rate of 78 g day^{-1}. This is equivalent to energy expenditures of 2 012 and 1 337 kJ day^{-1} for Macaroni and Rockhopper Penguins respectively. Mean body mass loss discounting feathers was 46 % of the initial mass for Macaroni Penguins and 43 % of the initial mass for Rockhopper Penguins.

Table 3.1. Mean mass loss (± one S.E.) and estimated energy expenditure of Macaroni and Rockhopper Penguins during moult.

	Mean initial mass (g)	Mean final mass (g)	Mean feather mass (g)	Mean body mass loss (g day^{-1})	Energy expenditure[a] (kJ day^{-1})	MR/RMR[b]	MR/IMR[c]
Macaroni Penguins	6 385	3 240	225	132 ± 7	2 012	1.36	1.96
Rockhopper Penguins	3 840	2 053	135	78 ± 5	1 337	1.32	1.79

[a] Using 36.4 % fat and 4.9 % non-feather protein for Macaroni Penguins and 40.2 % fat and 7.2 % non-feather protein for Rockhopper Penguins (Williams *et al.* 1977).

[b] Using a RMR of 307 kJ $kg^{-1}day^{-1}$ for Macaroni Penguins and 344 kJ $kg^{-1}day^{-1}$ for Rockhopper Penguins, measured on resting, non-moulting adult birds during the chick feeding period (Chapter 1).

[c] Using IMR's of 213 and 254 kJ $kg^{-1}day^{-1}$ for Macaroni and Rockhopper Penguins respectively (Chapter 2).

Discussion

Energy expenditure from oxygen consumption

The steady decrease in daily energy expenditure (kJ day^{-1}) observed for Macaroni and Rockhopper Penguins throughout the period of moult studied probably reflects the progressive loss of body mass of the birds. Mass specific energy expenditure (kJ $kg^{-1}day^{-1}$), on the other hand, varied during moult. Moult is recognized as being a complex process, divisible in penguins into a number of different physical and biochemical phases (Croxall 1984). Although generalized descriptions of moult, and its place in the breeding cycle are available for most species of penguin (eg. Richdale 1957, Penney 1967, Stonehouse 1960, Warham 1963, 1971, Strange 1982), detailed descriptions of moult processes and the events associated with them are less common. However, Le Maho *et al.* (1976) observed different rates of mass loss at different stages of moult in the Emperor Penguin (*Aptenodytes forsteri*), and Groscolas (1978, 1982) recognized three moult stages in this species based on observations of rates of mass loss, feather growth, body temperature and plasma lipid levels. The changes in mass specific energy expenditure observed in Macaroni and Rockhopper Penguins may therefore be indicative of the processes of moult and of the energetic cost associated with them when compared to the energy expenditure of non-moulting birds.

Resting Metabolic Rate (RMR) and Incubating Metabolic Rate (IMR) in both Macaroni and Rockhopper Penguins have been measured (Chapters 1 and 2). RMR was significantly higher than IMR, possibly because RMR was measured on adult birds which were feeding chicks. These birds were more restless in the metabolic chambers than incubating birds which almost certainly led to elevated metabolic rates. IMR, however, approximated Basal Metabolic Rate (BMR) as predicted from allometric equations and may represent a better estimation of BMR than does RMR. For this reason, energy expenditure during moult is compared to IMR rather than RMR.

The general pattern of mass specific energy expenditure was similar in both species (Figs 3.1b and 3.2b). Mass specific energy expenditure prior to first feather loss (305 and 345 kJ $kg^{-1}day^{-1}$ for Macaroni and Rockhopper Penguins respectively) was the same as that previously measured for resting, non-moulting birds (Chapter 1) but 1.43 and 1.36 higher than IMR (Chapter 2). The measurement for Rockhopper Penguins prior to first feather loss was, however, from a single bird. Groscolas (1978) considers the period between when an Emperor Penguin first remains ashore and its first feather loss to be a part of moult, characterized by a significant increase in body temperature, a depression of plasma lipid levels and initial feather synthesis. Groscolas further suggested that moult might begin while the birds are still at sea. Duroselle and Tollu (1977) and Brown (Chapter 4) found

evidence of feather synthesis under the skin of Rockhopper Penguins coming ashore to moult, although there was no external evidence of moult. The mass specific metabolism of 1.43 times IMR in Macaroni Penguins and 1.36 times IMR in Rockhopper Penguins may thus represent the cost of feather synthesis above estimated basal levels.

Mass specific energy expenditure of Macaroni Penguins began increasing concurrently with first feather loss while that of Rockhopper Penguins began shortly after. Feather loss itself is a mechanical process, the old feathers being pushed out by the emerging new ones (King and Farner 1961, Voitkevich 1966). The first feathers lost in both Macaroni and Rockhopper Penguins were from the crest and tail, and loss of contour feathers began between one and three days later. Insulation during this stage is reduced (Groscolas 1978), and the increase in mass specific energy expenditure at this time is probably due, in part, to increased thermoregulatory demands brought about by old feather loss.

The second increase in mass specific energy expenditure in Macaroni Penguins occurred during late feather loss and reached a peak about 1.81 times incubating levels (1.26 times RMR). This increase occurred just after the period of maximum feather loss when between half and three-quarters of the new plumage was visible. In Emperor Penguins, the end of active feather synthesis, indicated by an increase in plasma lipids, occurs about eight days before the end of visible moult (Groscolas 1978). The corresponding period in

Macaroni Penguins would occur some 12 - 13 days after first feather loss. This second increase therefore probably represents the peak thermoregulatory cost of body temperature maintenance during a period of increased heat loss through the highly vascularized emerging feather shafts (King and Farner 1961) and reduced plumage insulation. If this is the case, then thermoregulatory demands during moult are about 27 % greater than that of feather synthesis in Macaroni Penguins. Le Maho *et al.* (1976) and Groscolas (1978) observed an increase in the rate of mass loss in Emperor Penguins during feather loss and attributed this to increased energy demands for feather synthesis and thermoregulation during a period of reduced insulation.

In Rockhopper Penguins there was no obvious two phase increase in mass specific metabolic rate, which peaked at a level about 1.50 times IMR during late feather loss. Peak thermoregulatory demand is thus about 10 % greater than that of feather synthesis.

The decrease in mass specific energy expenditure began in both species concurrently with final feather loss. The corresponding stage in Emperor Penguins coincides with the extrusion of the part of the new feathers that were under the skin (Groscolas 1978). The decrease in mass-specific energy expenditure observed in this study may similarly result from reduced heat conductance due to gradual devascularization of the new feathers and increased insulation as their length increases.

The peak energetic cost of moult in Macaroni Penguins was greater than that of Rockhopper Penguins. This is surprising since the Macaroni Penguin, being the larger of the two species, has the more favourable surface area to volume ratio which may be of particular importance during the period of high heat conductance that occurs during maximum feather replacement. The reason for the relatively higher cost of moult is not readily explicable.

Energy expenditure from mass loss

Rates of mass loss measured in this study were relatively high for both species. Croxall (1982) reported mass loss of Macaroni Penguins during moult to be 125 g day^{-1} for free birds of both sexes, while Williams *et al.* (1977) reported a mass loss of 105 g day^{-1} for captive birds housed outdoors. Previously observed rates of mass loss in Rockhopper Penguins are 71 g day^{-1} (Warham 1963), 82 g day-1 (Williams *et al.* 1977), and *c.* 72 g day^{-1} (Duroselle and Tollu 1977). Energy expenditure, based on these observed rates of mass loss and the composition data of Williams *et al.* (1977), range from 1 603 - 2 012 kJ day^{-1} for Macaroni Penguins and from 1 219 - 1 407 kJ day^{-1} for Rockhopper Penguins, with the results of the present study representing the highest values for Macaroni Penguins. The ratio of energy expenditure to IMR from these data range from 1.63 - 1.96 and 1.66 - 2.06 for Macaroni and Rockhopper Penguins respectively. The range of moult costs for penguins in general, estimated from rates of mass loss, is

1.62 - 2.39 (mean = 1.96) times predicted BMR (Croxall 1982). The mean percentage mass loss over the period of the study (46 and 43 % of initial body mass in Macaroni and Rockhopper Penguins respectively) is similar to that recorded for other penguins (Richdale 1957, Penney 1967, Cooper 1978).

Comparison between oxygen consumption and mass loss estimates

The pattern of mass specific energy expenditure was not reflected by the mass specific mass, loss which is probably related to changes in the composition of the mass loss (Groscolas 1978). Consequently, mass loss may at best provide an average rate of energy expenditure over the measured period. BMR has been generally predicted from the mass of penguins at the midpoint of the moult fast (Croxall 1982). Consequently, energy expenditure from rates of mass loss are compared here with the mean energy expenditure calculated from oxygen consumption measurements (ie. 1 519 and 1 056 kJ day^{-1} for Macaroni and Rockhopper Penguins respectively). Estimates of energy expenditure from rates of mass loss during moult were 32 and 27 % greater in Macaroni and Rockhopper Penguins respectively than energy expenditure estimated from $\dot{V}O_2$ measurements.

A possible explanation for the observed differences in energy expenditure from the two techniques is that estimates by Williams *et al.* (1977) of the amount of fat oxidized may

be too high. Using the rates of mass loss of 132 and 78 g day^{-1} observed in the present study and the mean energy expenditure calculated from oxygen consumption, and assuming the proportion of protein oxidized to be the same as that estimated by Williams *et al.* (1977), it can be calculated that the proportion of fat oxidized by the penguins in this study accounts for 27.6 and 31.6 % of the daily mass loss in Macaroni and Rockhopper Penguins respectively. These are about 9 % lower than the estimates of Williams *et al.*(1977). Cooper (1978), estimated that fat comprised only 23 % of the daily mass loss of moulting Jackass Penguins (*Spheniscus demersus*).

Little information is available on moult costs in other non-passerines. Energy expenditure during moult in passerines, however, ranges from 1.05 - 1.35 greater than that of resting, non-moulting birds (Payne 1972, King 1980). The peak moult costs of 1.26 and 1.10 times greater than resting, non-moulting Macaroni and Rockhopper Penguins respectively, are within this range, although Resting Metabolic Rates of both species were significantly higher than IMR (a better estimate of BMR). Peak moult costs were 1.81 and 1.50 times IMR, somewhat higher than that measured for passerines. This is probably due to the relative intensity of the moult in penguins. Penguins which come ashore to moult with insufficient fat reserves may approach terminal starvation before completing the moult or may have insufficient reserves to return to the foraging area after moulting. Yellow-eyed Penguins (*Megadyptes*

antipodes) have a critical mass, and if body mass at the end of moult falls below this the birds have little chance of survival (Richdale 1957). Moulting penguins are sedentary (Penney 1967, pers.obs.) and the increased energy expenditure required for moult may be offset by the reduced activity. It is probably only by reducing activity to a minimum during moult that penguins can stretch their fat reserves to enable them to complete moult successfully.

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CHAPTER 4

FEATHER GROWTH, MASS LOSS AND DURATION OF MOULT IN MACARONI AND ROCKHOPPER PENGUINS

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SUMMARY

The development of new feathers, loss of body mass and the duration of moult were investigated in Macaroni Penguins *Eudyptes chrysolophus* and Rockhopper Penguins *E. chrysocome* at Marion Island, southern Indian Ocean. New feathers began developing under the skin before the birds returned ashore to moult, and only began protruding through the skin about five days later when they were already over half their final length. Feather synthesis was complete by 21 days after the birds returned ashore. Loss of body mass was similar to previous observations for the species, but previous reports on the duration of moult do not take into account that moult begins while the birds are still at sea.

INTRODUCTION

Penguins undergo an annual moult in which all the feathers are replaced over a period of two to five weeks. The general process has been described for most species (e.g. Richdale 1957; Stonehouse 1960; Warham 1963; 1971; Penney 1967), and the moult divided into several stages based on visual observation of the initiation and progression of old feather loss. Old feathers, however, are initially pushed out by the emerging new feathers, and their loss is subsequently a mechanical process. Loss can therefore be affected by friction, agitation, wind and handling, and the measurement of new feather length thus provides a better determination of the progress of moult than do plumage observations (Groscolas 1976). The present study investigates the growth of new feathers, rate of loss of body mass and duration of moult in Macaroni *Eudyptes chrysolophus* and Rockhopper Penguins *E. chrysocome*.

METHODS

The study was carried out at sub-Antarctic Marion Island ($46^{o}52'S$; $37^{o}51'E$). Eight Rockhopper Penguins were caught and weighed within two hours of returning ashore to moult and eight Macaroni Penguins were caught and weighed within 18 h of their return ashore. All birds were fitted with

temporary, numbered, plastic flipper-tags and were confined to large crates out of doors for the duration of the study.

Birds were weighed to the nearest 10 g every second day from day 1 (day of return ashore = day zero). The lengths of 14 - 18 new feathers protruding through the skin were measured every second day to the nearest 0,5 mm with a ruler, and between 14 and 18 of the new feathers were plucked at random from the back and front of each bird every second day and measured to the nearest 0,5 mm. Before the emergence of new feathers through the skin, their internal length was equal to their total length. Once the new feathers began protruding through the skin, internal length was calculated by subtracting the mean external length of the protruding feathers from the mean total length of the plucked feathers. A sample of old feathers from both species was collected and total length measured for comparison with new feathers.

A single Rockhopper Penguin was collected within two hours of returning ashore, skinned, and the internal length of its developing new feathers measured. All measurements quoted are mean $\pm$ 1 standard deviation.

Rate of mass loss during moult was obtained for each bird by least squares linear regression, and the mean slope calculated. All birds were released after their visible moult was completed (i.e. all their old feathers had been lost) and when there was no further increase in the total

length of their new feathers and, because moulting penguins have a critical mass below which their chances of survival are reduced (Richdale 1957), the birds were released before they became too emaciated. Consequently, the external length of the new feathers in some birds had not yet reached their maximum length when the birds were released.

To establish the duration of moult, a further 22 Macaroni Penguins and 20 Rockhopper Penguins were caught at their colonies on the day they returned ashore, fitted with temporary, numbered flipper-tags and then released. The birds were not weighed or handled subsequent to fitting of the tags, but were monitored at intervals during the moult, and daily towards the end, until they left the colony.

RESULTS AND DISCUSSION

Feather growth

Lengths of the old feathers from the front and back were not significantly different in either species, nor were the lengths of new feathers from the front and back under the skin of the collected Rockhopper Penguin ($P>0,05$), so all feather measurements for each species were pooled (Figs 4.1 & 4.2).

Moult in penguins has generally been regarded as the period between when the birds first remain ashore and their return to sea after renewing all their feathers, whereas the period prior to the first loss of old feathers has been

Figure 4.1. Feather growth (mean $\pm$ 1 standard deviation) during moult in Macaroni Penguins. Closed circles, total length of the new feathers; open circles, external length of the new feathers; closed triangles, internal length of the new feathers.

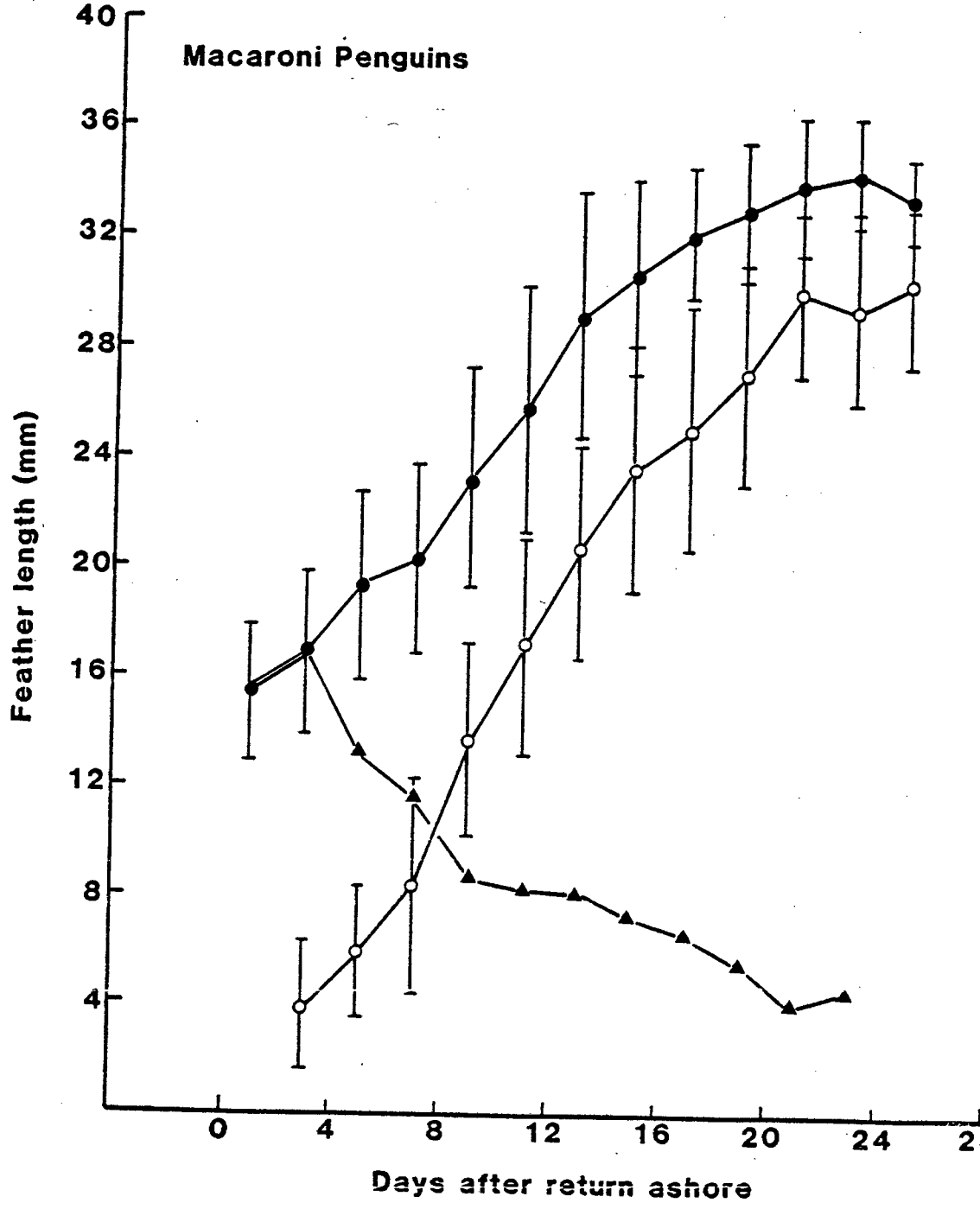
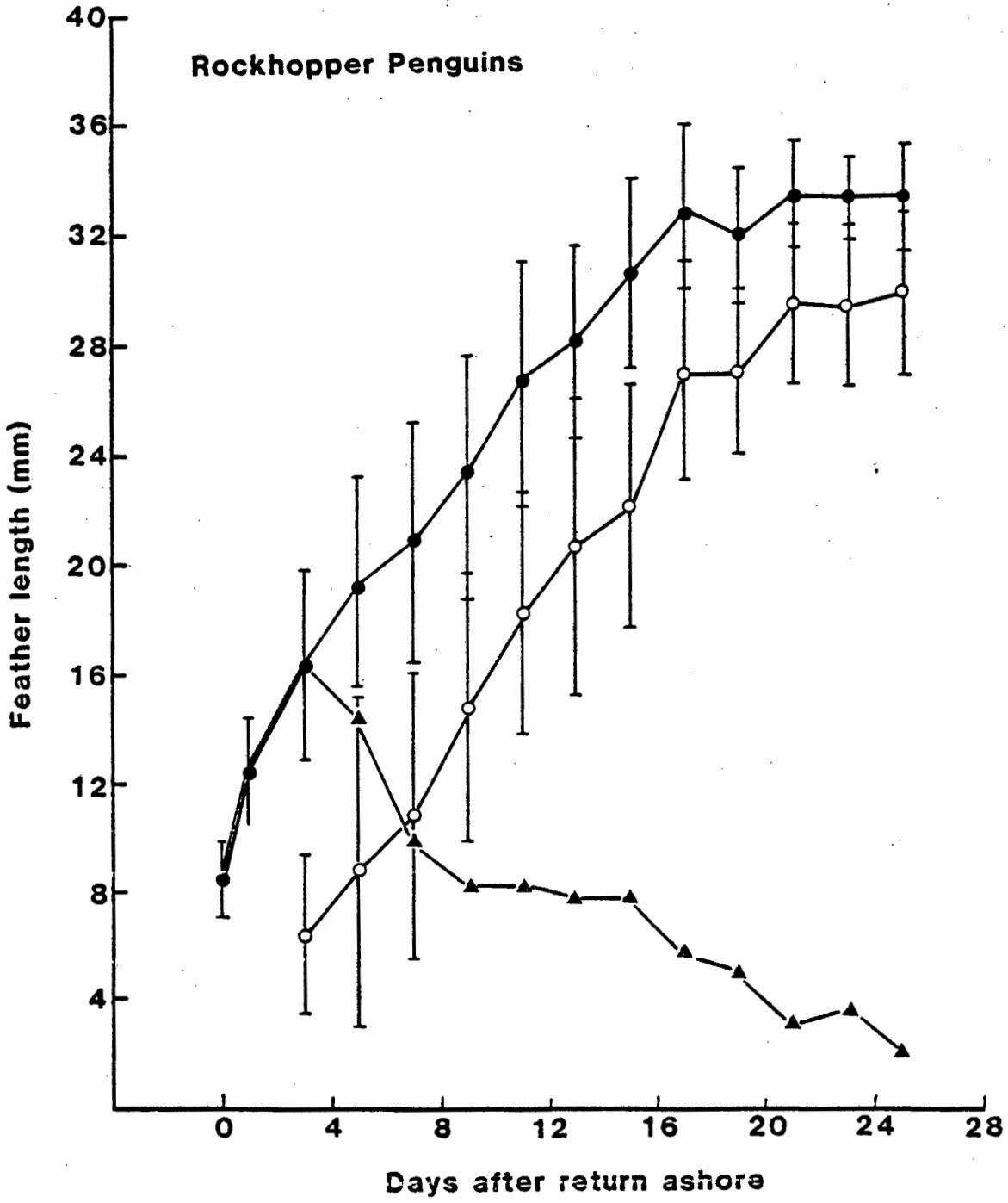

Macaroni Penguins
Feather length (mm)
40
36
32
28
24
20
16
12
8
4
0
4
8
12
16
20
24
28
Days after return ashore

Figure 4.2. Feather growth (mean ± 1 standard deviation) during moult in Rockhopper Penguins. Closed circles, total length of the new feathers; open circles, external length of the new feathers; closed triangles, internal length of the new feathers.


Rockhopper Penguins
Feather length (mm)
40
36
32
28
24
20
16
12
8
4
0
4
8
12
16
20
24
28
Days after return ashore

regarded as pre-moult (Richdale 1957; Warham 1963; Penney 1967). Groscolas (1976) recognized that moult in penguins actually begins while the birds are still at sea. Duroselle & Tollu (1977) found evidence of feather synthesis under the skin of Rockhopper Penguins coming ashore to moult, and the new feathers under the skin of the collected Rockhopper in this study already averaged 8,5 mm (n=65) long at this time (Fig 4.2). Also, new feathers under the skin of Macaroni and the other Rockhopper Penguins exceeded 12 mm within 24 h of their return ashore (Figs 4.1 & 4.2). New feather growth between arrival ashore and the emergence of the new feathers through the skin is quite rapid (approximately 2 mm per day in Rockhopper Penguins). From this it can be estimated that new feather growth probably begins between three and five days before the birds first return ashore.

Feather synthesis, growth beneath the skin, extrusion of the new feathers and total feather lengths were, as might be expected in closely related species, very similar (Figs 4.1 & 4.2). Initially new feathers grew internally, and first protruded through the skin about five days after the birds returned ashore (Table 4.1), when their mean total length in both species was 19,5 mm, over half their final total length (Figs 4.1 & 4.2).

Old feather loss began when the external length of the new feathers was approximately 17,5 mm and 15,0 mm in Macaroni and Rockhopper Penguins respectively and, on

average, began earlier and lasted longer in Rockhopper Penguins than in Macaroni Penguins (Table 4.1). Old feather loss , however, was almost certainly affected by confinement and handling and the timing of the event may be somewhat different in non-captive birds.

Synthesis of new feathers after their extrusion through the skin occurred at an average rate of 1,0 mm per day in both species. Active feather synthesis, estimated from the recession of new feather papillae under the skin, began decreasing in Macaroni Penguins between 13 - 18 days after an individual's return ashore (Table 4.1), when external feather length was about 25,5 mm. Papillae had receded completely in all individuals of both species by 21 days when the external length of the new feathers was about 30 mm. Mean total feather length at this stage was not significantly different in both species (34,5 $\pm$ 2,5 mm in Macaroni Penguins, 34,0 $\pm$ 2,0 mm in Rockhopper Penguins; t = 2,25; 174 *d.f.*; P>0,05), and that of Rockhopper Penguins was close to the mean length of 34,5 mm measured for old feathers (t = 1,69; 178 *d.f.*; P>0,05). New feathers in Macaroni Penguins, however, were significantly shorter than old feathers (mean = 38,0 $\pm$ 2,5 mm; t = 12,3; 212 *d.f.*; P<0,001).

Moult progression based on measurements of new feather growth has previously been described only for Emperor Penguins *Aptenodytes forsteri* (Groscolas 1976). Groscolas

TABLE 4.1

APPROXIMATE TIMING OF MAIN MOULT EVENTS IN EIGHT MACARONI AND EIGHT ROCKHOPPER PENGUINS AFTER THEIR RETURN ASHORE. FIGURES ARE MEANS WITH RANGES IN PARENTHESES

Event (days)	Macaroni Penguin	Rockhopper Penguin
New feathers protrude through skin	5 (3 - 7)	5 (3 - 7)
Old feather loss begins	11 (9 - 13)	8 (5 - 15)
Old feather loss ends	20 (17 - 23)	19 (15 - 24)
Duration of old feather loss	9 (8 - 12)	12 (9 - 15)
New feather papillae recession begins	15 (13 - 18)	*
Feather synthesis ends	19 (15 - 21)	19 (15 - 21)

* Not noted.

described three moult stages based on new feather measurements, body temperatures and rates of mass loss: an initial stage of internal feather growth and emergence of the new feathers through the skin, a second stage of continued new feather growth at a constant rate and the loss of old feathers with an associated drop in plumage insulation, and a final stage during which feather synthesis ends, external feather length reaches its maximum and plumage insulation increases. Although the total feather length is less and the moult period shorter in the smaller Macaroni and Rockhopper Penguins, the general pattern of feather growth and replacement is very similar to that of the Emperor Penguin and may be common to most other species of penguin.

Mass loss

Changes in rates of mass loss at different stages of moult have been observed in Emperor Penguins (Groscolas 1976; Le Maho *et al.* 1976) and in King Penguins *Aptenodytes patagonicus* (Barre 1975). Mass loss was relatively constant in Macaroni and Rockhopper Penguins during the moult and no such changes in rates of mass loss were evident. Mean initial mass of Macaroni Penguins after their return ashore was 6 170 $\pm$ 470 g (range 5 550 - 6 900 g; n = 8) and that of Rockhopper Penguins was 3 880 $\pm$ 200 g (range 3 630 - 4 230 g; n = 8). When released, final masses averaged 3 420 $\pm$ 260 g (range 3 050 - 3 840 g) and 2 130 $\pm$ 110 g (range 2 050 -

2 300 g) in Macaroni and Rockhopper Penguins respectively. Macaroni Penguins lost an average of 44 % of their initial mass during moult at a mean rate of 120 ± 11 g per day and Rockhopper Penguins lost 45 % at a mean rate of 95 ± 13 g per day. Of this total daily mass loss, feathers comprise 7,2 and 7,6 % respectively (Chapter 3). Mean body mass loss was therefore estimated to be 111 g per day in Macaroni Penguins and 88 g per day in Rockhopper Penguins. The observed body mass loss in Macaroni Penguins is within the range previously reported for the species, but that of Rockhopper Penguins was slightly higher (Warham 1963, 1971; Williams *et al.* 1977; Croxall 1982; Chapter 3). Overall mass loss during moult (44 and 45 % of initial mass in Macaroni and Rockhopper Penguins respectively) was, however, similar to that previously cited for the species and also for other species of penguins (e.g. Richdale 1957; Penney 1967; Cooper 1978; Strange 1982; Chapter 3).

Duration of moult

Of the 22 Macaroni Penguins and 20 Rockhopper Penguins tagged, seven of each species were not observed again at their respective colonies or lost their tags which were subsequently found loose on the ground. Birds of both species spent between 20 and 30 days (mean = 25 ± 3 days) ashore during the moult. Half the tagged Macaroni Penguins had left the colony by 26 days and half the Rockhoppers by 25 days. This is similar to previous observations. Richdale

(1957) reports a 19 - 26 day moult period for Macaroni Penguins and Warham (1971) and Croxall (1982) cite about 28 and 24 days respectively. Moult period in Rockhopper Penguins has been reported as 23 days (Richdale 1957), about 23 - 30 days (Warham 1963) and approximately 24 - 26 days (Strange 1982). These periods, however, do not take into account that moult begins while the birds are still at sea, an estimated three to five days before their return ashore. The total moult period is thus about 25 - 35 days in both Macaroni and Rockhopper Penguins.

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CHAPTER 5

EGG TEMPERATURE AND EMBRYONIC METABOLISM OF MACARONI AND ROCKHOPPER PENGUINS

Submitted to *S. Afr. J. Zool.*

ABSTRACT

Macaroni and rockhopper penguins lay two eggs but rear only one chick to independence. The eggs are markedly dimorphic in size and, although the smaller A-egg is laid several days before the B-egg, in nests where both eggs are incubated, the incubation periods are such that the larger B-egg always hatches first. Incubation temperatures and embryonic oxygen consumption were measured to determine whether the observed hatching sequence could be accounted for by differences in egg temperatures or rate of embryonic development. Lowest egg temperatures were recorded from A-egg incubated in the less favourable anterior position in the brood patch and highest temperatures from A-eggs incubated singly and B-eggs. Differences, however, were not significant. Levels of embryonic oxygen consumption of A-eggs of the same age showed a similar pattern to egg temperatures, but differences were slight. A-eggs incubated singly, and those incubated for several days after laying in a hot-room, still had incubation periods longer than B-eggs, suggesting that egg temperature alone does not account for differences in the hatching sequence. Consequently, it appears that there are inherent differences in embryonic metabolism of A- and B-eggs that result in the B-egg, which represents the greater parental investment, hatching first.

Introduction

Crested penguins of the genus *Eudyptes* lay two eggs which are markedly dimorphic in size (Gwynn 1953). This dimorphism is most pronounced in macaroni penguins *E. chrysolophus* and rockhopper penguins *E. chrysocome* in which the first laid A-eggs average 59% and 44% lighter, respectively, than the second laid B-eggs (Williams 1980a). Although both eggs are viable, only one chick is ever reared , brood reduction in macaroni penguins usually occurring through loss or ejection of the smaller A-egg from the nest before the B-egg is laid (Warham 1963, 1971; Williams 1980b). However, in rockhopper penguins, A-eggs are incubated with B-eggs in about 30% of nests (Williams 1980b). The laying interval between A- and B-eggs averages 4 - 5 d, but the incubation periods are such that the larger B-eggs hatch before or on the same day as the A-egg (Williams 1981a). Williams (1980a) suggested two possible reasons for this. Firstly, in nests where both eggs are incubated, incubation of the A-egg only began once the B-egg was laid. Also, because eggs are positioned one in front of the other in the elongated brood patch and the birds incubate in a semi-upright position, the anterior eggs are more exposed. A-eggs are more frequently placed in the anterior position. Consequently, A-eggs are incubated for the same period as B-eggs but generally experience lower and less steady temperatures during incubation (cf. Burger & Williams 1979) which might retard embryonic growth.

Secondly, the time required for embryonic development is different for A-and B-eggs.

In this study I investigated egg temperatures and embryonic oxygen consumption of A-and B-eggs of macaroni and rockhopper penguins. In order to test the suggestions of Williams (1980a), egg temperatures and embryonic oxygen consumption were measured on 1) A-eggs incubated normally with B-eggs, 2) A-eggs incubated alone and 3) A-eggs which were incubated at temperatures above 30°C from day of laying.

Methods

The study was carried out at sub-Antarctic Marion Island (46°52'S, 37°51'E), between October and December 1985. Selected nests of both macaroni and rockhopper penguins were numbered prior to egg laying and nests were checked daily for eggs, whose laying dates were recorded. Because the A-egg of macaroni penguins is usually lost prior to laying of the B-egg, A-eggs were substituted for B-eggs in a number of nests at the beginning of incubation. In order to obtain rockhopper penguin nests in which A-eggs were incubated alone, B-eggs were removed from several nests on the day they were laid. Because A-eggs of rockhopper penguins are not normally incubated until the B-egg is laid, A-eggs were removed from four nests and "pre-incubated" at 33 - 35°C in

a hot-room. These eggs were then replaced in their nests once the B-eggs were laid.

Measurement of egg temperatures

Egg temperatures of B-eggs of macaroni penguins and A- and B-eggs of rockhopper penguins were measured using previously collected and blown eggs of the respective species filled with water and containing previously calibrated Model T or Model L minimitters (Minimitter Co., Indianapolis). Minimitters were held in place in the centre of the eggs by cut off, perforated, plastic syringe barrels inserted into the eggs through a hole in the blunt end and glued into place in the long axis of the eggs. Water and the minimitter were introduced into each egg through the hole in the blunt end which was then sealed using the rubber plunger from the syringe.

Eggs containing transmitters were substituted for fertile eggs in the field when the latter were removed for measurements of oxygen consumption and were readily accepted and incubated by the birds. Because the macaroni penguin colony was about 2,5 km from the research station, temperatures of the dummy eggs were measured prior to replacement of the fertile eggs, between 3-4 h and 24 h after their initial removal. Temperatures were then recorded at 5-min intervals over a period of 15-30 min. Rockhopper penguins, however, nest under some of the buildings of the research station and on the adjacent point. Consequently, a

series of egg temperature measurements was usually made, when convenient, over periods of 12-24 h. The mean egg temperature over each period was subsequently used.

Embryonic oxygen consumption

Measurements of embryonic oxygen consumption were made at approximately 5-d intervals from 6 - 10 d into incubation. Dummy eggs containing transmitters were substituted for fertile eggs in the nests and fertile eggs taken to the laboratory, a trip of less than 5 min for eggs of rockhopper penguins, but 25 min for those of macaroni penguins, which were wrapped in cotton wool for the trip. In the laboratory, eggs were weighed to the nearest 0,01 g on a Mettler analytical balance and placed in a hot-room at 33 - 35°C, within the range of egg temperatures previously measured for penguins (Burger & Williams 1979 and references therein).

Embryonic oxygen consumption was measured in closed respiratory systems consisting of plexiglass syringes of 2 800 ml (macaroni penguin eggs) or 1 400 ml (rockhopper eggs) maximum volume. Chamber volume depended on how far back the plunger was drawn and, because this was varied depending on the size of the egg and the age of the embryo, chamber volume was calculated for each measurement. The net volume of air in the chamber was calculated by subtracting the volume of each egg (measured by water displacement) from the calculated chamber volume. Eggs were left for 1-3 h to come

into thermal equilibrium with the hot-room air before being placed in a chamber. Chambers were then flushed with air and the open ends sealed off with three-way stopcocks. Eggs were left in the chambers for periods estimated to reduce the oxygen concentration in the chamber by 0,5 - 2,0%. This required as long as 24 h for young embryos (7 - 10 days) to 5 - 10 min for pipped eggs and hatchlings. Final oxygen concentration in the chambers was measured by injecting the chamber air through a tube of soda asbestos and Silica gel into a Taylor Servomex OA 570 paramagnetic oxygen analyzer. Initial oxygen concentration in the hot-room was measured by pumping hot-room air through the analyzer with a hand-held aspirator. Embryonic oxygen consumption (VO_2) was calculated from equation 1 of Vleck, Hoyt & Vleck (1979) and corrected to STPD. Eggs were returned to their nests after measurement.

Oxygen consumption was measured throughout incubation or until the embryo died. Measurements from embryos which died were only used from that portion of incubation in which oxygen consumption was similar to that of eggs which hatched. All means are given $\pm$ 1 standard deviation.

Results

A-eggs of rockhopper penguins incubated alone had slightly shorter incubation periods (mean = 38,8 $\pm$ 1,7 days; range 36-41; n = 6) than did those incubated in two-egg clutches

(mean = 39,9 ± 1,3 days; range 38-42; n = 7), although the difference was not significant (t = 1,383; P > 0,02). Two A-eggs that were incubated above 30°C from laying hatched in 39 days; the remaining two pre-incubated eggs were found next to their nests once the B-eggs had hatched and were presumably ejected from their nests (Williams 1980b). Overall incubation periods and fresh egg masses of A- and B-eggs of macaroni and rockhopper penguins, recorded during the present study (Table 5.1), were similar to those previously measured for the species at Marion Island (Williams 1980, 1981a) and at other localities (Warham 1963, 1971; Strange 1982). Incubation periods of B-eggs of both species were close to expected values for eggs of equivalent mass, but those of A-eggs exceeded expected values by 20% in macaroni penguins and 30% in rockhopper penguins (Table 5.1).

Egg temperatures

Egg temperatures of rockhopper penguins measured over 12 - 24 h fluctuated by as little as 1°C to as much as 7°C, presumably as a result of egg turning, changes in adult attentiveness, nest ventilation and the position of the egg in the nest.

There were slight differences in temperatures of dummy eggs placed in different positions within rockhopper penguin nests, with single eggs (33,4 ± 1,0°C, n = 9) being

FIGURE 5.1. Embryonic oxygen consumption of A- and B-eggs of macaroni penguins in relation to age. Solid circles = unpipped eggs, stars = fractured eggs, open circles = pipped eggs (holed) and diamond = hatchlings $\pm$ 1 S.D. Data for A-eggs based on 76 measurements on seven eggs and that of B-eggs on 98 measurements on nine eggs. Equations relate to unpipped eggs only

Table 5.1 Incubation periods and fresh egg mass of A- and B-eggs of macaroni and rockhopper penguins at Marion Island

		Macaroni penguins		Rockhopper penguins	
		A-eggs	B-eggs	A-eggs	B-eggs
Incubation period (days)	Mean	38,8	34,6	39,1	33,6
	S.D	1,3	1,8	1,3	1,1
	Range	37-41	32-39	38-42	31-35
	N	4	12	14	20
	Predicted[a]	32,2	35,9	30,4	33,0
Egg mass (g)	Mean	99,2	163,3	77,5	111,9
	S.D.	7,7	16,0	8,5	12,9
	Range	87,7-109,3	138,7-179,0	63,4-91,4	98,1-131,8
	N	8	9	8	7

[a] From the equation of Ar & Rahn (1978); $I = 11,64\ W^{0.221}$ where W is the fresh egg mass in grams.

incubated at a higher temperature than eggs placed in the posterior position in a two-egg clutch (32,7 ± 1,1°C, n = 4) and lowest temperatures being recorded from eggs placed anteriorly in a two-egg clutch (31,9 ± 1,9°C, n = 3). Differences, however, were not significant (P > 0,05), probably because of the small sample sizes involved, and results were pooled. A single macaroni penguin B-egg recorded prior to 7 d after laying had a temperature of 27,9°C. However, from the second week of incubation until hatching there was no consistent trend in dummy egg temperatures of either macaroni penguins or A- and B-eggs of rockhopper penguins (Table 5.2).

Overall egg temperature of macaroni penguins averaged 34,0 ± 2,1°C and those of rockhopper penguins A-eggs (32,2 ± 1,4°C) averaged slightly, but not significantly, lower than those of B-eggs (33,5 ± 1,2°C, t = 1.90, P > 0,20) (Table 5.2).

Embryonic oxygen consumption

Oxygen consumption (VO_2) increased throughout incubation in A- and B-eggs of macaroni and rockhopper penguins (Figures 5.1 & 5.2). Mean VO_2 prior to fracture of the egg shell averaged 821 and 1 337 ml day^{-1} for A- and B-eggs of macaroni penguins, respectively (Table 5.3). In the first 10 - 25 days of incubation, A-eggs of rockhopper penguins which were pre-incubated for the first 3 - 4 days in the hot-room

Table 5.2 Egg temperatures of macaroni and rockhopper penguins during natural incubation at Marion Island. Figures are means ± standard deviation, range and sample size

Day of incubation	Egg temperature (°C)		
	Macaroni penguins	Rockhopper penguins	
		A-eggs	B-eggs
1 - 7	27,9 [1]	---	---
8 - 14	33,6 ± 0,8 (33,0-34,9) [5]	31,0 ± 0,6 (30,4-31,6)[3]	31,2 [1]
15 - 21	34,0 ± 1,8 (31,1-35,9) [6]	33,9 (33,7-34,0)[2]	33,8 ± 0,7 (33,0-34,4)[4]
22 - 28	35,4 ± 1,1 (33,2-36,1) [6]	32,8 (31,9-33,6)[2]	33,5 ± 0,7 (32,7-34,0)[3]
29 - 35	34,1 [1]	---	33,7 (32,8-34,5)[2]
Overall	34,0 ± 2,1 (27,9-36,1) [19]	32,3 ± 1,4 (30,4-34,0)[7]	33,5 ± 1,2 (31,2-34,5)[10]

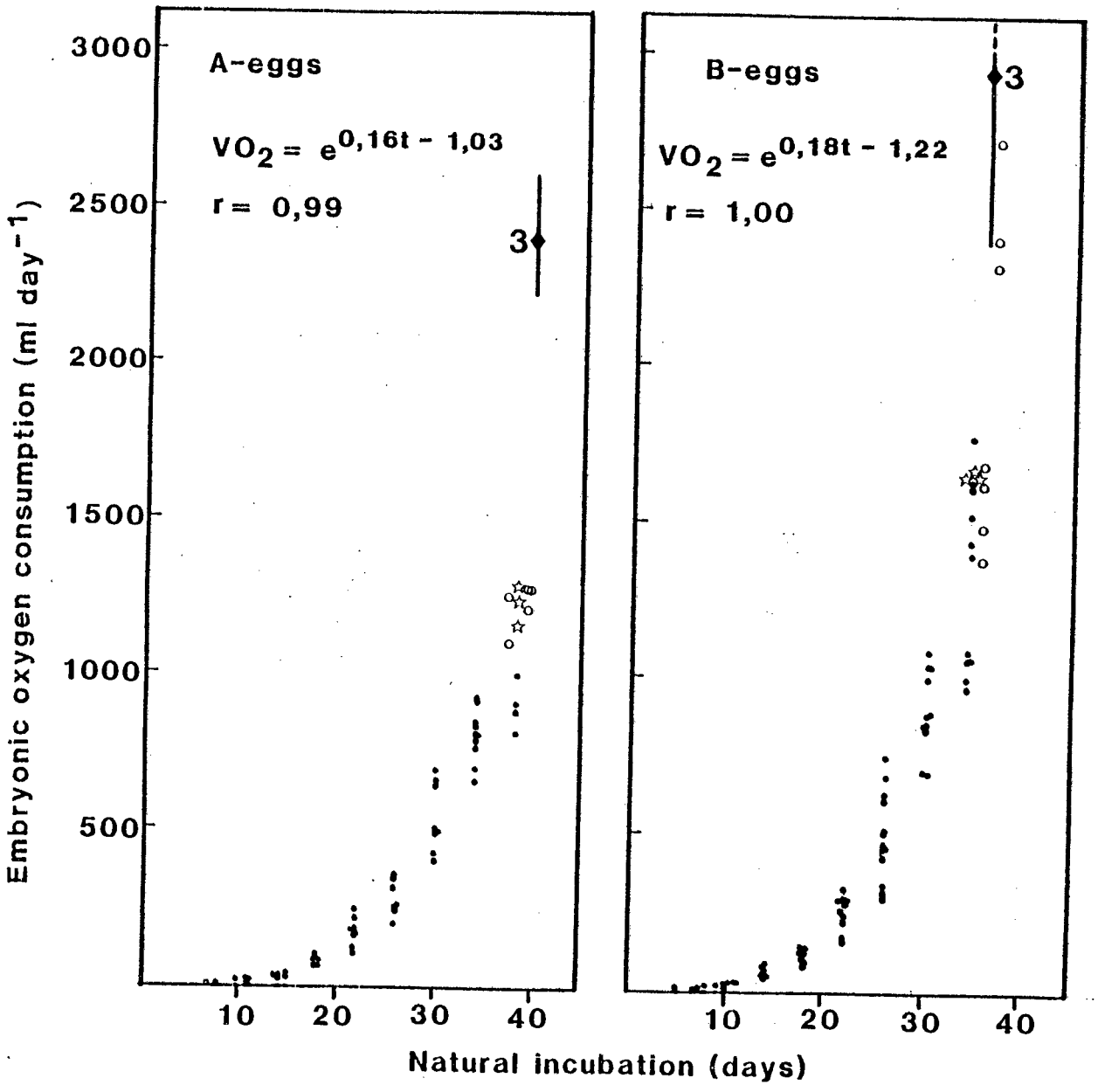
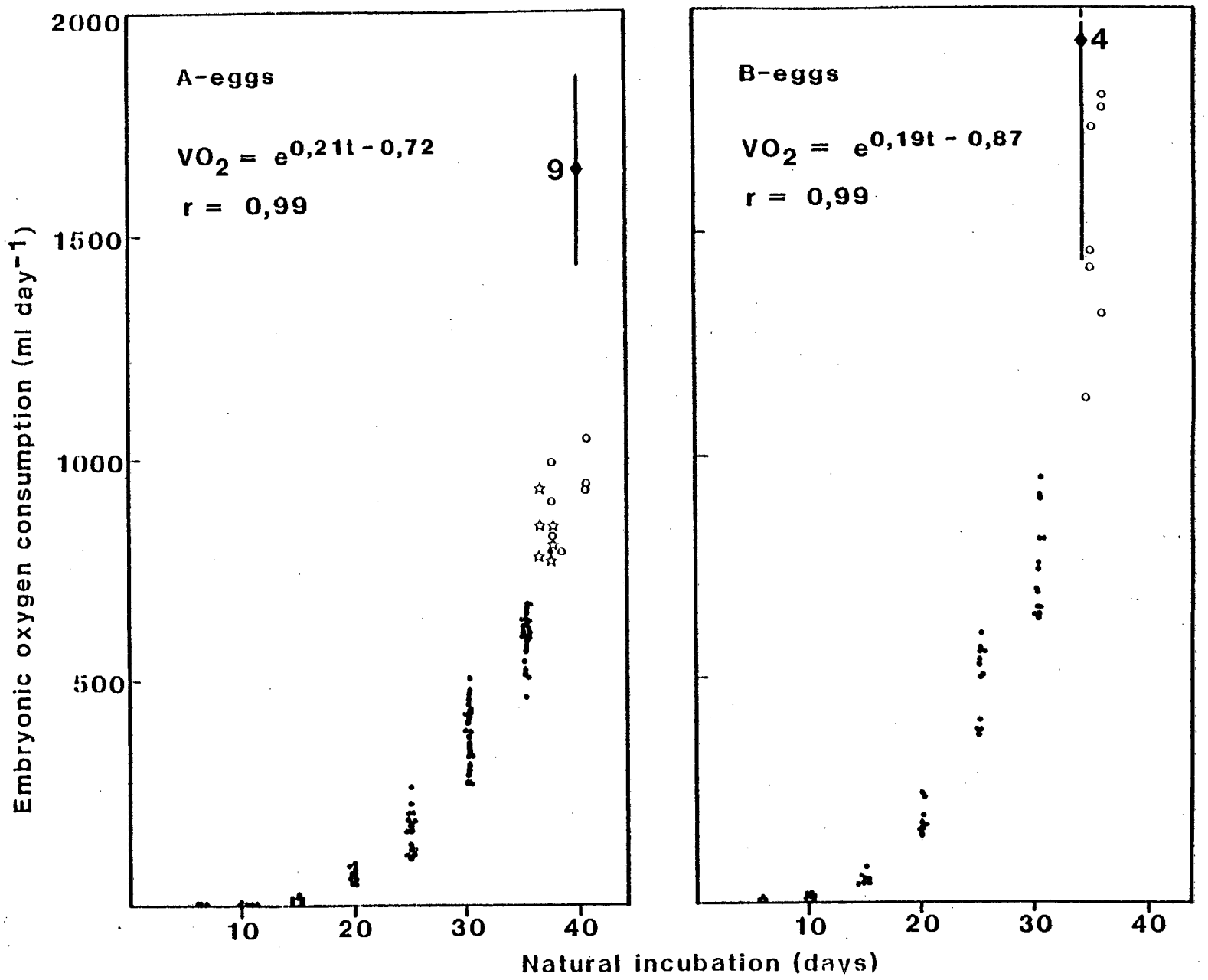

A-eggs
$VO_2 = e^{0,16t - 1,03}$
r = 0,99
B-eggs
$VO_2 = e^{0,18t - 1,22}$
r = 1,00
3
3
3000
2500
2000
1500
1000
500
10
20
30
40
10
20
30
40
Embryonic oxygen consumption (ml day^{-1})
Natural incubation (days)

FIGURE 5.2. Embryonic oxygen consumption of A- and B-eggs of rockhopper penguins in relation to age. Symbols as for Figure 1. Data for A-eggs based on 149 measurements on 17 eggs and that of B-eggs based on 68 measurements on nine eggs. Equations relate to unpipped eggs only.


A-eggs
$VO_2 = e^{0,21t - 0,72}$
r = 0,99
9
B-eggs
$VO_2 = e^{0,19t - 0,87}$
r = 0,99
4
8
2000
1500
1000
500
Embryonic oxygen consumption (ml day^{-1})
10
20
30
40
Natural incubation (days)

had rates of VO_2 similar to those incubated alone on the nest, both of which were slightly higher than A-eggs incubated in two-egg clutches. However, differences in mean VO_2 on comparable days of incubation were not significant, nor were differences in the slopes of the semilog transformed data relating VO_2 to incubation time (P's > 0,05). Consequently, results for all A-eggs were pooled, overall pre-pipping VO_2 averaging 593 ml day^{-1} (Table 5.3). Pre-pipping VO_2 of rockhopper penguin B-eggs averaged 732 ml day^{-1} (Table 5.3). Pre-pipping VO_2 of rockhopper penguin B-eggs, however, was measured about three days prior to initial fracture of the shell and is thus probably a slight underestimate of actual pre-pipping VO_2.

Mean embryonic VO_2 of both macaroni and rockhopper penguin B-eggs was always significantly greater than that of A-eggs measured on the same day of incubation (macaroni penguins P's < 0,02; rockhopper penguins P's < 0,001), although there was no difference in the slopes of the semilog transformed data relating embryonic VO_2 to incubation time (macaroni penguins t = 1,527; P > 0,10; rockhopper penguins t = 1,183; P > 0,20).

After initial pipping, VO_2 increased markedly in all eggs measured and reached a peak in hatchlings at levels 2 - 3 times pre-pipping levels (Figures 5.1 & 5.2). Although hatchlings from B-eggs of both species had higher metabolic rates than hatchlings from A-eggs, differences were not

Table 5.3 Mean pre-pipping oxygen consumption (VO_2) of macaroni and rockhopper penguin embryos at Marion Island

	Pre-pipping VO_2 ml O_2/day	Day of incubation	No. of eggs
Macaroni penguins			
A-eggs	820,6 ± 90,3	38	7
B-eggs	1 337,0 ± 295,0	33	4
Rockhopper penguins			
A-eggs	592,6 ± 55,0	35	12
B-eggs	732,3 ± 78,7	30	7

significant (macaroni penguins t = 2,04; P > 0,05; rockhopper penguins t = 1,67; P > 0,01). Total oxygen consumption during embryonic development, estimated from graphical integration of the areas under the curves in Figures 5.1 & 5.2, was 12,6 and 14,5 l O_2 for A- and B-eggs of macaroni penguins, respectively, and 7,0 and 10,6 l O_2 for those of rockhopper penguins (Table 5.4), of which 70 - 74% was consumed prior to pipping.

Discussion

Egg temperature

Incubation temperatures measured for both A- and B-eggs of macaroni and rockhopper penguins in the present study were within the range measured for several other species of penguins (Table 5.5). In particular, those of rockhopper penguins were similar to those measured for the same species by Burger & Williams (1979) during the second half of incubation. However, Burger & Williams (1979) reported low egg temperatures in both macaroni and rockhopper penguins during the first half of incubation, which they suggested might result from retarded vascularization of the brood patch in females which undertake most of the incubation during this period. In contrast, egg temperatures of both species in the present study were maintained above 30°C from eight and 10 days after laying, respectively (see Table 5.2).

Table 5.4 Total embryonic oxygen consumption of macaroni and rockhopper penguins

	Total VO_2		Pre-pipping VO_2		Pip-to-hatch VO_2	
	ml	ml/g egg	ml	% total	ml	% total
Macaroni penguins						
A-eggs	12 558	126,6	9 314	74,2	3 244	25,8
B-eggs	14 540	89,0	10 700	73,6	3 840	26,4
Rockhopper penguins						
A-eggs	6 985	90,1	4 955	70,9	2 030	29,1
B-eggs	10 552	94,2	7 788	73,8	2 764	26,2

Consistent with Burger & Williams (1979), B-eggs of rockhopper penguins were maintained at a higher temperature than were A-eggs, although in the present study the differences were not very marked. Burger & Williams (1979) attributed differences in temperature to the position of the eggs in the nest, B-eggs being found more frequently in the posterior position where they are more covered by the brood patch and less exposed to cool ambient temperatures than are A-eggs. Differences in temperatures of eggs placed singly or in different positions in a two-egg clutch in the present study, although slight, support this, temperatures of A-eggs incubated alone and those placed posteriorly in two-egg clutches being close to those of B-eggs. Yom-Tov, Wilson & Ar (1986) also found differences in temperatures between two eggs of a clutch in jackass penguins *Spheniscus demersus*, but differences were not correlated with the relative position of the eggs under the brood patch, nor were there consistent differences in egg temperatures between nests with one and two eggs.

Egg temperatures of macaroni penguins measured by Haftorn (1986) were made with thermistors placed near the egg surface and are consequently more representative of brood patch temperatures than of central egg temperatures measured in the present study (see Farner 1958; Yom-Tov *et al.* 1986).

Egg temperatures measured in the air cell of live eggs tend to be quite variable and to underestimate central egg

Table 5.5 Egg temperatures of penguins during incubation, measured with transmitters (M) and thermistors or thermocouples (T) on dummy (D), infertile (I) or in the centre (L) or air space (A) of live eggs

Species	Egg temperature (°C) Mean	Range	Method	Reference
Emperor penguin	32,6 ± 0,7		MD	Bucher *et al.* (1986)
	32,7 ± 0,4			
Adèlie penguin	33,7	(29,2-36,8)	MD	Eklund & Charlton (1959)
	35,2	(30,0-38,0)	TL	Derksen (1977)
	35,9 ± 1,1	(34,7-37,2)	TL	Rahn & Hammel (1982)
Chinstrap penguin	37,4 ± 0,5	(34,8-38,0)	TI	Haftorn (1986)
	34,5 ± 2,9	(29,0-38,0)		
Gentoo penguin	32,9 ± 4,0	(16,8-37,9)	TA	Burger & Williams (1979)
Yellow-eyed penguin	35,2[a]		--	Farner (1958)
Macaroni penguin A-egg[b]	11,7	(1,3-33,0)	TA	Burger & Williams (1979)
B-egg	23,4	(17,2-32,5)	TA	
	37,3 ± 0,6	(34,0-37,8)	TI	Haftorn (1986)
	34,0 ± 2,1	(27,9-36,1)	MD	This study
Rockhopper A-egg	32,9	(22,8-37,9)	TA	Burger & Williams (1979)
	32,3 ± 1,4	(30,4-34,0)	MD	This study
B-egg	25,9 ± 10,1	(8,4-37,9)	TA	Burger & Williams (1979)
	33,5 ± 1,2	(31,2-34,5)	MD	This study
Jackass penguin	34,9[c]	(14,0-36,0)	--	Yom-Tov *et al.* (1986)
	34,5 ± 1,5	(31,9-36,0)	TA	Burger & Williams (1979)

[a] Estimated as the midpoint between the egg-brood patch interface and the egg-nest substratum interface.

[b] Measured on day of laying.

[c] Calculated indirectly from water-vapour pressure difference between the egg and the nest microclimate.

temperatures, and temperatures measured on dummy eggs are probably more typical of early incubation when embryonic heat production is negligible. Although central egg temperatures throughout incubation have not been measured for developing penguin eggs, temperatures of live Adélie penguin *Pygoscelis adeliae* eggs late in incubation (Derksen 1977; Rahn & Hammel 1982), were 1 - 2°C higher than those measured on dummy eggs (Table 5.5), presumably as a result of embryonic heat production. In contrast, temperatures of dummy eggs of incubating macaroni and rockhopper penguins in this study remained relatively constant throughout most of incubation, suggesting that these species do not regulate egg temperature by changes in behaviour, blood flow or metabolic rate. This has also been suggested for some albatrosses and petrels (Grant, Pettit, Rahn, Whittow & Paganelli 1982).

Embryonic metabolism

Low egg temperatures in penguins are known to retard embryonic development (Weinrich & Baker 1978) and the slightly higher rates of embryonic oxygen consumption of pre-incubated A-eggs of rockhopper penguins, and those of A-eggs incubated singly, are consistent with the slightly higher incubation temperatures and slightly shorter incubation periods observed in these eggs compared to those incubated in two-egg clutches. However, even A-eggs which were incubated singly or at temperatures similar to those of

B-eggs from day of laying had incubation periods longer than B-eggs. Furthermore, the incubation period of macaroni penguin A-eggs was 2 - 4 days longer than those of B-eggs, even though the A-eggs were substituted for B-eggs on the day of laying and consequently occupied the posterior position in the brood patch throughout incubation (Williams 1981a; this study). Similarly, a comparison of macaroni penguin A-eggs and rockhopper penguin B-eggs, both of which are similar in size (see Table 5.1), are incubated posteriorly in the brood patch and produce similarly sized hatchlings Williams 1980a, pers. obs.), shows that A-eggs of macaroni penguins have rates of oxygen consumption significantly lower than those of rockhopper penguin B-eggs at equivalent stages of incubation between 10 and 30 days (P's $< 0{,}005$). From the above observations, it is evident that the different temperatures experienced by A- and B-eggs of, in particular rockhopper penguins, do not, by themselves, account for the differences in incubation periods which result in B-eggs hatching earlier than A-eggs.

Embryonic metabolism of A-eggs could be retarded if oxygen conductance across the eggshell was limiting. Because conductances of oxygen and water across eggshells is proportional to their respective diffusion coefficients, oxygen conductances of eggshells (GO_2) can be calculated from their water vapour conductances using the relationship $GO_2^{38} = 1{,}08\ GH_2O^{25}$ (Hoyt, Board, Rahn & Paganelli 1979). Water vapour conductances of A- and B-eggs of both macaroni

and rockhopper penguins have been measured (C.R. Brown unpubl. data) and oxygen conductances calculated from these have values of 19,5 and 27,0 ml d^{-1} $torr^{-1}$ for A- and B-eggs of macaroni penguins, respectively, and 15,9 and 19,2 ml d^{-1} $torr^{-1}$ for those of rockhopper penguins. Higher oxygen conductances of B-eggs are consistent with their larger size and larger functional pore area, but oxygen conductances of rockhopper penguin B-eggs, which had oxygen uptakes significantly greater than macaroni penguins A-eggs of similar size, were the same. Consequently, it must be concluded that oxygen conductance of the shell does not limit embryonic metabolism in A-eggs. This suggests that Williams' second suggestion, that the time required for embryonic development of A-and B-eggs is different, is more likely. Presumably, embryos have to reach a particular level of development and metabolism before hatching can occur. The generally higher levels of metabolism in B-eggs result in this level being attained earlier than in A-eggs. A-eggs have proportionately less albumen than do B-eggs (Williams, Siegfried & Cooper 1982). Since the proportion of albumen has a controlling effect on post-hatching development (c.f. Nisbet 1978), Williams (1980a) suggested that it might also affect embryonic development.

Williams (1980a) hypothesized that ancestral *Eudyptes* penguins were inshore foragers which laid two eggs of similar size and were capable of rearing two chicks, as do

present inshore-foraging species. He speculated that the ability to raise only a single chick resulted from a move to offshore-foraging, characteristic of present *Eudyptes* penguins. Under these circumstances, where feeding frequency is reduced, early brood reduction would allow all energy delivered by the adults to be channelled into the single chicks which would survive, rather than wasting it on a second chick which could not be raised. Chicks from large eggs grow larger, survive better and, in penguins, are fed preferentially (Williams 1981b). Consequently, an inherently slower rate of embryonic metabolism, and presumably slower embryonic development, brought about through differences in egg composition, ensures that hatching of eggs in *Eudyptes* penguins is such that the larger B-egg, which represents the greater parental investment, always hatches first. Clearly, however, the relationship between egg composition and embryonic development in these and other species of *Eudyptes* penguins needs to be investigated further.

Embryonic metabolism has previously been measured only for emperor penguins *Aptenodytes forsteri* and Adélie penguins (Bucher, Bartholomew, Trivelpiece & Volkman 1986). Relevant results are compared with those from macaroni and rockhopper penguins in Table 5.6. Adélie penguin eggs and hatchlings are of similar masses to those of B-eggs of rockhopper penguins and pre-pipping $\dot{V}O_2$, total embryonic $\dot{V}O_2$ and hatchling $\dot{V}O_2$ for the two species are also similar

Table 5.6 Metabolic rates of penguin embryos during development

Species		Pre-pipping oxygen consumption (ml/day)	Total embryonic oxygen consumption (ml)	Total embryonic oxygen consumption (ml/g egg)	Hatchling oxygen consumption (ml/day)	Hatchling oxygen consumption (ml/g day)
Emperor penguin[a]		1 621	43 997	94,5	----	----
Adélie penguin[a]		830	11 865	99,7	1 640	20,2
Macaroni penguin	A-eggs[b]	821	12 558	126,6	2 393	28,4
	B-eggs	1 337	14 540	89,0	2 946	27,6
Rockhopper penguin	A-eggs[b]	593	6 985	90,1	1 634	30,8
	B-eggs	732	10 552	94,2	1 934	23,9

[a] Bucher *et al.* (1986)

[b] This study

(Table 5.6). Overall, despite the large range of egg sizes (78 g for rockhopper penguin A-eggs to 466 g for emperor penguin eggs), total embryonic $\dot{V}O_2$ per gram fresh egg mass was, with the single exception of macaroni penguin A-eggs, very similar for all species.

On the basis of egg composition and the ability of their chicks to leave the nest and fend for themselves (Nice 1962, Williams *et al.* 1982), penguins have generally been classified as semi-altricial species. However, Bucher *et al.* (1986) compared measured embryonic and hatchling metabolic rates with those predicted for altricial and precocial species and concluded that embryos and hatchlings of emperor and Adélie penguins had metabolic rates more characteristic of semi-precocial and precocial species than with those of semi-altricial species. Although embryonic oxygen consumption of macaroni and rockhopper penguins shows no indication of a plateau in the days immediately preceeding pipping, a feature characteristic of precocial species (Vleck *et al.* 1979), pre-pipping, total, and hatchling $\dot{V}O_2$ of both species were, as with emperor and Adélie penguins, more closely predicted by equations for precocial species than by those for altricial species. However, it is notable that post-natal metabolism of macaroni and rockhopper penguins is consistent with that of semi-altricial chicks (Chapter 6).

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CHAPTER 6

ENERGY REQUIREMENTS FOR GROWTH AND MAINTENANCE IN MACARONI AND ROCKHOPPER PENGUINS

In press, *Polar Biol.* (1987). 7:

Summary.

Energy requirements for growth and maintenance of macaroni and rockhopper penguin chicks at Marion Island, southern Indian Ocean, were estimated from rates of oxygen consumption and body composition analysis.

Mass-specific energy expenditures of both species increased to levels 1.5 times that of hatchlings within 14 - 21 d of hatching and subsequently decreased. Lipid was initially accumulated slowly but the rate of accumulation increased after 30 d of age when male parents joined the females in feeding the chicks. Lipid, however, decreased markedly after 45 d of age and was presumably metabolized. Protein was laid down throughout the growth period, but doubled its initial rate of accumulation between 22 and 35 d of age. Thereafter the rate decreased until independence.

Daily energy requirements of macaroni and rockhopper penguins increased from 417 and 211 kJ d^{-1}, respectively, in the first week after hatching to peaks of 1 540 and 1 170 kJ d^{-1} about halfway through the growth period before decreasing until independence. Total energy requirement for growth and maintenance was estimated to be 76 200 kJ for macaroni penguins and 59 400 kJ for rockhopper penguins, of which growth energy comprised 38% and 28% respectively. Based on the energy requirements and population data,

macaroni and rockhopper penguin chicks at Marion Island consume an estimated 4 200 and 700 t of food, respectively, each year.

Introduction

Penguins are important consumers of resources in some marine ecosystems. This is particularly so in the sub-Antarctic where Croxall (1984) has estimated that 80% of the avian biomass is made up of penguins, of which 50% are macaroni penguins (*Eudyptes chrysolophus*). Four species of penguin breed at sub-Antarctic Marion Island, southern Indian Ocean. The small population of gentoo penguins (*Pygoscelis papua*; 888 pairs, Adams and Wilson, in press) and the very much larger population of king penguins (*Aptenodytes patagonicus*; 215 230 pairs, Siegfried *et al.* 1978) are year-round residents, the former breeding in the austral winter and the latter all year round. However, the impact of penguins on the surrounding marine resources increases markedly with the influx of an estimated 405 084 and 93 286 pairs, respectively, of summer-breeding macaroni penguins and rockhopper penguins (*E. chrysocome*) (Siegfried *et al.* 1978; Watkins, in press). The energy demands of these penguins are particularly high when both species are rearing chicks. Estimates of energy requirements for chick growth and development may be made from direct measurements of food intake rates of the chicks and this method has been used for several species of seabirds (eg. Dunn 1975; Cooper 1977) and, more particularly, for macaroni and rockhopper penguins (Williams 1982). Because chick energy demands change during growth, this method requires detailed information on meal

size and feeding frequency throughout the growth period which is both time and labour intensive. In addition, although measurements of food intake rates allow estimates of overall energy requirements, they provide no indication of how the energy is partitioned between growth and maintenance. Such estimates are best obtained from direct measurements of the chicks' energy expenditures and energy accumulated as chick biomass (Ricklefs 1974). This method has been used for few seabirds (Ricklefs *et al.* 1980, Ricklefs and White 1980), and not at all for penguins. In the present study I construct an energy budget for macaroni and rockhopper penguin chicks from hatching to independence from measurements of the chicks' energy expenditures, derived from measurements of oxygen consumption, and body composition analysis (cf Ricklefs 1974), and estimate the total energy, and hence food, requirements of the chicks.

Materials and methods

The study was carried out at Marion Island (46°52'S, 37°51'E) during the austral summers of 1981/82 and 1984/85. Both macaroni and rockhopper penguins at Marion Island lay two eggs 4-5 d apart (Williams 1981). The eggs are dimorphic in size, the second laid B-egg being larger than the first laid A-egg in both species (Warham 1963, 1971; Williams 1980a). In macaroni penguins the A-egg is usually lost before the B-egg is laid, but in rockhopper penguins two eggs are incubated in about 35% of nests and two chicks are

hatched in about 6% of nests, although only one is ever reared to independence (Williams 1980a). Eggs of macaroni penguins begin hatching in early December and those of rockhopper penguins in late December. The fledging period of both species is 70 ± 3 days (Williams 1980a).

In both seasons, about 40 previously marked nests of each species were checked daily each season during the hatching period until all chicks had hatched. In order to obtain chicks from A-eggs of rockhopper penguins, A-eggs were substituted for B-eggs, or B-eggs were removed, from 28 rockhopper penguin nests. Because chicks of both species are brooded and guarded only for about 21 d (Warham 1963, 1971), after which they may leave their nests to form small creches, chicks from marked nests were fitted with temporary, numbered flipper tags prior to the end of the guard stage.

Energy expenditure

Energy expenditure of was measured on two to five chicks at weekly intervals from hatching until immediately prior to independence. Chicks were taken from their respective colonies to the laboratory, a trip of about 35 min for macaroni penguins but less than five min for rockhopper penguins. In the laboratory, chicks were weighed to the nearest 1 g (small chicks) or 10 g (large chicks) on appropriate Pesola spring balances and placed in

translucent, airtight, metabolic chambers of 10, 25 or 74 l volume, depending on the age and size of the chicks. Ambient air, drawn from outside the laboratory, was pumped through a regulating flowmeter and a Rotameter flowmeter before entering the chamber. Air exiting the chamber passed through a Silica gel/Carbosorb tube, to remove water vapour and carbon dioxide, before entering a Taylor-Servomex OA 570 paramagnetic oxygen analyzer. Air flow through the chamber was set to obtain a 1-2% decrease in oxygen concentration between chamber inlet and outlet and ranged from 400 to 3 200 ml min^{-1}, depending on the size of the chicks. Oxygen content of ambient air was assumed to be 20.94% and the calibration of the oxygen analyzer was checked before and after each experiment. Chamber temperatures, measured with a thermocouple inserted into the chamber through a rubber bung, could not be controlled and ranged from 10 to 20°C, between 5 and 10°C warmer than average temperatures in the field, but within the range the chicks might experience at Marion Island during summer (Schulze 1971).

Before commencing an experiment, a period of at least 60 min was allowed for a chick to settle in the chamber and the chamber air to equilibrate. Thereafter, readings of chamber temperature, flow rate and percentage oxygen in the effluent air were recorded at 15-min intervals over a period of 2-3 h. Chicks were returned to their nests or colonies immediately after an experiment.

Oxygen consumption of the chicks was calculated from the equation of Hill (1972) for dry, CO_2-free air and corrected to standard temperature and pressure. Oxygen consumption was converted to energy equivalents using 1 l O_2 = 20.083 kJ.

It was not established whether the chicks were fed before measurement of oxygen consumption. However, because chicks up to about 21 - 26 days are fed daily it is unlikely that they were post-absorbtive. Also, 50 - 56% of older chick fasts last between 24 and 48 h and 93% of fasts <96 h (Williams 1982). Because effects of the heat increment of feeding (or specific dynamic action SDA) appear to persist for several days (Ricklefs 1974), it is probable that most measurements of oxygen consumption include an SDA component. However, this could not be quantified.

Body composition

Accumulation of lipid and ash-free, non-lipid (protein) dry matter during development was estimated from the body composition of nine macaroni and 16 rockhopper penguin chicks, collected at approximately 15-d intervals from hatching until 60 d of age. The chicks were weighed to the nearest 1 g or 10 g on Pesola spring balances and frozen for later analysis. In the laboratory, chicks were thawed and their stomach contents removed and weighed. The entire chicks were then dissected, minced, and dried to constant mass at 60°C in a forced-draught oven to estimate water

content. Aliquots of the dried samples were analysed for lipid content by hexane extraction for 45 min at 70°C. Further aliquots were ashed in a muffle furnace for 6 h at 450°C. Energy content was obtained by bomb calorimetry in a Digital Data Systems CP 500 bomb calorimeter.

Results

Energy expenditure

Mass, energy expenditure and mass-specific energy expenditure of macaroni and rockhopper penguin chicks from hatching until immediately prior to independence are presented in Figs 6.1 and 6.2 respectively. Mass of macaroni penguins increased to a peak at 56 d of age, thereafter remaining relatively constant until independence (Fig 6.1a). Mass of A and B-chicks of rockhopper penguins peaked at 56 and 63 d of age, respectively, and then decreased until independence (Fig. 6.2a). Although A-chicks generally weighed less than B-chicks at the same age, differences were significant ($P < 0.05$) only at 49, 56 and 63 d of age over which period the clear trend in heavier B-chicks disappeared.

Energy expenditure of macaroni penguin chicks increased rapidly in the first 14 d after hatching and peaked at about 42 d of age, before decreasing until independence (Fig 6.1b). Energy expenditure of both A and B-chicks of rockhopper penguins increased until 28 d of age, thereafter

Figure 6.1: Mass, energy expenditure and mass-specific energy expenditure of macaroni penguin chicks from hatching to independence. Numbers relate to sample sizes and bars show $\pm$ 1 S.D.

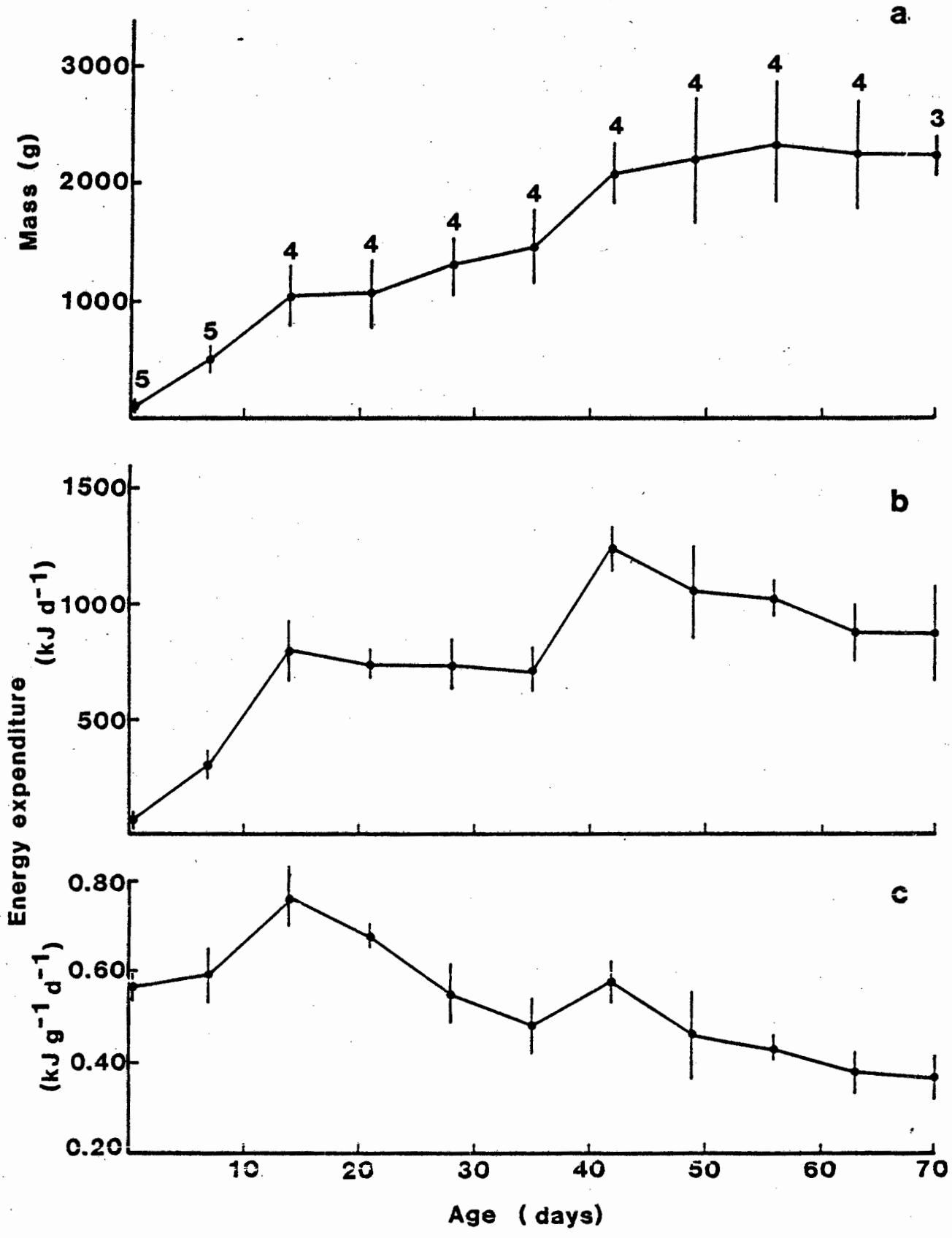
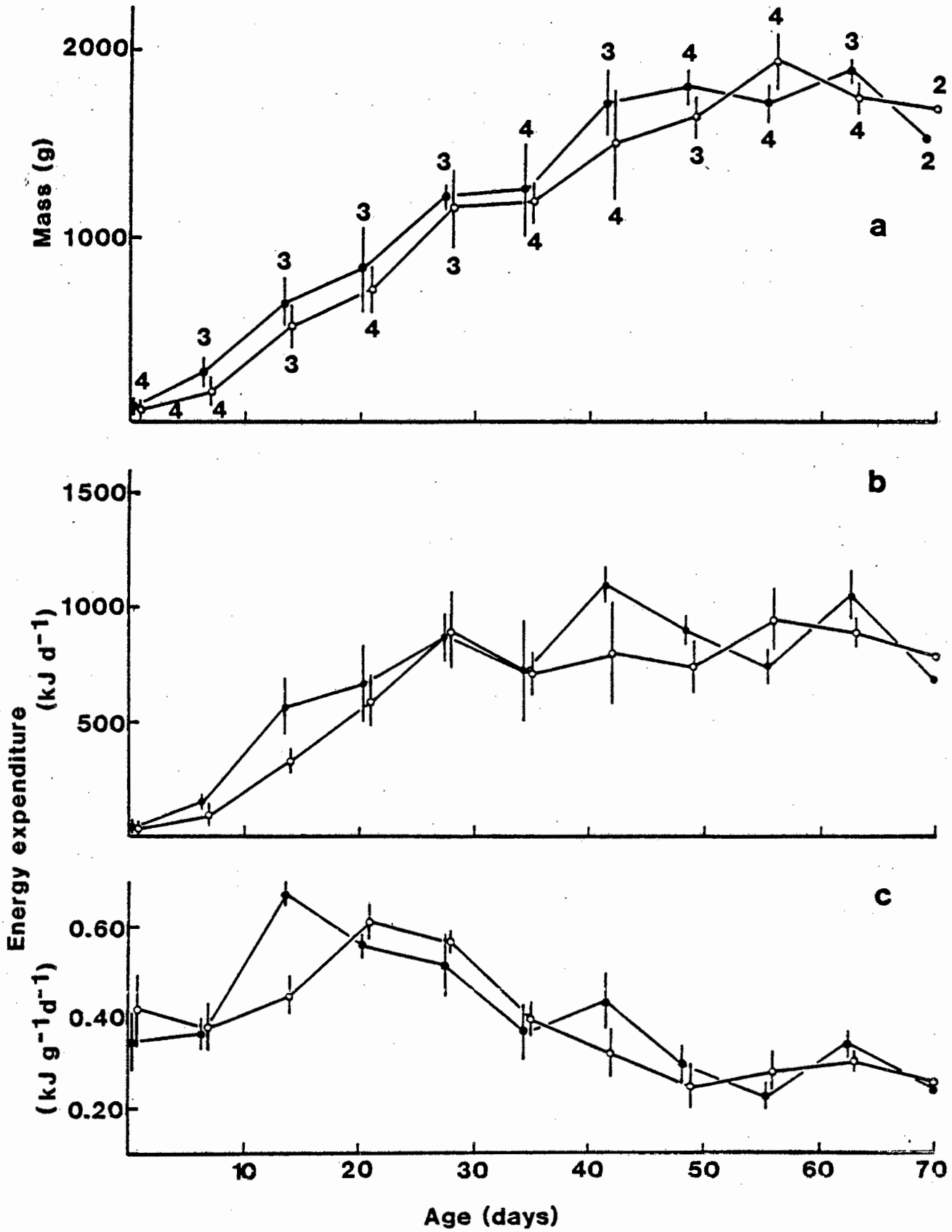

a
Mass (g)
3000
2000
1000
5
5
4
4
4
4
4
4
4
3
b
Energy expenditure
(kJ d-1)
1500
1000
500
c
(kJ g-1 d-1)
0.80
0.60
0.40
0.20
10
20
30
40
50
60
70
Age (days)

Figure 6.2: Mass, energy expenditure and mass-specific energy expenditure of A- (open circles) and B- (closed circles) rockhopper penguin chicks from hatching to independence. Numbers relate to sample sizes and bars show $\pm$ 1 S.D.


Mass (g)
2000
1000
a
b
1500
1000
500
Energy expenditure
(kJ d⁻¹)
c
0.60
0.40
0.20
(kJ g⁻¹d⁻¹)
10
20
30
40
50
60
70
Age (days)

showing no systematic trend (Fig. 6.2b). Mass-specific energy expenditure of both species increased to a level almost 1.5 times that of hatchlings within the first 14 - 21 d of nestling life, thereafter decreasing until independence (Figs. 6.1c and 6.2c).

Williams (1980b) reported significant differences in mass between A- and B-chicks of rockhopper penguins at hatching, with B-chicks growing significantly faster during the first 35 d of nestling life. Differences in growth between A- and B-chicks were, for the most part, not evident in the present study, possibly because of the small sample sizes. In addition, the patterns and levels of energy expenditure and mass-specific energy expenditure were similar for both A- and B-chicks (Fig. 6.2). Consequently, for the remainder of this paper, results for A- and B-chicks are combined and discussed together.

Body composition

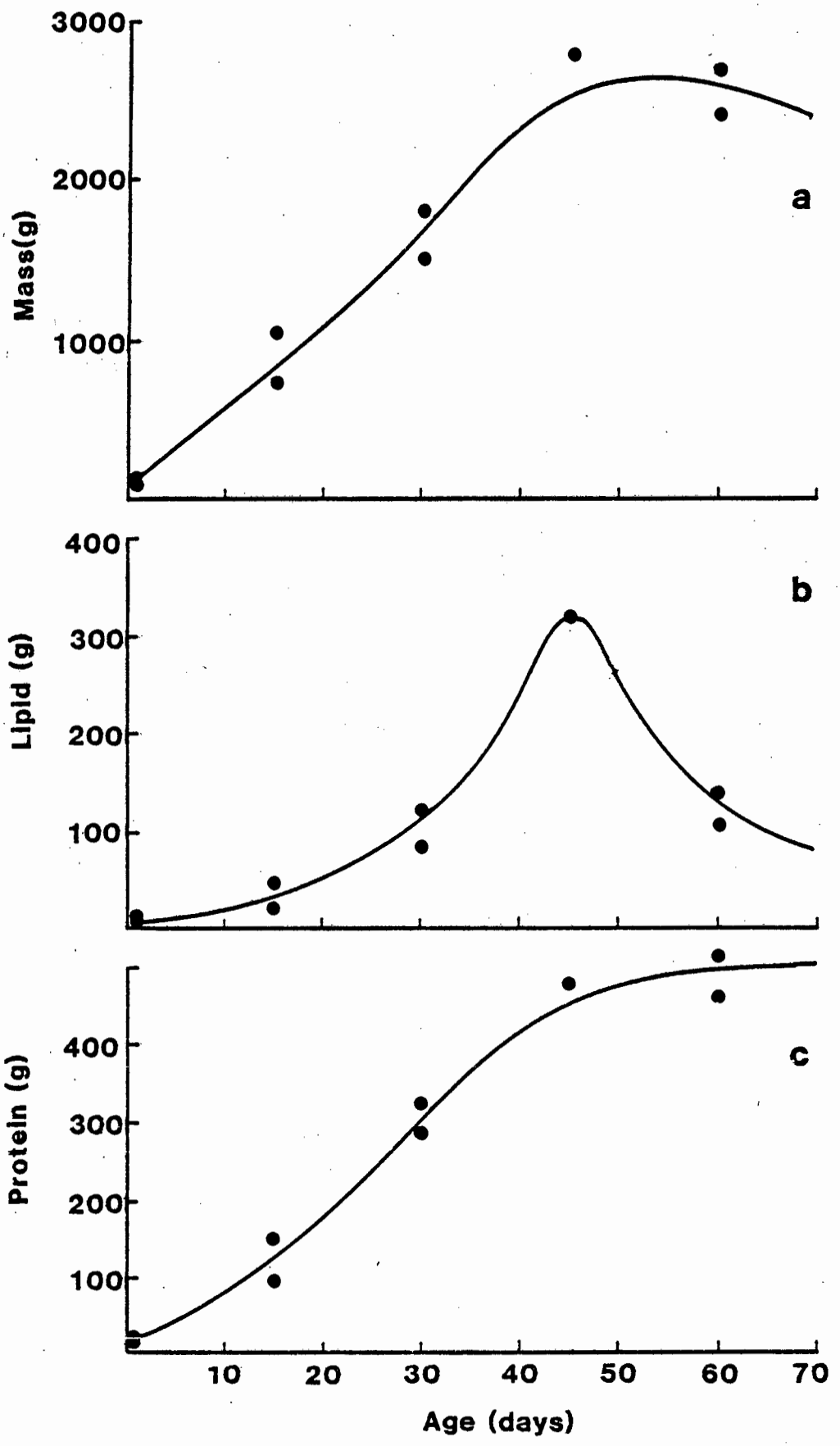
Total body water in chicks of macaroni penguins decreased from 81% of body mass at hatching to 74% at 60 d of age and that of rockhopper penguins from 79% at hatching to 71% at 60 d of age (Table 6.1). In both species, the largest decrease occurred between 15 and 30 d of age. Ash comprised a relatively constant proportion of dry body mass in both species throughout growth, averaging 8.3 $\pm$ 1.6% (5.7 - 9.5%)

Table 6.1. Water content (% fresh mass) and ash content (% dry mass) of macaroni and rockhopper penguin chicks in relation to age

	Age (days)	No. birds	Fresh body mass (g)	Body water content (%)	Ash content (%)
Macaroni penguins	0	2	106	80.9	7.8
	15	2	879	80.2	9.3
	30	2	1 653	72.8	9.5
	45	1	2 776	69.5	5.7
	60	2	2 569	73.3	9.0
Mean				75.4	8.3
S.D				4.9	1.6
Rockhopper penguins	0	2	79	78.6	9.1
	15	4	518	76.1	8.4
	30	2	943	70.6	11.7
	45	4	1 680	71.9	6.9
	60	4	1 629	71.0	8.6
Mean				73.6	8.9
S.D				3.5	1.7

in chicks of macaroni penguins and 8.9 ± 1.7% (6.9 - 11.7%) in those of rockhopper penguins (Table 6.1).

General patterns of lipid and protein accumulation appeared to be similar for both species (Figs. 6.3 and 6.4). Lipid increased between hatching and about 45 d, after which it decreased markedly, presumably being metabolized (Figs. 6.3b and 6.4b). Rates of accumulation were initially low (Tables 6.3 and 6.4), but more than doubled after about 30 d of age, corresponding to the stage when the male parents join the females in feeding the chicks (Williams 1982). Protein in both species was laid down throughout the growth period. The rate of accumulation increased until about 35 d of age, after which it decreased until independence, when it was negligible (Fig. 6.3c and 6.4c). Energy content of macaroni penguin chicks increased significantly from 22.8 ± 0.4 kJ g^{-1} dry mass at hatching to a maximum of 27.5 kJ g^{-1} at 45 d of age (Table 6.2), consistent with the increase in lipid content of the chicks, subsequently decreasing to a minimum of 21.7 kJ g^{-1} at 60 d of age as lipid stores were metabolized. Mean energy content of rockhopper penguin chicks decreased slightly from 23.5 kJ g^{-1} at hatching to a minimum of 21.1 kJ g^{-1} at 30 d of age before increasing significantly to a maximum of 24.9 kJ g^{-1} at 45 d (Table 6.2). Energy content at independence was 22.5 kJ g^{-1}.


3000
2000
1000
Mass(g)
a
400
300
200
100
Lipid (g)
b
400
300
200
100
Protein (g)
c
10
20
30
40
50
60
70
Age (days)

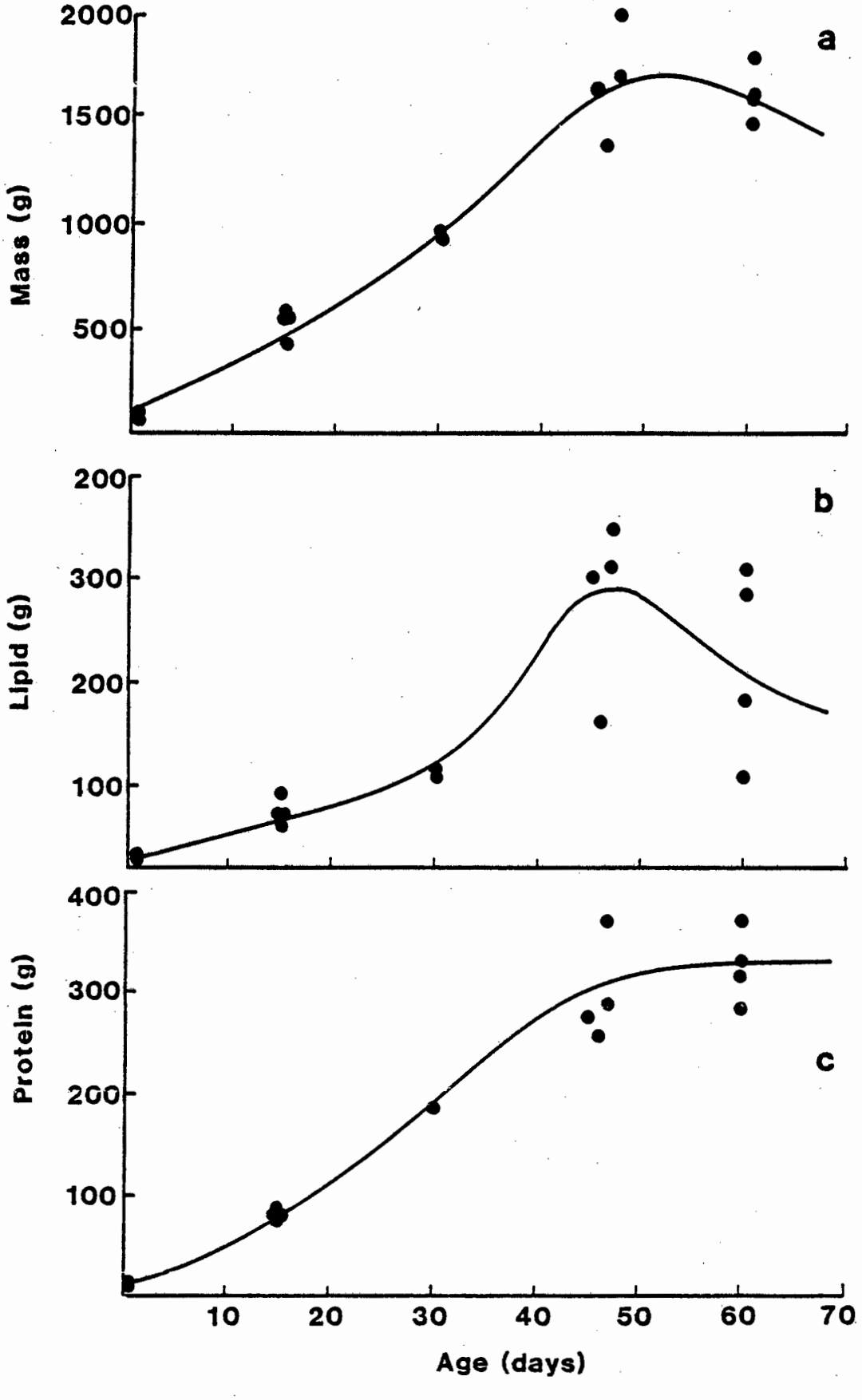

2000
1500
1000
500
Mass (g)
a
200
300
200
100
Lipid (g)
b
400
300
200
100
Protein (g)
c
10
20
30
40
50
60
70
Age (days)

Table 6.2. Energy content of macaroni and rockhopper penguin chicks in relation to age. Number of birds as for Table 6.1

Age (days)	Energy content (kJ g-1 dry mass)[a]	
	Macaroni penguins	Rockhopper penguins
0	22.8	23.5
15	23.2	23.5
30	23.2	21.1
45	27.5	24.9
60	21.7	22.5

[a] Means of 2 - 6 determinations.

metabolic rates in chicks of precocial species are attained soon after hatching and decrease to adult levels towards the end of the nestling period. The pattern of mass-specific metabolic rates in macaroni and rockhopper penguins in the present study, and in king penguins (Barrė 1978), is intermediate between these two extremes, consistent with the semi-altrical mode of development of penguins (Williams *et al.* 1982).

The increase in mass-specific metabolism in developing chicks parallels the development of homeothermic capacity (Ricklefs 1974). The peak and subsequent decrease in mass-specific energy expenditure of macaroni and rockhopper penguins thus suggests that homeothermy in chicks of these species is attained between two and three weeks of age. Although there are no empirical data, circumstantial evidence suggests that this is essentially correct. By about 15 d of age the chicks become too large to be effectively covered by the adults and stand next to them on their nests. In addition, mesoptile down, with an associated improvement in insulation (Taylor 1986), develops from between 7 and 14 d of age (Williams 1980b). King penguin chicks attain homeothermy at about 20 d of age (Barrė 1978), and those of chinstrap (*Pygoscelis antarctica*) and gentoo penguins attain homeothermy by 15 d of age (Taylor 1985).

Body composition

Previous information on the body composition of penguin chicks is limited to the study of Myrcha and Kaminski (1982) who measured body water, ash and energy content of 46 chinstrap and 38 gentoo penguins during growth. Body water content of these two species decreased linearly from about 85% at hatching to less than 65% at independence, a greater and more regular decrease than that observed for macaroni and rockhopper penguin chicks. Ash content of chinstrap and gentoo penguin chicks was similar to that of macaroni and rockhopper penguin chicks, increasing from about 9% at hatching to between 11.5 and 12.5% at independence. Energy content of chinstrap and gentoo penguin chicks also varied in a similar manner to that of macaroni and rockhopper penguin chicks, increasing from about 21 kJ g^{-1} dry mass at hatching to 27 kJ g^{-1} about halfway through growth as water content decreased and fat reserves increased; energy content subsequently decreased slightly, but not significantly, to 26 kJ g^{-1} (Myrcha and Kaminski 1982).

Energy requirement for growth

Following the method described by Ricklefs *et al.* (1980), I constructed energy budgets for chicks of macaroni penguins (Table 6.3) and rockhopper penguins (Table 6.4). Energy accumulated as biomass was estimated from rates of lipid and protein accumulation (Figs. 6.3 and 6.4), converted to

energy equivalents. Energy cost of biosynthesis was assumed to be equivalent to one-third the accumulated energy (Ricklefs 1974) and was added to accumulated energy to obtain energy requirement for growth. Energy requirement for maintenance is the energy expenditure, estimated by graphical integration of the areas under the energy expenditure curves in Figs. 6.1 and 6.2, minus the cost of biosynthesis. Total energy requirement is the sum of the growth and maintenance requirements. Faecal energy is, for the moment, not taken into account.

Energy requirements of macaroni and rockhopper penguin chicks increased rapidly from about 417 and 211 kJ d^{-1}, respectively, in the first week after hatching, to peaks of 1 540 and 1 170 kJ d^{-1}, respectively, about halfway through the growth period (Fig. 6.5). Energy requirements subsequently decreased by 50% in macaroni and by 30% in rockhopper penguins prior to independence. The proportion of total energy allocated to growth decreased from about 85% in macaroni and 70% in rockhopper penguins in the first week of nestling life to average about 40-45% between two and seven weeks of age, subsequently decreasing markedly after this to <10% when chicks no longer laid down lipid and the rate of protein accumulation decreased.

Based on the above calculations, the total energy requirement for growth and maintenance of an normal chick was estimated to be 76 200 kJ for macaroni and 59 400 kJ for

Figure 6.3: Total body mass and lipid and protein content of macaroni penguins in relation to age. Curves fitted by eye.

Table 6.3. Calculation of the energy budget of Macaroni penguin chicks

Age interval (days)	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
0-7	2.4	6.1	91	122	213	204	283	134	417
8-14	2.4	8.3	91	166	257	516	342	431	773
15-21	4.3	10.0	163	200	363	883	483	763	1246
22-28	4.3	12.9	163	258	421	795	560	656	1216
29-35	10.5	12.1	399	242	641	900	853	688	1541
36-42	10.5	10.3	399	206	605	863	805	663	1468
43-49	10.5	5.0	399	100	499	1045	664	880	1544
50-56	--	2.6	--	52	52	941	69	924	993
57-63	--	1.7	--	34	34	896	45	885	930
64-70	--	0.7	--	14	14	749	19	744	763

Figure 6.4: Total body mass and lipid and protein content of rockhopper penguins in relation to age. Curves fitted by eye.

(1) Rate of accumulation of lipid (g d^{-1}), estimated from the slopes of the curves in Fig. 6.3b.

(2) Rate of accumulation of protein (g d^{-1}), estimated from the slopes of the curves in Fig. 6.3c.

(3) Energy equivalent of lipid accumulation (kJ d^{-1}) = (1) X 38 kJ g^{-1}.

(4) Energy equivalent of protein accumulation (kJ d^{-1}) = (2) X 20 kJ g^{-1}.

(5) Energy equivalent of tissue accumulation (kJ d^{-1}) = (3) + (4).

(6) Energy expenditure (kJ d^{-1}) estimated from the area under the curves in Fig. 6.1b.

(7) Total energy requirement for growth (kJ d^{-1}), assuming a production efficiency of 75% = (5) X 1.33.

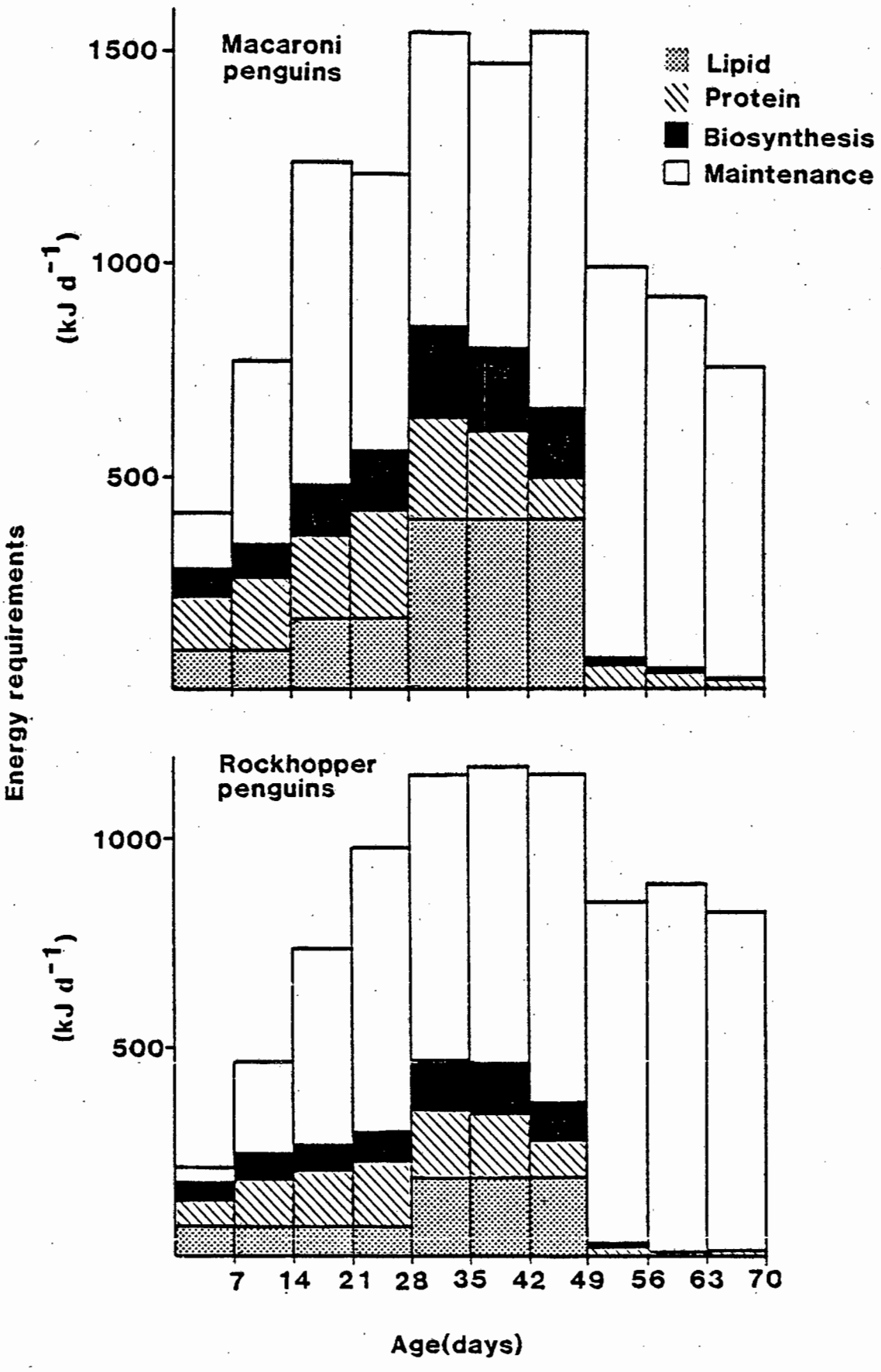
(8) Total energy requirement for maintenance (kJ d^{-1}) = (6) - 0.33 X (5).

(9) Total energy expenditure for growth and maintenance = (7) + (8).

Table 6.4. Calculation of the energy budget of Rockhopper penguin chicks. Conventions as for Table 6.3

Age interval (days)	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
0-7	1.9	3.1	72	62	134	77	178	33	211
8-14	1.9	5.7	72	114	186	283	247	222	469
15-21	1.9	6.6	72	132	204	538	271	471	742
22-28	1.9	7.7	72	154	226	752	301	677	978
29-35	5.1	8.2	194	164	358	794	476	676	1152
36-42	5.1	8.0	194	160	354	818	471	701	1172
43-49	5.1	4.3	194	86	280	874	372	782	1154
50-56	--	1.1	--	22	22	843	29	836	865
57-63	--	0.3	--	6	6	893	8	891	899
64-70	--	0.3	--	6	6	839	8	837	845

Figure 6.5: Estimated daily energy budgets of macaroni and rockhopper penguins in relation to age, based on energy expenditures and rates of lipid and protein accumulation.


Macaroni penguins
Lipid
Protein
Biosynthesis
Maintenance
1500
1000
500
Energy requirements
(kJ d⁻¹)
Rockhopper penguins
1000
500
(kJ d⁻¹)
7
14
21
28
35
42
49
56
63
70
Age(days)

rockhopper penguins of which the growth energy requirement comprised 38% and 28%, respectively. Despite the generally lower ambient temperatures and wind and rain experienced by chicks in the field, metabolic rates of chicks measured in chambers in the laboratory are regarded as realistic. Although the thermal neutral zones of macaroni and rockhopper penguin chicks are not known, Barré (1984) has shown that the thermal neutral zone of king penguin chicks in summer lies between 4.8 and 25°C and that there is no shivering above 0°C. Taylor (1985) reported that chicks of chinstrap and gentoo penguins (closer in size to macaroni and rockhopper penguins than are king penguins) have lower critical temperatures of -4.0 and -6.5°C, respectively, by 25 days of age and that these decrease to -13.0 and -15.5°C by 40 days. Consequently, older chicks of these species live within their thermal neutral zones in their natural environment and do not incur any extra energy expenditure for thermoregulation. Furthermore, the insulative properties of the down, and later the feathers, of chicks suggest that these species remain within their thermal neutral zones even during strong winds (Taylor 1986). Because king, gentoo, macaroni and rockhopper penguins breed sympatrically through much of their respective ranges, the latter two species are, presumably, similarly adapted and energy expenditure in the field is unlikely to elevate metabolic rates significantly above those measured in the laboratory.

Penguin chicks are, for the most part, inactive, being brooded and guarded on the nest for the first 21 - 26 days and thereafter spending most of their time huddling in groups or sheltering under rocks (Warham 1963, 1971, pers. obs). However, older chicks may chase parents to solicit food, wander within their colonies and, in the final 10 days or so prior to independence, exercise their flippers vigorously (Warham 1963, 1971; Strange 1982; pers. obs). Energy expenditure during these activities has not been taken into account, but is not considered to contribute greatly to the energy expenditure of the chicks over the entire 70 day fledgling period.

The estimated energy requirements of macaroni and rockhopper penguin chicks in the present study are compared with the few relevant studies on other penguins in Table 6.5. Energy requirements for chick growth alone range from 16 537 kJ in the rockhopper penguin to 46 652 kJ for the much larger gentoo penguin. Despite the different methods used to estimate energy requirements, relative values for the different species are in reasonable agreement. Energy cost of growth per gram of chick, where comparable, range from 9.4 to 12.9 kJ g^{-1}. With the exception of the present study, estimates of total energy requirements are available only for jackass penguin (*Spheniscus demersus*) chicks. Captive, hand-reared jackass penguin chicks consumed an estimated 186 255 kJ of energy, twice that estimated for chicks in the field (Cooper 1977). Total energy requirement

Table 6.5. Energy requirements for growth and maintenance in penguin chicks

Species	Fledgling minus hatchling mass (g)	Energy requirements (kJ)			Energy requirements per gram of chick (kJ)		
		Growth	Maintenance	Total	Growth	Maintenance	Total
Macaroni[1] penguin	2 237	28 861	47 376	76 237	12.9	21.2	34.1
Rockhopper[1] penguin	1 533	16 527	42 882	59 409	10.8	28.0	38.8
Jackass[2] penguin	2 403[3]	------	------	186 255[a]	----	----	77.5
		------	------	93 150[b]	----	----	38.8
Chinstrap[4] penguin	3 475[5]	35 146	------	------	10.1	----	----
Gentoo[4] penguin	4 965[5]	46 652	------	------	9.4	----	----

[1] This study.

[2] From Cooper (1977), estimated from food intake and energy content of food for (a) captive, hand-reared chicks and (b) naturally reared chicks.

[3] From Williams and Cooper (1984).

[4] From Myrcha and Kaminski (1982) and multiplied by 1.33 to account for cost of biosynthesis.

[5] From Despin (1977).

per gram of fledgling in naturally reared jackass penguins is similar to that of macaroni and rockhopper penguin chicks. The relatively greater energy requirement for growth and smaller energy requirement for maintenance in macaroni relative to rockhopper penguins may be related to differences in body size: macaroni and rockhopper penguins are, respectively, the largest and smallest of the *Eudyptes* penguins (Warham 1975).

Food requirements

Food requirements for successful fledging of macaroni and rockhopper penguin chicks can be estimated from knowledge of their energy requirements (see above), the energy content of their foods and their assimilation efficiencies. Both macaroni and rockhopper penguin chicks are fed on crustaceans, fish and cephalopods (Chapter 7). The energy content of an average meal, measured by bomb calorimetry, was 4.6 kJ g^{-1} wet mass (C.R. Brown, unpubl.data). Assuming an assimilation efficiency of 76% for penguin chicks (Cooper 1977), the energy requirements of macaroni and rockhopper penguin chicks throughout their growth period would be met by 21.8 and 16.6 kg of food, respectively. Williams (1982) estimated from chick feeding rates and mass increases that macaroni penguin chicks were fed about 33 kg of food during development and rockhoppers about 15 kg. The latter figure is quite close to the food requirements estimated for rockhopper penguin chicks in the present study, but the

amount of food fed to macaroni penguin chicks, as estimated by Williams (1982), is 50% more than their requirement of 22 kg estimated from their energy expenditures and body composition. The reason for this difference is not readily apparent.

An estimated 175 116 macaroni and 27 179 rockhopper penguin chicks are reared to independence annually at Marion Island, and a further 50 516 and 32 121 chicks, respectively, die during the guard and post guard stages (calculated from mortality figures in Williams 1980a). Based on these population figures, chicks of macaroni penguins at Marion Island consume about 4 200 t of food during growth and those of rockhopper penguins about 700 t, about 90% of which comprises crustaceans, 8% fish and 2% cephalopods by mass (Chapter 7). Williams (1982) estimated a total food consumption for chicks of both species to be 8 800 t, compared to the 4 900 t estimated in the present study. The difference is accounted for by the 10% lower population estimate, based on a more recent census, and the 50% lower food requirement of macaroni penguin chicks in the present study.

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CHAPTER 7

SEASONAL AND ANNUAL VARIATION IN DIETS OF MACARONI AND SOUTHERN ROCKHOPPER PENGUINS AT SUB-ANTARCTIC MARION ISLAND

Published in *J. Zool., Lond.* (1987). 212: 7-28. with N.T. Klages as a junior co-author.

SUMMARY

The diets of adult Macaroni penguins *Eudyptes chrysolophus chrysolophus* and Southern rockhopper penguins *E. chrysocome chrysocome* were analysed quantitatively at Marion Island, southern Indian Ocean, throughout two successive chick-rearing seasons. The diets were broadly similar. Crustaceans were the predominant prey type comprising, overall, 90 % by mass and 98 % by numbers in Macaroni penguins and 96 % by mass and 99 % by numbers in Rockhopper penguins. *Nauticaris marionis* was the predominant crustacean eaten by both penguin species in 1983-84, but *Euphausia vallentini* and *Thysanoessa vicina* predominated in 1984-85. *Themisto gaudichaudii* was present in appreciable numbers only in Macaroni penguins. Fish was not found in measurable quantities in either species in 1983-84, but contributed 5 % and 4 % of the mass of the diet in Macaroni and Rockhopper penguins respectively when calculated in terms of the original biomass of food ingested. In 1984-85, however, fish comprised 10 and 6 % of observed mass and c. 25 and 14 % of original biomass ingested in Macaroni and Rockhopper penguins respectively. Pelagic myctophids, predominantly *Krefftichthys anderssoni*, *Protomyctophum tenisoni* and *P. normani* between 0.01 and 8.3 g, were the most commonly identified fish prey, but Macaroni penguins took an appreciable number of *Electrona carlsbergi* in 1983-84. Cephalopods made up between 1 and 3 % of the diet by mass in

both penguin species and between 5 and 13 % of original biomass ingested. Predominant cephalopods eaten were *Kondakovia longimana* and an unidentified octopus species. The relative proportions of each prey type changed throughout chick-rearing, with pelagic fish and cephalopods comprising a larger proportion later in the season when the penguins were assumed to be foraging farther from their breeding sites. Dietary segregation of the two species appears to be related to the difference in the timing of the breeding season, which begins three to four weeks earlier in Macaroni penguins.

Introduction

Macaroni penguins *Eudyptes chrysolophus chrysolophus* are widely distributed between 62° and 46°S in the Southern Ocean and are one of the most abundant penguins in the sub-Antarctic (Wilson, 1983). A second subspecies, the Royal penguins *E. chrysolophus schlegeli*, breeds only at Macquarie Island (54°S, 158°E). Southern rockhopper penguins *E. chrysocome chrysocome* are less abundant than are Macaroni penguins and are distributed between 55° and 46°S (Wilson, 1983), with a separate subspecies, the Northern rockhopper penguin *E. chrysocome moseleyi*, being found north to 37°S. Southern rockhopper penguins breed sympatrically with Macaroni penguins throughout much of their ranges.

Despite the importance of Macaroni penguins in terms of biomass and food consumption (Croxall, 1984), quantitative investigations of their diet have only recently been made at the South Shetland Islands (Croxall & Furse, 1980) and at South Georgia (Croxall & Prince, 1980). These localities lie towards the southern limits of the species' range and, more particularly, they lie south of the Antarctic Polar Front (APF, formerly known as the Antarctic Convergence), which is regarded as a major biogeographical boundary for many prey species that occur in the diets of Southern Ocean seabirds (Deacon, 1982). Penguins breeding at localities north of the APF might therefore be expected to differ in diet from their

southern counterparts. Horne (1985) has reported on the diets of the Royal penguin and the Southern rockhopper penguin at Macquarie Island, but sampling was conducted only over 12 days of the 70-day chick-rearing period. Nevertheless, this is the only important published study from north of the APF in which the diets of the two species have been compared at the same locality. The diet of the Southern rockhopper penguin has also been described at the Falkland Islands, but samples were only collected over a period of one week during early chick rearing (Croxall, Prince, Baird & Ward, 1985). Other information on diets of Macaroni and Rockhopper penguins at their more northerly breeding localities is largely anecdotal (Duroselle & Tollu, 1977; Williams & Laycock, 1981).

This paper presents a quantitative analysis of the diet of Macaroni and Southern rockhopper penguins during two successive chick-rearing seasons at Marion Island, one of the northernmost breeding localities where both species occur sympatrically.

Study site

Marion Island (46°52'S, 37°51'E) is the larger of two islands which make up the Prince Edward group, which lies between 200 and 250 km north of the Antarctic Polar Front (Lutjeharms & Valentine, 1984). Marion Island has an estimated breeding population of 405 000 pairs of Macaroni

penguins (FitzPatrick Institute, unpubl. data) and 93 290 pairs of Rockhopper penguins (Williams, Siegfried, Burger & Berruti, 1979). Whereas Macaroni penguins breed at about 30 colonies around the island (Williams, 1978), Rockhoppers nest in scattered colonies along most of the coastline.

Rockhopper penguin food samples were collected from a small colony of *c.* 350 pairs which breed under some of the buildings of the research station and on the adjacent point at Transvaal Cove. Macaroni penguin food samples were collected from Macaroni Bay, a colony of *c.* 1 165 pairs some 3 km south of the research station.

Methods

Collection of food samples

Thirty stomach samples of Macaroni penguins were collected between 20 December 1983 and 25 February 1984 and a further 45 samples between the same dates during 1984-85. Thirty-four and 50 Rockhopper penguin stomach samples were collected between 2 January and 11 March in 1984 and 1985 respectively. Whereas in 1983-84 samples were not collected on a regular basis, in 1984-85 five samples were collected from each species per week. Birds were caught when they came ashore at their respective colonies and stomach pumped using the wet-offloading technique of Wilson (1984). Contrary to Lishman (1985), the technique worked well, although most birds, particularly those with full stomachs, needed to be

pumped two or three times to empty the stomach (cf. Ryan & Jackson, 1986). Samples were drained through a 0.5 mm sieve and returned to the laboratory for analysis.

Analysis of food samples

In the laboratory, the samples were drained a second time, blotted dry and weighed to the nearest 1 g. Relatively undigested samples were placed in a large bowl under a slowly running tap and the crustacean component floated off, leaving behind the heavier fish and cephalopod components, including fish otoliths and cephalopod mandibles (beaks). The fish and cephalopod components, and any remaining crustaceans, were then separated as far as possible and weighed to the nearest 0.5 g. The difference between the combined mass of the fish and cephalopod components and the original sample mass was assumed to comprise the crustacean component. However, many samples particularly those from 1983-84, contained a large proportion of inseparable, unidentifiable material in a highly digested state. Identifiable components from these samples were sorted as far as possible by hand and the unidentifiable material was assumed to be distributed in proportion to the composition of the identifiable material (Croxall *et al.*, 1985).

Crustaceans

In relatively undigested samples, a random 100 g subsample was removed prior to sorting the entire sample,

and was sorted for all intact, measurable crustaceans. In well digested samples, and in samples weighing less than 100 g , the whole sample was searched for intact crustaceans. These were measured to the nearest millimetre between the anterior margin of the eyes and the tip of the telson, and stored in alcohol for later identification using published keys (Bowman & Gruner, 1973; Kirkwood, 1982, 1984).

The number of crustaceans in each sample was estimated by weighing 50 - 100 individuals of small, medium and large specimens chosen at random from eight samples. The mean mass of these specimens was then divided by the mass of the crustacean component in each sample, using the mean masses in proportion to the size class of crustaceans present.

Fish

Otoliths recovered from the food samples were cleaned in tap water, dried, counted and stored for later identification. Relatively intact fish, when present, were stored in alcohol. Fish and otoliths were later identified either by direct comparison with material held in the reference collection of the Port Elizabeth Museum or from the literature (Schwarzhans, 1978; Hecht & Hecht, 1981; North, Burchett, Gilbert & White, 1984). Uncorroded otoliths were measured using an ocular micrometer under a binocular microscope, and paired by species and size in order to estimate the number of fish consumed. Large numbers of otoliths which could not be paired were divided by two to

obtain the number of fish consumed and odd otoliths were assigned to an additional fish. Regressions relating otolith diameter (OD) to standard length (SL), total length (TL) and mass (M) (see **Appendix**) were used to estimate the original biomass of fish ingested in each sample. Heavily eroded otoliths were assumed to be from a previous meal and were excluded from calculations. Regressions were derived from data logged in the Port Elizabeth Museum's reference collection, with the exception of the regression for *Notothenia magellanica* which came from Hecht & Cooper (1986).

Cephalopods

Intact and partially digested cephalopods recovered from food samples were stored in alcohol for later identification. Cephalopod beaks recovered from food samples were counted to estimate the number of cephalopods eaten, and the lower rostral length (LRL) measured according to Clarke (1962) with Vernier calipers or using an ocular micrometer under a dissecting microscope. Lower beaks were identified by comparison with material held in the Port Elizabeth Museum or by reference to the literature (Clarke, 1962, 1980, 1985; Filipova, 1972). Intact and partially digested cephalopods found in stomachs were identified from the literature (Roper, Young & Voss, 1969; Filipova, 1972), and were used to confirm identifications made from beaks. The identification of very small beaks (LRL < 2 mm) could

only be established to family level, since beaks of this size do not usually show sufficient characteristics to permit identification to genus or species. Regressions relating LRL to dorsal mantle length (DML) and mass (M) (see **Appendix**) were used to estimate the original biomass of cephalopods consumed. Beaks which were too eroded to measure were assumed to have come from previous meals and were not included when calculating original biomass of cephalopods ingested.

Results

General composition of the diet

Stomach samples collected from Macaroni penguins in 1983-84 did not differ significantly in mean mass from those collected in 1984-85 (t = 1.74, P>0.05). Overall mean mass for both years was 273 $\pm$ 141 g (Range 41 - 815 g). The mean mass of stomach samples from Rockhopper penguins in 1984 was 149 $\pm$ 42 g (range 80-294 g), significantly less than the 195 $\pm$ 84 g (range 80-430 g) recorded in 1985 (t = 2.99, P<0.005).

The total mass of all stomach samples collected in 1983-84 was 7 148 g for Macaroni penguins and 5 204 g for Rockhopper penguins, of which 54 and 20 % respectively consisted of unidentifiable material. Stomach samples in 1983-84 were, however, frequently stored in the refrigerator for several days before being sorted. In 1984-85 all samples

were sorted within 24 h of collection and were generally better preserved, with only 11 % of a total sample mass of 13 286 g in Macaroni and 2 % of 9 732 g in Rockhopper penguins comprising unidentifiable material.

In both species of penguin, crustaceans formed by far the predominant prey in terms of frequency of occurrence (Table 7.1), mass (Table 7.2) and number (Table 7.3), but made up slightly less of the diet by mass in 1984-85 when both penguin species contained quantities of relatively undigested fish (Table 7.2). Whole fish was not found in measurable quantities in 1983-84, although traces, in the form of fine bones, scales, eye lenses and otoliths, were present in many of the samples (see Table 7.1 and Table 7.3). However, fish comprised about 5 and 4 % of the diet of Macaroni and Rockhopper penguins respectively when expressed as original biomass of prey ingested (Table 7.4). In 1984-85, fish made up 25 % of the diet of Macaroni and 14 % of the diet of Rockhopper penguins when estimated on the basis of original biomass ingested (Table 7.4).

Cephalopods comprised only a small percentage of the mass (Table 7.2) and numbers (Table 7.3) of the prey of Macaroni and Rockhopper penguins in both years, but made up between 8 and 13 % of the original biomass of prey ingested by Macaroni and 5 % of that ingested by Rockhopper penguins (Table 7.4).

TABLE 7.1

Frequency of occurrence (%) of prey in the stomach contents of Macaroni and Rockhopper penguins at Marion Island. N equals the total number of samples

Species	Year	N	Crustaceans	Fish	Cephalopods
Macaroni penguins	1983-84	30	100	83	77
	1984-85	45	93	84	64
Rockhopper penguins	1984	35	100	40	46
	1985	50	100	68	46

TABLE 7.2

Composition by mass of food in the stomach contents of Macaroni and Rockhopper penguins at Marion Island. Unidentifiable material was assumed to be distributed in proportion to the composition of the identified components

Species and year		Crustaceans	Fish	Cephalopods
Macaroni penguins				
1983-84	mass (g)	7 024	---	124
	%	98.3	---	1.7
1984-85	mass (g)	11 724	1 281	281
	%	88.2	9.6	2.2
Rockhopper penguins				
1984	mass (g)	5 188	---	16
	%	99.7	---	0.3
1985	mass (g)	8 887	606	239
	%	91.3	6.2	2.5

TABLE 7.3

Composition by numbers of crustaceans, fish and cephalopods in the stomach contents of Macaroni and Rockhopper penguins at Marion Island

pecies		Crustaceans		Fish		Cephalopods	
		1983-84	1984-85	1983-84	1984-85	1983-84	1984-85
acaroni	Mean	3 577 (99.4 %)	4 056 (96.9 %)	14 (0.4 %)	112 (2.7 %)	9 (0.3 %)	17 (0.4 %)
enguins	S.D.	990	3 212	19	105	18	48
	Range	2 269 - 5 806	0 - 14 276	0 - 86	0 - 404	0 - 93	0 - 311
ockhopper	Mean	2 344 (99.3 %)	3 062 (99.4 %)	13 (0.6 %)	11 (0.4 %)	3 (0.1 %)	7 (0.2 %)
enguins	S.D.	787	1 570	34	17	5	14
	Range	1 194 - 4 388	239 - 6 314	0 - 195	0 - 65	0 - 20	0 - 53

TABLE 7.4

Composition of the diet of Macaroni and Rockhopper penguins at Marion Island based on the original biomass of crustaceans, fish and cephalopods ingested

Species and year		Crustaceans	Fish	Cephalopods
Macaroni penguins				
1983-84	mass (g)	6 974	388	651
	(%)	87.0	4.9	8.1
1984-85	mass (g)	11 217	4 455	2 385
	(%)	62.1	24.7	13.2
Rockhopper penguins				
1984	mass (g)	5 086	212	257
	(%)	91.6	3.8	4.6
1985	mass (g)	8 815	1 528	569
	(%)	80.8	14.0	5.2

Crustaceans

Juveniles of the hippolytid shrimp *Nauticaris marionis*, were the predominant crustaceans in the diets of both penguin species in 1983-84, comprising 42 and 60 % of all identified crustaceans in Macaroni and Rockhopper penguin samples respectively (Table 7.5). The euphausiid *Euphausia vallentini* comprised the rest of the crustacean component in Rockhopper penguins in 1984 but only a small proportion of identified crustaceans in Macaroni penguins, the remainder consisting of amphipods, predominantly *Themisto gaudichaudii*, and the euphausiid *Thysanoessa vicina* (Table 7.5). In 1984-85, however, *E. vallentini* and *T. vicina* were the predominant crustaceans identified from both penguin species, comprising 83 % of all crustaceans identified from Macaroni penguins and 95 % from Rockhopper penguins (Table 7.5). No *N. marionis* were identified from the stomach contents of Macaroni penguins in 1984-85 and very few from Rockhopper penguins. *Themisto gaudichaudii* made up only 10 % of crustaceans identified from Macaroni penguin samples in 1984-85, compared to 32 % in 1983-84. Several other species of amphipod were also found in small numbers in Macaroni samples, but none was found in Rockhopper stomach samples in 1984 and few in 1985.

The overall mean lengths of crustaceans eaten by Macaroni and Rockhopper penguins were closely similar at 20.0 mm and 20.9 mm respectively. There were, however, differences in

Figure 6.1: Mass, energy expenditure and mass-specific energy expenditure of macaroni penguin chicks from hatching to independence. Numbers relate to sample sizes and bars show $\pm$ 1 S.D.

Table 6.3. Calculation of the energy budget of Macaroni penguin chicks

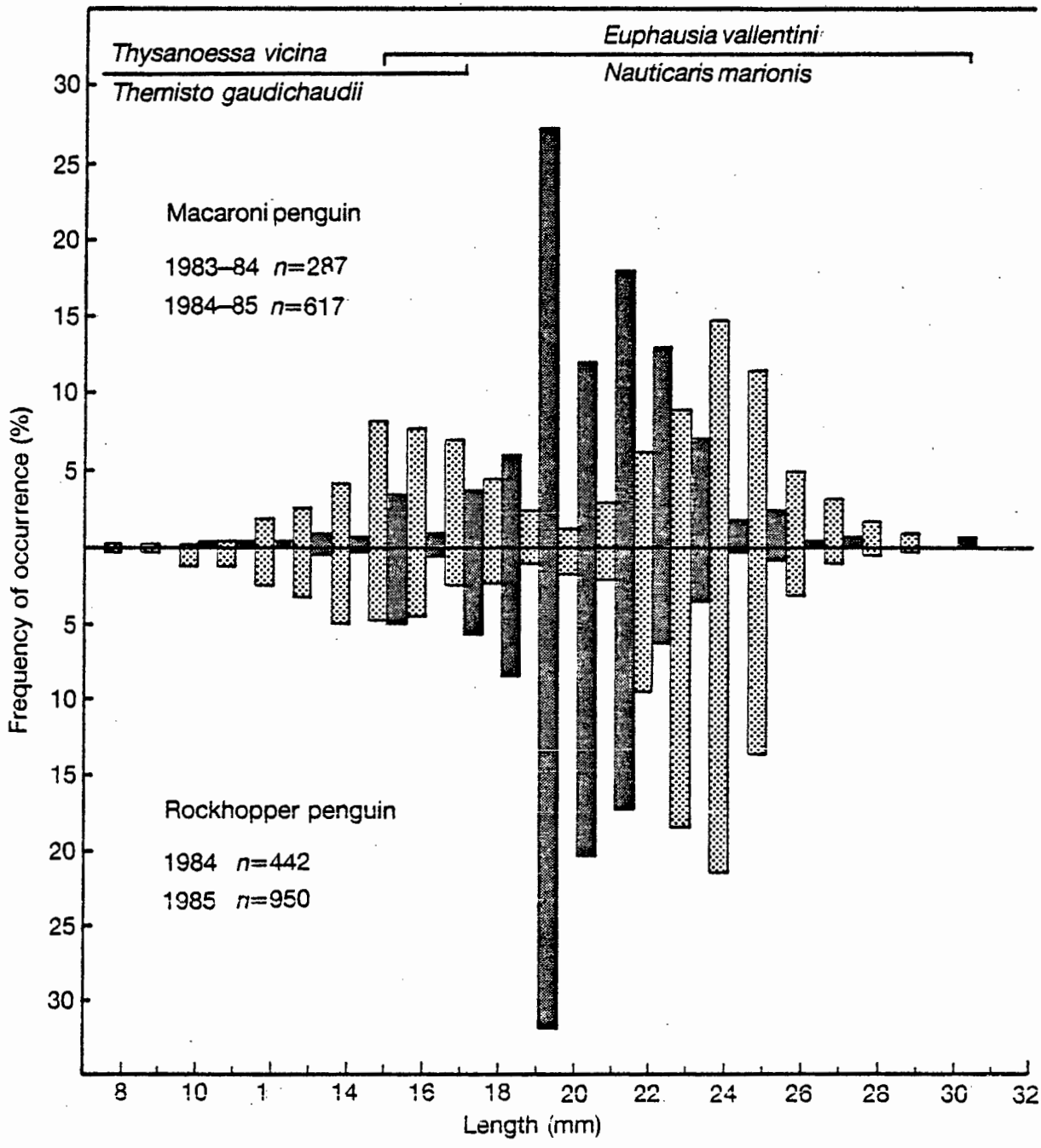
Age interval (days)	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
0-7	2.4	6.1	91	122	213	204	283	134	417
8-14	2.4	8.3	91	166	257	516	342	431	773
15-21	4.3	10.0	163	200	363	883	483	763	1246
22-28	4.3	12.9	163	258	421	795	560	656	1216
29-35	10.5	12.1	399	242	641	900	853	688	1541
36-42	10.5	10.3	399	206	605	863	805	663	1468
43-49	10.5	5.0	399	100	499	1045	664	880	1544
50-56	--	2.6	--	52	52	941	69	924	993
57-63	--	1.7	--	34	34	896	45	885	930
64-70	--	0.7	--	14	14	749	19	744	763

Figure 6.5: Estimated daily energy budgets of macaroni and rockhopper penguins in relation to age, based on energy expenditures and rates of lipid and protein accumulation.

TABLE 7.5

Composition (%) of identified crustacean prey in the stomach contents of Macaroni and Rockhopper penguins

Taxa	Macaroni penguins		Rockhopper penguins	
	1983-84	1984-85	1984	1985
Natantia				
Nauticaris marionis	42.3	---	60.0	0.4
Nematocarcinus longirostris	1.3	0.2	---	---
Euphausiacea				
Euphausia vallentini	6.4	49.7	40.0	72.5
Thyssanoessa vicina	9.0	33.2	---	---
Euphausia spp.	---	4.2	---	4.5
Amphipoda				
Themisto gaudichaudi	32.1	9.9	---	0.1
Primno spp.	7.6	0.5	---	0.1
Vibilia spp.	---	---	---	0.2
Cyllopus sp.	---	1.6	---	---
Hyperiella sp.	---	0.2	---	---
Unidentified crustaceans	1.3	0.5	---	---
Total number identified	78	636	90	1 028


Thysanoessa vicina
Themisto gaudichaudii
Euphausia vallentini
Nauticaris marionis
Macaroni penguin
1983–84 n=287
1984–85 n=617
Rockhopper penguin
1984 n=442
1985 n=950
Frequency of occurrence (%)
30
25
20
15
10
5
5
10
15
20
25
30
8
10
1
14
16
18
20
22
24
26
28
30
32
Length (mm)

the size distributions of crustaceans eaten by both species between years. Over 75 % of all intact crustaceans measured in 1983-84 were between 18 and 23 mm in length (Fig.7.1), reflecting the predominance of juvenile *Nauticaris marionis*, which had a maximum length of 23 mm, and adult *E. vallentini* which have a total length of 15 - 28 mm (Mauchline & Fisher, 1969). Smaller individuals measured were *Themisto gaudichaudii* and, probably, juvenile *E. vallentini*. The size-frequency distributions of crustaceans in the diets in 1984-85 were bimodal(Fig.7.1), with the smaller peak reflecting the high proportion of *Thysanoessa vicina* taken in this year. These have a maximum adult length of about 17 mm (Mauchline & Fisher, 1969). The second peak is accounted for by adult *E. vallentini*.

Fishes

Over 95 % of the fish identified from the stomach contents of Macaroni and Rockhopper penguins belonged to the family Myctophidae (lantern fishes). Three species in particular, *Protomyctophum tenisoni*, *P. normani* and *Krefftichthys anderssoni*, accounted for over 90 % of the fish diet of Macaroni penguins in 1984-85 and over 80 % in Rockhopper penguins (Table 7.6). *P. tenisoni* and *K. anderssoni* also comprised 74 % of the fish eaten by Macaroni and 97 % of that eaten by Rockhoppers in 1983-84, but *P. normani* was absent except in small numbers in Macaroni penguin samples (Table 7.6). *Electrona carlsbergi* accounted

TABLE 7.6

Composition (%) of fish prey identified from otoliths recovered from Macaroni and Rockhopper stomach contents at Marion Island.

Taxa	Macaroni penguins		Rockhopper penguins	
	1983-84	1984-85	1984	1985
Myctophidae				
Krefftichthys anderssoni	9.1	25.7	52.6	14.3
Protomyctophum tenisoni	65.3	53.6	44.3	44.8
P. normani	2.0	12.8	---	23.5
P. bolini	---	0.1	---	---
Protomyctophum spp.	---	0.1	---	---
Gymnoscopelus sp.	---	0.1	---	---
Electrona carlsbergi	21.9	0.8	---	---
E. subaspera	---	1.1	---	---
Unidentified Myctophidae	---	4.6	---	0.2
Notothenidae				
Notothenia magellanica	---	---	0.3	3.4
N. squamifrons	---	0.1	---	---
Notothenia sp.	---	0.1	---	---
Paralepis coreginoides	---	0.2	---	---
Dissostichus eleginoides	---	0.1	---	---
Unidentified fish	1.7	1.1	2.8	14.0
Total number of fish identified	352	4 815	399	494

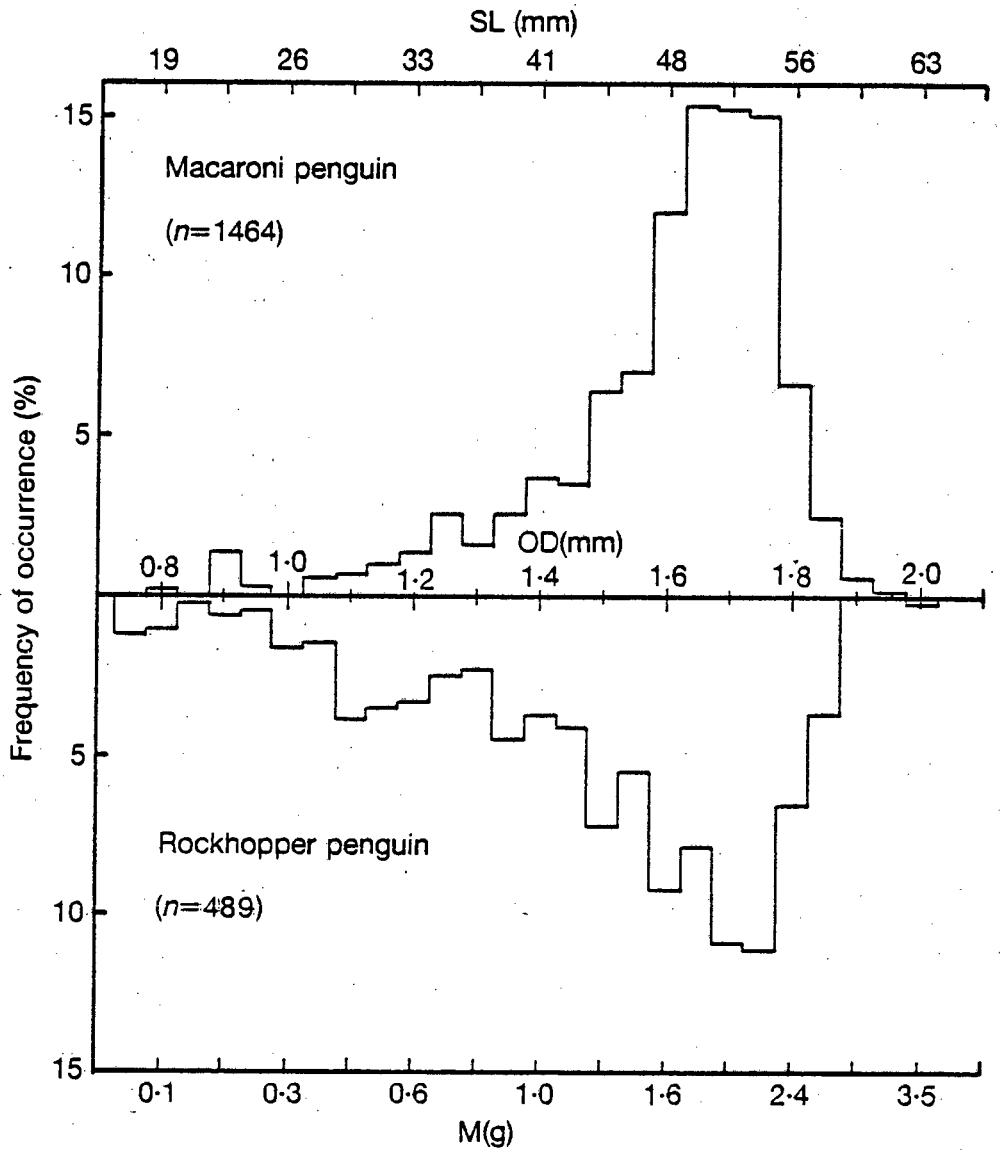
for the remainder of the fish consumed by Macaroni penguins in 1983-84, but was present only in a few samples in 1985. No *Electrona* were found in Rockhopper stomach contents. Other fish species were present only in very small numbers.

The size-frequency distribution of *Protomyctophum tenisoni* eaten by both Macaroni and Rockhopper penguins was skewed (Fig. 7.2), but mean lengths (45 mm SL, *c.* 1.3 g) and modal lengths (52 mm SL, *c.* 2.0 g) were the same for both penguin species. Overall size range was 19 - 63 mm SL or about 0.1 - 3.5 g. *P.normani* eaten by both penguin species were larger than *P.tenisoni*, with individuals between 56 and 85 mm SL being taken (Fig.7.3). The mean size eaten by Rockhoppers (74.8 $\pm$ 4.5 mm SL) was, however, significantly larger (t = 13.7, P<0.001) than that taken by Macaroni (68.5 $\pm$ 7.0 mm SL). Macaroni penguins, by contrast, generally consumed larger *Krefftichthys anderssoni* than did Rockhoppers (Fig.7.4). However, the size-frequency distribution of *K. anderssoni* taken by Rockhoppers had a bimodal distribution, incorporating a large proportion of small fish. *Electrona* spp. eaten by Macaroni penguins ranged in size from 27 to 95 mm SL (0.3 to 13.2 g), and *Notothenia magellanica* eaten by Rockhopper penguins ranged from 12 to 85 mm SL (0.04 and 13.4 g).

Cephalopods

In both penguin species, cephalopod beaks with a lower rostral length (LRL) >2 mm were identified predominantly as

FIG. 7.1. Length-frequency distribution of crustaceans eaten by Macaroni and Rockhopper penguins at Marion Island. Solid bars are from 1983-84 samples and stippled bars from 1984-85.


SL (mm)
19
26
33
41
48
56
63
15
10
5
Macaroni penguin
(n=1464)
OD(mm)
0·8
1·0
1·2
1·4
1·6
1·8
2·0
Frequency of occurrence (%)
5
10
15
Rockhopper penguin
(n=489)
0·1
0·3
0·6
1·0
1·6
2·4
3·5
M(g)

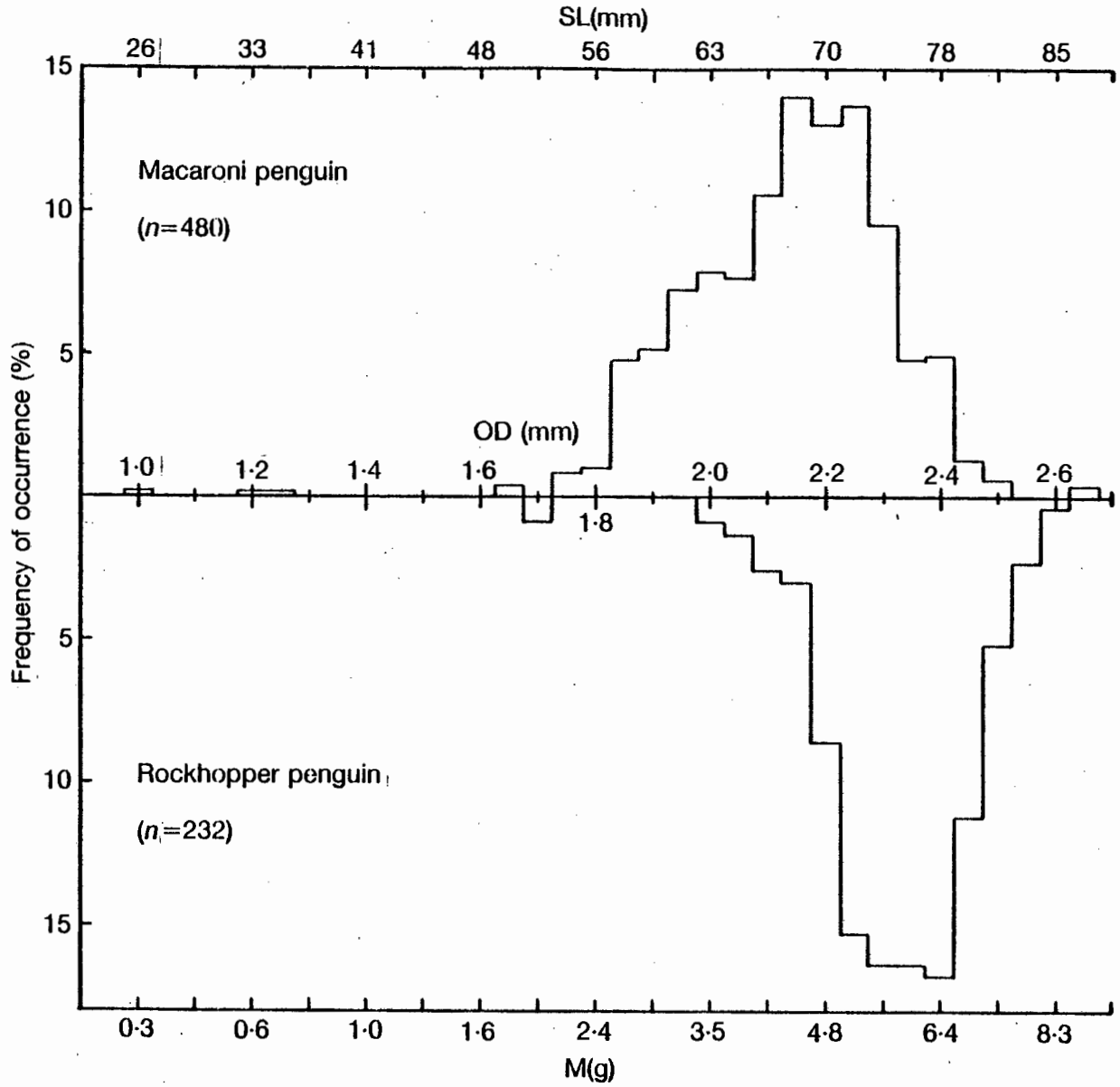
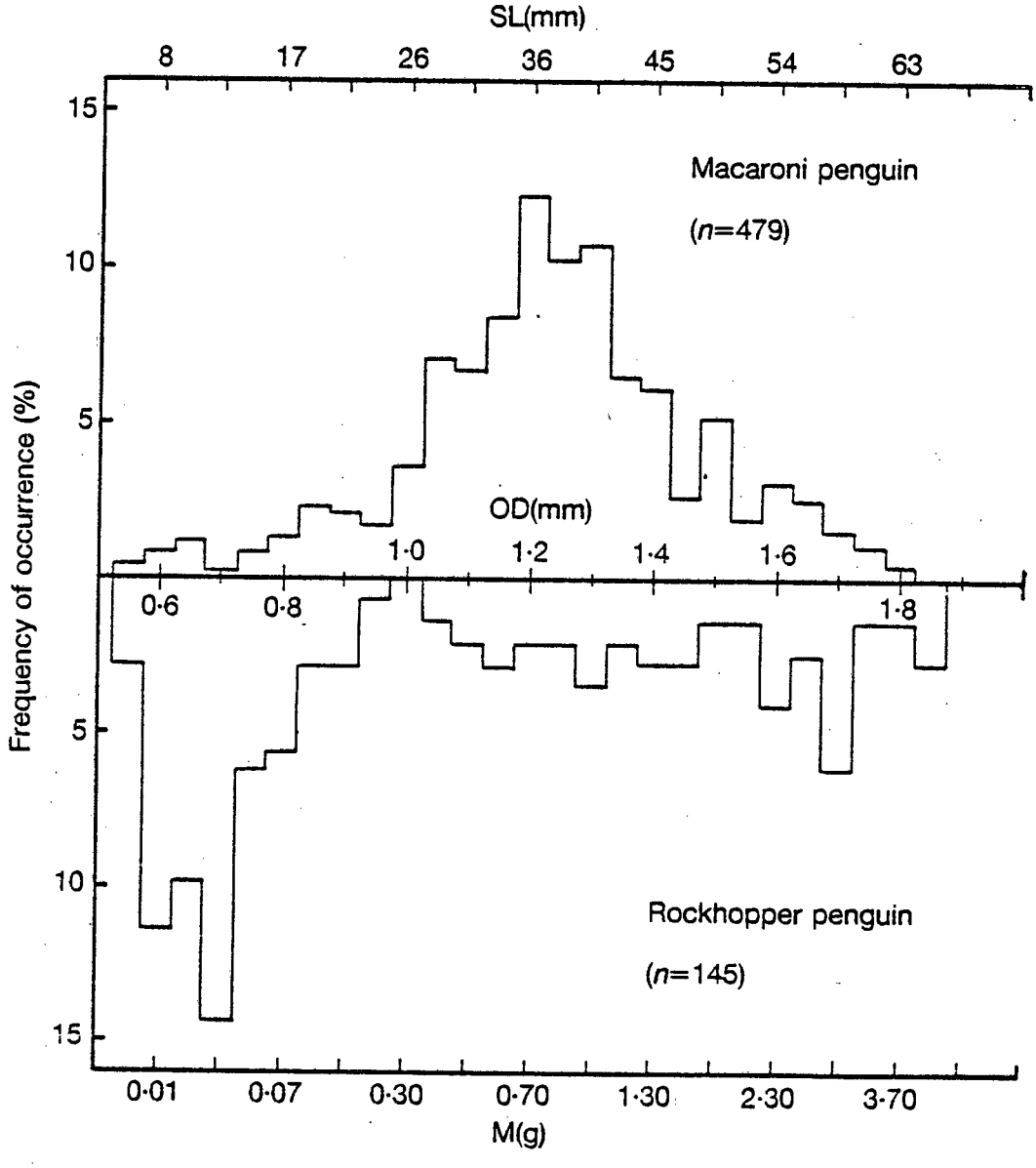

SL(mm)
26
33
41
48
56
63
70
78
85
15
10
5
Macaroni penguin
(n=480)
OD (mm)
1·0
1·2
1·4
1·6
1·8
2·0
2·2
2·4
2·6
Frequency of occurrence (%)
5
10
15
Rockhopper penguin
(n=232)
0·3
0·6
1·0
1·6
2·4
3·5
4·8
6·4
8·3
M(g)

FIG. 7.3. Size-frequency distribution of *Protomyctophum normani* eaten by Macaroni and Rockhopper penguins at Marion Island. OD = otolith diameter. Estimated standard length (SL) and mass (M) are included on separate scales.

FIG.7.4. Size-frequency distribution of *Krefftichthys anderssoni* eaten by Macaroni and Rockhopper penguins at Marion Island. OD = otolith diameter. Estimated standard length (SL) and mass (M) are included on separate scales.


SL(mm)
8
17
26
36
45
54
63
15
10
5
Macaroni penguin
(n=479)
OD(mm)
1·0
1·2
1·4
1·6
0·6
0·8
1·8
Frequency of occurrence (%)
5
10
15
Rockhopper penguin
(n=145)
0·01
0·07
0·30
0·70
1·30
2·30
3·70
M(g)

Kondakovia longimana, although *Moroteuthis knipovitchi* was also present (Table 7.7). Both species are of the family Onychoteuthidae. A large proportion of the beaks 1 - 2 mm LRL was identified as onychoteuthids, and their general appearance suggested that they probably belonged to the same species mentioned above. Very small beaks (<1 mm) could not be classified further than Decapoda, Oegopsida.

Octopods represented <6 % of cephalopods recovered from Macaroni penguins in 1983-84 and 1984-85 (Table 7.7). In contrast, octopods comprised *c.* 37 and 82 % of cephalopods identified from Rockhopper penguins in 1984 and 1985 respectively. All octopods recovered were very small (crest length *c.* 0.5 mm, total length 10 mm) and are, as yet, unidentified.

The size of onychoteuthid squid taken by Macaroni and Rockhopper penguins were generally <1 mm LRL and were estimated to weigh <0.5 g (Table 7.8), although squid up to 5 mm LRL weighing about 82 g were recovered from Macaroni penguins. The largest squid found in Rockhopper penguins had *c.* 3 mm LRL and weighed about 13 g.

Seasonal variation in diet

Changes in the relative proportions of crustaceans, fish and cephalopods in the penguins' diets at weekly intervals throughout their respective chick-rearing periods in 1984-85 (Fig. 7.5) show that both species fed predominantly on

TABLE 7.7

Composition (%) of cephalopod prey in food samples from Macaroni and Rockhopper penguins at Marion Island

Taxa	Macaroni penguins		Rockhopper penguins	
	1983-84	1984-85	1984	1985
Onychoteuthidae				
Kondakovia longimana	26.1	62.1	20.2	8.9
Moroteuthis knipovitchi	0.4	---	---	---
Unidentified Onychoteuthidae	58.4	1.3	32.3	1.9
Unidentified decapods	12.4	31.2	10.1	7.4
Neoteuthidae				
Alluroteuthis sp.	---	0.2	---	---
Unidentified octopods	2.7	5.2	37.4	81.8
Total number of cephalopods identified	260	911	99	385

TABLE 7.8

Size-frequency distribution of all decapods eaten by Macaroni and Rockhopper penguins at Marion Island in 1984 and 1985. LRL = lower rostral length, DML = dorsal mantle length, and M = mass

Species	LRL (mm) DML (mm) M (g)	<1 <10 <0.5	1 - 1.9 33.6 2.6	2 - 2.9 71.0 12.8	3 - 3.9 108.3 37.0	4 - 4.9 145.6 81.7
Macaroni penguins	Frequency	415	140	161	8	1
	%	57.2	19.3	22.2	1.1	0.2
Rockhopper penguins	Frequency	60	30	42	-	-
	%	45.5	22.7	31.8	-	-

crustaceans during early chick-rearing. Fish comprised a greater proportion of the diet of Macaroni penguins, but was not taken in large quantities (>20 %) until mid-January when their chicks were approximately 30 days old; in Rockhoppers fish was not taken in large quantities until mid-February when their chicks were about 47 days old. The proportionate importance of fish and cephalopods increased in both species until late February, the end of chick-rearing in Macaroni, when they accounted for 100 % of the diet of Macaroni and over 50 % of the diet of Rockhopper penguins. Subsequently, in the last three weeks of chick-rearing in Rockhoppers, the proportions of fish and cephalopods in this species' diet decreased to the point that crustaceans accounted for over 99 % of the biomass of food samples in the final two weeks. A similar pattern was evident in 1983-84, but was less clear because of less regular sampling.

Discussion

Biases in analysis

Stomach contents obtained from penguins are frequently in a well digested state and, in many cases, prey components are inseparable and unidentifiable (Croxall & Prince, 1980; Croxall *et al.*, 1985; Adams & Klages, 1987; CRB, pers. obs). Problems associated with analyzing such samples and in interpreting results have been discussed in some detail by Croxall *et al.* (1985). Several of these problems were, to

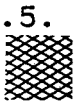
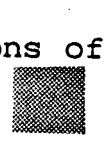
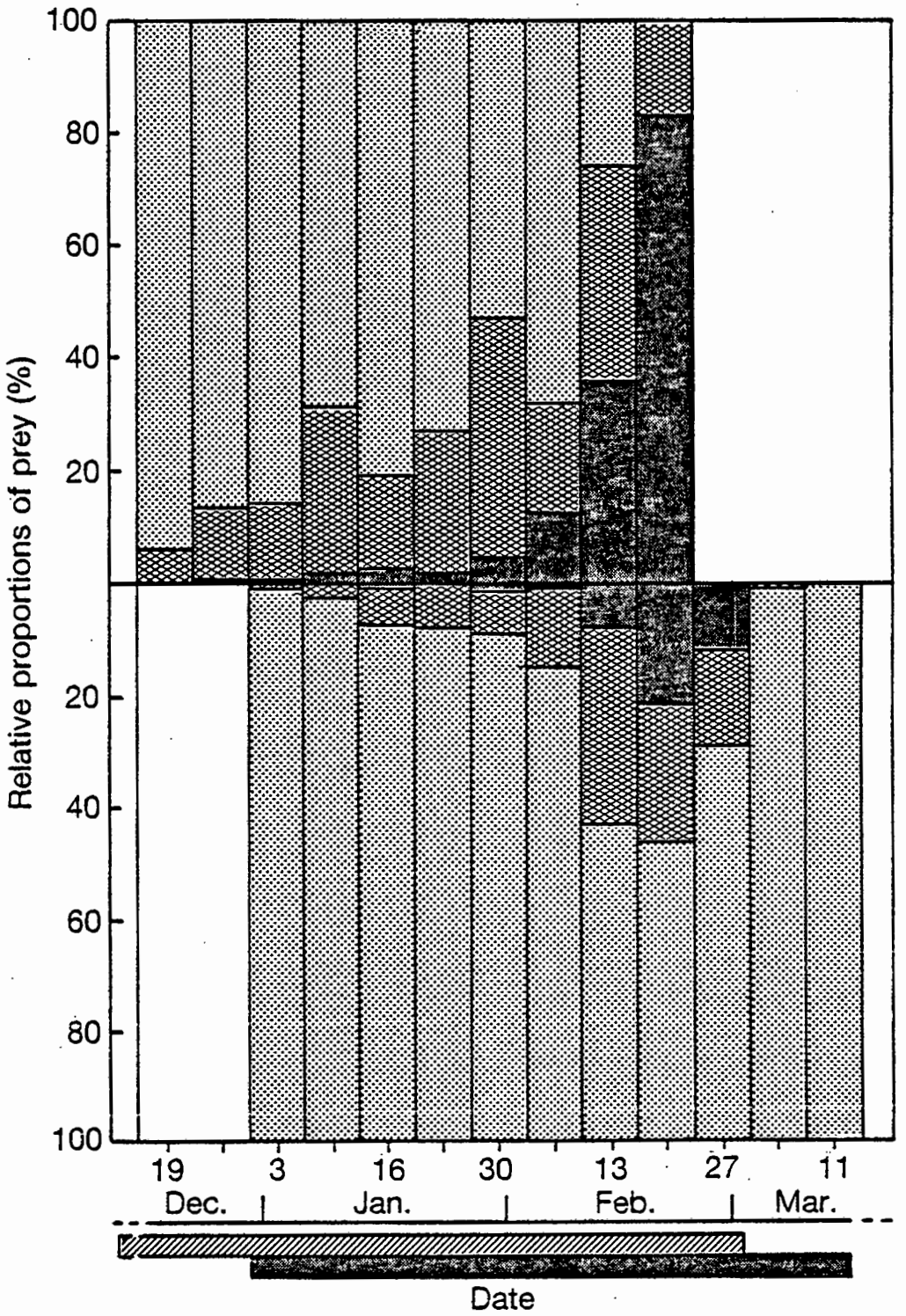



FIG. 7.5. Relative proportions of crustaceans , fish and cephalopods in the diets of Macaroni penguins (top) and Rockhopper penguins (bottom) during the 1984-85 chick-rearing periods at Marion Island. Data based on estimated biomass of prey ingested calculated at weekly intervals from five samples collected each week. Approximate spans of the chick-rearing periods are given on a separate axis (Macaroni penguins = hatched bar, Rockhopper penguins = solid bar).


100
80
60
40
20
20
40
60
80
100
Relative proportions of prey (%)
19
Dec.
3
16
Jan.
30
13
Feb.
27
11
Mar.
Date

some extent, avoided in the present study. First, as far as possible, whole stomach samples were sorted rather than subsamples, thus avoiding bias in samples which were not homogeneous. Secondly, the samples were sorted soon after collection, not stored for later analysis (e.g. Croxall *et al.*, 1985; Horne, 1985). Storage for any length of time in alcohol, formalin or by freezing often results in further disintegration and deterioration of the samples (CRB, pers.obs), making later analysis more difficult. Furthermore, storage in formalin dissolves otoliths (Croxall *et al.*, 1985) leading to underestimates of the relative importance of fish in penguins which utilize this resource.

Even if sorted immediately after collection, well digested, unidentifiable remains still frequently comprise a large proportion of some stomach samples, particularly those obtained from penguins with foraging trips lasting longer than 24 h. In such samples, the differential digestion of different prey types, and the differential retention of hard structures, such as cephalopod beaks and fish otoliths, from prey are persistent problems in analysing and interpreting food samples from penguins. Such biases have been discussed by Adams & Klages (1987).

Meal size

The mean mass of stomach contents from Macaroni penguins collected at Marion Island (273 $\pm$ 141 g) was similar to that

of samples collected by Croxall & Furse (1980) at the South Shetland Islands (347 ± 119 g; t = 1.78, P>0.05), but was significantly less than those collected by Croxall & Prince (1980) at South Georgia (692 ± 227 g; t = 12.2, P<0.001). Rockhopper stomach samples collected at Marion Island in 1984 (149 ± 42 g) also averaged less than the value of 219 ± 42 g reported by Croxall *et al.* (1985) from the Falkland Islands (t = 6.64, P<0.001), although those collected at Marion Island in 1985 (195 ± 84 g) were similar (t = 1.44, P>0.1). Although birds in the other studies were sacrificed, and samples consequently represent the entire stomach contents, it is unlikely that this could account for significant differences in meal sizes. Birds in the present study were stomach pumped several times, and samples from the last pumping frequently contained green bile and small stones, indicating that the stomachs were then empty (Wilson, 1984; Adams & Klages, 1987). Observed differences in meal size between localities may, however, reflect local differences in the availability of food. Chicks of Macaroni penguins at South Georgia grow faster, and adults have a shorter pre-moult fattening period, than at Marion and other sub-Antarctic Islands (Croxall, 1984), suggesting that food may be more readily available to penguins at South Georgia. The stomach samples collected by Horne (1985) at Macquarie Island, however, were particularly small compared to those from elsewhere, averaging only *c.* 50 g for Royal and 31 g for Rockhopper penguins. These low sample masses are

surprising, especially since Horne states that the Royal penguins were feeding large chicks at the time of collection. At Marion Island, adults of both species were frequently found to have a small bolus of relatively undigested food, often surrounded by a mucous layer, present at the top of the stomach. This was usually regurgitated first, the bulk of the more digested stomach contents only being given up when the birds were stomach pumped a second time (cf. Ryan & Jackson, 1986). Strange (1982) also reports a mucous layer around food fed to Rockhopper penguin chicks at the Falkland Islands. Because Horne (1985) only pumped her birds once, it is possible that in many cases she did not obtain the entire stomach contents.

Crustaceans

Macaroni and Rockhopper penguins feed on broadly similar species and size ranges of crustaceans. *Nauticaris marionis*, the predominant crustacean in both species' diets in 1983-84, is apparently abundant in the waters around Marion Island (Boden & Parker, 1986) and comprised 30 % by mass of the diet of Gentoo penguins *Pygoscelis papua* at Marion Island in September 1982 (La Cock, Hech & Klages, 1984), of which juveniles accounted for 6 %. Its absence in the diet of Macaroni and Rockhopper penguins in 1984-85 was possibly due to a scarcity around Marion Island in that year, since it was found only in very small numbers in food samples of Gentoo penguins in January and February and not at all in

March in 1985 (Adams & Klages, in prep.). *Euphausia vallentini* and *Thysanoessa vicina* have a circumpolar distribution on both sides of the APF (Mauchline & Fisher, 1969), and both species are commonly caught in net hauls in the immediate vicinity of Marion Island (Miller, 1982). *Themisto gaudichaudii* is widely distributed in the Southern Ocean (Kane, 1966) and it frequently forms the most common and abundant species in net hauls from the upper 100 m around Marion Island (Boden & Parker, 1986). *Vibilia antarctica, V. armata* and *Primno macropa* are also common species from net hauls around Marion Island and are likely to have been the amphipod species found in the penguin stomach samples.

Crustaceans identified from the stomach contents of Macaroni and Rockhopper penguins include species regarded as having an Antarctic distribution as well as species generally regarded as sub-Antarctic and sub-tropical. Zooplankton samples from net hauls in the vicinity of the Prince Edward Islands, however, also commonly include sub-Antarctic, sub-tropical and Antarctic species (Allanson, Boden, Parker & Duncombe-Rae, 1985), probably as a result of periodic incursions of the sub-tropical and Antarctic species through advection and eddies of foreign water masses past the islands (Miller, 1985; Boden & Parker, 1986). Such periodic incursions of species beyond their normal ranges might account for some of the year-to-year variations in the

crustacean component in net hauls and in the stomach samples of the penguins.

Fishes

The fish component of the diet of Macaroni and Rockhopper penguins at Marion Island was dominated by pelagic myctophids. *Krefftichthys anderssoni*, *Protomyctophum tenisoni* and *P. normani* are broadly Antarctic species that occur from south of the APF north to the Subtropical Convergence, and they are frequently caught in mid-water trawls between 50 and 150 m depth (Hulley, 1981). *K. anderssoni* is probably sexually mature at about 54 mm SL and *P. tenisoni* at about 45 mm SL (Hulley, 1981). Size-frequency distributions thus indicate that both penguin species consume predominantly juvenile *K. anderssoni*, whereas both adult and juvenile *P. tenisoni* were eaten in approximately equal proportions by Rockhopper penguins and predominantly adults (74 %) by Macaroni penguins. *K. anderssoni* < 15 mm SL, which were found almost entirely in Rockhopper stomach samples collected in February 1985, may represent the recruitment of a new cohort into the population around Marion Island at this time. Available data indicate that *P. normani* may be sexually mature from about 48 mm SL (Hulley, 1981). This implies that almost all individuals eaten by Macaroni and Rockhopper penguins were adult, with many considerably exceeding the maximum size (56 mm) observed by Hulley in the western Atlantic off Patagonia. Since it is

unlikely that the smaller Rockhoppers select larger fish than do Macaroni penguins, and there was no evidence from otoliths recovered in the samples of fish growth over the sampling period, the significant difference in the size of fish taken by the two penguins may be due to natural size variation between shoals. *Electrona carlsbergi* and *E. subaspera* have a broadly Antarctic distribution between the Antarctic continent (Linkowski, 1983) to as far north as the Subtropical convergence (Krefft, 1974) and occur at depths between 100 and 600 m. *E. subaspera* has been caught in mid-water trawls in the top 100 m of the water column in the vicinity of Marion Island (Miller, 1985) and has been identified in stomach samples from Greatwinged petrel *Pterodroma macroptera* chicks at Marion and Prince Edward Islands (Schramm, 1986). Both *E. carlsbergi* and *E. subaspera* are considered to be sexually mature at 83 mm SL (Hulley, 1981) implying that 86 % of individuals consumed by Macaroni penguins were juvenile. About 60 otoliths of juvenile *E. carlsbergi* have also been recorded from the stomach contents of a single Chinstrap penguin *Pygoscelis antarctica* at Bouvet Island (54^{o}S, 03^{o} E) (Cooper, Enticott, Hecht & Klages, 1984). Myctophid fish, predominantly *Krefftichthys anderssoni, Protomyctophum tenisoni* and *Electrona carlsbergi*, are also a major component in the diet of the King penguin *Aptenodytes patagonicus* at Marion Island (Adams & Klages, 1987).

Specimens of adult *Notothenia magellanica, N. squamifrons* and *Dissostichus eleganoides* have all been recorded previously from around Marion Island (Arnaud & Hureau, 1979), but details of their biology, especially the distribution and abundance of juveniles, are largely unrecorded.

Cephalopods

Apart from indirect evidence from the stomachs of various species of seabirds (e.g. Berruti & Harcus, 1978; Imber & Berruti, 1981; La Cock *et al.*, 1984; Schramm, 1986; Brooke & Klages, 1986), information on the distribution and abundance of cephalopods from the waters surrounding the Prince Edward Islands is almost non-existent. *Kondakovia longimana* has in the past been regarded as an Antarctic species (Filipova, 1972), but Adams & Klages (1987) found it to be the most important squid in the diet of the King penguin at Marion Island, although King penguins took much larger individuals than did Macaroni and Rockhopper penguins. *K. longimana* has also been found in the diet of Gentoo penguins at Marion Island (La Cock *et al.*, 1984) and is evidently abundant in the vicinity. Since *K. longimana* spawns at a DML of >500 mm (Clarke, 1980), all individuals consumed by Macaroni and Rockhopper penguins were juveniles.

The octopods recovered from Macaroni and Rockhopper penguins may be *Octopus dolfleini*, a species known to

inhabit the waters around Marion Island (Lu & Mangold, 1978). However, octopus beaks recently recovered from the stomachs of giant petrels *Macronectes* spp. and a crown recovered from an Imperial cormorant *Phalacrocorax atriceps*, at Marion Island (N.T. Klages, pers.comm.) are clearly different from *O. dolfleini*, suggesting that another species may also be present.

Foraging parameters and diet

Both Macaroni and Rockhopper penguins feed in open water and few benthic prey species were evident in their diets. Although both species are generally regarded as offshore foragers (Williams & Siegfried, 1980; Croxall, 1984; Croxall *et al.*, 1985), chick-feeding intervals during the first 30 d or so after hatching are short, increasing from an initial 12 h at hatching to between 36 and 84 h as the chicks get older (Williams, 1982). Foraging range during the first *c.* 30 d increases from as little as 4 km to about 50 km in Rockhopper penguins (Chapter 8), thus accounting for the general absence of pelagic fish and cephalopods in the diet during early chick-rearing. The foraging range of Macaroni penguins is probably similar to Rockhoppers when their chicks are younger than 30 d. On completion of guarding after *c.* 30 d, however, both adults feed the chicks and foraging range in Macaroni penguins at Marion Island is up to 300 km, although about 180 km is probably more normal (Chapter 8). The increased foraging range in Macaroni and,

probably, Rockhopper penguins accounts for the increased incidence of pelagic fish and cephalopods observed in their diets during the middle and latter half of the chick-rearing periods. In the Falkland Islands, Strange (1982) observed a change from pink to purple in the colour of the excreta of Rockhopper penguin chicks at *c.* 20 days of age, reflecting a change in diet from mainly crustaceans to predominantly squid.

The reason for the further change in diet in Rockhopper penguins at Marion Island to almost entirely crustaceans by the end of chick-rearing is not clear. Although chicks at this time are still fed infrequently and at long intervals (Williams, 1982), the absence of fish and cephalopods and the high incidence of relatively undigested crustaceans in food samples collected (pers.obs) suggest that in the absence of the far more numerous Macaroni penguins, which have now completed breeding and left the island on their pre-moult foraging trip (pers.obs), the Rockhoppers may again be feeding relatively close to the island.

Whereas both Macaroni and Rockhopper penguins have the potential to forage up to 300 km from their respective breeding sites at Marion Island (Chapter 8), there is no dietary evidence that either species forages south of the APF since all Antarctic prey recorded are known to be present in the immediate vicinity of Marion Island.

Although the normal diving depths of Macaroni and Rockhopper penguins are not yet known, maximum diving depths of c. 100 m have been recorded for Rockhopper penguins at Marion Island (C.R.Brown, unpubl. data) and most penguin species of similar size are capable of dives to similar depths (Adams & Brown, 1983; Lishman & Croxall, 1983; Wilson & Bain, 1984). Most crustaceans, fish and cephalopods present in the diets of Macaroni and Rockhopper penguins at Marion Island are present in the upper 100 m of the water column (Boden & Parker, 1986), making them readily available to the penguins.

Comparison with other studies

Numerous food samples have been collected from Macaroni and Rockhopper penguins at Marion Island on an opportunistic basis in previous years (FitzPatrick Institute, unpubl. data). Although no quantitative data are available from these samples, several species were identified (Table 7.9). Of these, the euphausiids *Thysanoessa macrura* and *Euphausia lucens* were not found in the present study, but both are common in the vicinity of Marion Island and were the most abundant euphausiids in net hauls in 1982 and 1983 (Boden & Parker, 1986). The myctophid fish *G. nicholsi* may be the species found in small numbers in the present study. It is common in the Southern Ocean in the upper 100 m (Hulley, 1981).

TABLE 7.9

Prey species identified from stomach samples of Macaroni and Rockhopper penguins at Marion Island prior to the present study

Taxa	Macaroni penguin	Rockhopper penguin
Crustaceans		
Nauticaris marionis	---	1982
Thysanoessa vicina	---	1982
T. macrura	1973/74[a]	1973/74[a]
Euphausia lucens	1973/74[a]	1973/74[a], 1982
Themisto gaudichaudii	1982	1982
Fish		
Protomyctophum tenisoni	1981	1982
P. bolini	1981/82	1982
P. normani	1981/82	1982
Krefftichthys anderssoni	1981	1981
Electrona carlsbergi	1981/82	---
Gymnoscopelus nicholsi	---	1983
Gymnoscopelus sp.	1981	---
Cephalopods		
Onychoteuthidae	1982	1982
Octopus sp.	1982	1982

[a] Williams & Laycock (1981)

The known diets of Macaroni and Rockhopper penguins from localities other than Marion Island are summarized in Table 7.10. In general, it appears that Macaroni and Rockhopper penguins feed relatively opportunistically on a wide range of open-water prey species, although inshore, benthic species have been found in the diet at some localities (Duroselle & Tollu, 1977; Horne, 1985; this study). Relative proportions of crustaceans, fish and cephalopods vary considerably between localities and, at Macquarie Island, the diets of Royal penguins were markedly different on the east and west coasts (Horne, 1985). Crustaceans often comprise a large proportion of the diet and are evidently abundant relatively close to the breeding sites at many localities. The more pelagic fish and cephalopods are taken later in chick-rearing at Marion Island, the Falkland Islands and, probably, at Macquarie Island, when the adults forage farther afield, and may form the bulk of the diet at this time. Thus many of the observed differences in the relative proportions of crustaceans, fish and cephalopods in the diets of Macaroni and Rockhopper penguins at different localities may result from the timing of food sampling.

Euphausiids frequently form the major component of the diets of both penguin species (Tables 7.5 & 7.10), with species differences in their composition probably reflecting local distribution and abundance. *Euphausia superba* is the dominant crustacean in the diet of Macaroni penguins at the more southerly breeding localities and is replaced by the

TABLE 7.10

Diets of Macaroni and Rockhopper penguins from localities other than Marion Island. Bold figures represent % mass of each prey type, F indicates % frequency of occurence, N, % numbers and V % by volume. All other figures are % mass, T indicates traces and + indicates species present in unspecified proportions

	Macaroni penguin[a]					Rockhopper penguin[b]					
Taxa Locality --	1	2	3	4a	4b	4	5	6	7	8	9
CRUSTACEANS	75	96	98	27	11	70	45				25
Euphausiacea	75	96	98	26	3	70	45				
Euphausia superba	37	96	98								
E. vallentini				85F	69F	94F	19N	+			
E. lucens							66N				
E. similis					T						
E. triacantha			T								
E. frigida			T								
Thysanoessa gregaria				45F	92F	19F	15N				
T. macrura	38										
T. vicina											
Thysanoessa sp.	+									40V	
Amphipoda				<1	8	<1					
Themisto gaudichaudii			T	50F	60F	T	T		++		
Hyperia galba									+		
H. antarctica					T						
Primno macropa				75F	76F	T					
Other crustaceans											10
FISH	25	4	2	62	54	17	<2	+			10
Myctophidae											
Krefftichthys anderssoni				+	+						
Electrona sp.				+	+						
Notothenidae											
Notothenia magellanica						+					
N. rossii			T								
N. larseni			T								
Other fish											
Harpagifer bispinis				+	+						
Zanchlorhynchus spinifer						+					
Champsocephalus gunnari			T								
CEPHALOPODS				10	35	6	53				50
Teuthowenia sp.							100				
decapods		T						+			+
octopods											+

[a] Includes Royal penguin

[b] Includes Northern rockhopper penguin

Localities and references: 1 Elephant Island, South Shetland Islands (Croxall & Furse, 1980); 2 King George Island, South Shetland Islands (Jablonski, 1985); 3 Bird Island, South Georgia (Croxall & Prince, 1980); 4 Macquarie Island, a = east coast, b = west coast (Horne, 1985); 5 Beauchêne Island, Falkland Islands (Croxall *et al.*, 1985); 6 Falkland Islands (Strange, 1982); 7 Heard Island (Ealey, 1954); 8 Gough Island (Williams & Laycock, 1981); 9 Saint Paul Island (Duroselle & Tollu, 1977).

smaller *E. vallentini* and *E. lucens* farther north. *Thysanoessa macrura* is eaten by both penguin species throughout most of their range, but is replaced to a large extent by the smaller *T. vicina* at the more northerly breeding localities. Amphipods, particularly *Themisto gaudichaudii*, often form an important crustacean component in the diets of Macaroni penguins, but are of little importance to Rockhopper penguins at most localities (Tables 7.5 & 7.10), with the notable exception of Heard Island, which lies south of the APF. Although cephalopods comprise an important component of the diets at some localities, very little is known of the species consumed. The only species identified to date are *Teuthowenia* sp. at Beauchène Island (Croxall *et al.*, 1985) and *Kondakovia longimana* and *Moroteuthis knipovitchi* at Marion Island (this study). Juvenile octopods, which contributed a large proportion of cephalopods consumed by Rockhopper penguins at Marion Island, have otherwise only been reported in the diet of this species at Saint Paul Island (Duroselle & Tollu, 1977).

Species-specific differences in diets at Marion Island

Both Macaroni and Rockhopper penguins at Marion Island feed on crustaceans, fish and cephalopods, although there is a tendency for Macaroni penguins to take more fish and cephalopods than do Rockhopper penguins. Species composition of the prey is broadly similar with certain notable exceptions. Amphipods, in particular *Themisto gaudichaudii*,

were almost totally absent in Rockhopper penguin samples. This is surprising, especially in 1984 when *T. gaudichaudii* comprised over 30 % of crustaceans identified from Macaroni penguin samples. Its distribution, abundance and size make it potentially available to Rockhopper penguins and its absence in their diet at Marion Island and at most other localities is not readily explicable.

Electrona carlsbergi and *E. subaspera* were also absent from the diet of Rockhopper penguins, whereas Macaroni penguins ate *Electrona* between 61 and 95 mm SL. Although individuals at the upper end of this range may be too large for Rockhopper penguins to swallow, *Protomyctophum normani* up to 85 mm were recovered from Rockhopper penguin samples so size alone is unlikely to be the reason. In contrast to fish, size does appear to restrict the size of cephalopods consumed by Rockhopper penguins. Cephalopods are swallowed whole, and Rockhopper penguins do not appear to be able to handle individuals larger than about 70 mm DML, whereas Macaroni penguins are capable of consuming specimens up to about 150 mm DML. Conversely, Rockhopper penguins contained a much larger proportion of small octopods than did Macaroni penguins.

Macaroni penguins begin breeding three to four weeks before Rockhopper penguins at Marion Island and, consequently, chicks hatch earlier (Williams, 1982; pers.obs). Initially, chick-feeding intervals are short and

the birds forage close to the island and feed primarily on crustaceans. By the time Rockhopper penguin chicks hatch and the adults begin foraging for them, Macaroni penguins are foraging farther afield on a diet which includes a proportion of fish and cephalopods. Despite the similarities in the diets of the two species, the difference in the timing of the breeding cycle to a large extent reduces potential competition for food. Nevertheless, there is a period when both species are feeding large chicks at similar intervals on similar diets. Since foraging ranges are probably also similar at this time, dietary segregation of the two species is incomplete.

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Appendix

Regressions relating otolith diameter (OD) to standard length (SL), total length (TL) and mass (M) in fish. Regressions were derived from data from the Port Elizabeth Museum otolith reference collection. Dimensions are in mm and g.

The general relationship relating standard length to total length in myctophid fish was:

$$SL = 0.17 + 0.80\ TL \quad (r^2 = 0.97,\ SD = 0.018)$$

Protomyctophum tenisoni and *P. normani*

$$OD = 0.3 + 0.027\ SL \quad (r^2 = 0.85,\ n = 46)$$

$$M = 1.282 \times 10^{-5}\ TL^{2.868} \quad (r^2 = 0.90,\ n = 28)$$

Krefftichthys anderssoni

$$OD = 0.416 + 0.022\ SL \quad (r^2 = 0.88,\ n = 27)$$

$$M = 5.36 \times 10^{-6}\ TL^{3.080} \quad (r^2 = 0.90,\ n = 16)$$

Electrona carlsbergi and *E. subaspera*

$$OD = 0.254 + 0.042\ SL \quad (r^2 = 0.91,\ n = 90)$$

$$M = 7.43 \times 10^{-6}\ SL^{3.159} \quad (r^2 = 0.90,\ n = 60)$$

Notothenia magellanica (Hecht & Cooper, 1986)

$$TL = 30.96\ OD^{1.801} \quad (r^2 = 0.75,\ n = 82)$$

$$M = 2.19 \times 10^{-5}\ TL^{3.00} \quad (r^2 = 0.99,\ n = 133)$$

The regression relating lower rostral length (LRL) to dorsal mantle length (DML) and mass (M) for *Kondakovia longimana* is:

$$DML = -22.348 + 37.818\ LRL \quad (r^2 = 0.95,\ n = 13)$$

$$M = 0.713\ LRL^{3.152} \quad (r^2 = 0.99,\ n = 22)$$

CHAPTER 8

TRAVELLING SPEED AND FORAGING RANGE OF MACARONI AND ROCKHOPPER PENGUINS AT MARION ISLAND

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SUMMARY

Travelling speeds of breeding Macaroni and Rockhopper Penguins at Marion Island averaged 7.5 and 7.4 km/h, respectively. Macaroni Penguins rearing old chicks and Rockhopper Penguins rearing younger chicks spent 38% and 30% respectively of their time at sea travelling. Foraging ranges were 59 to 303 km for Macaronis during late chick rearing and 4 to 157 km for Rockhoppers during early chick rearing. Diet, chick feeding rates, travelling speed and probably foraging range are very similar for both species, and the principal factor segregating the two species at this time appears to be the three week difference in the onset of breeding.

INTRODUCTION

Penguins are difficult to observe at sea because of their low profiles, and observations of their foraging behaviour are rare. However, the recent development of remote sensing devices has greatly increased our potential for understanding penguin behavior at sea (e.g. Kooyman *et al.* 1971, 1983, Lishman and Croxall 1983, Wilson and Bain 1984a, 1984b). In this study, I investigated the travelling speed and foraging range of breeding Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*) at Marion Island, southern Indian Ocean, using an autoradiographic speed meter (Wilson and Bain 1984b), with the aim of determining any species specific differences.

An estimated 405,000 pairs of Macaroni and 93,000 pairs of Rockhopper Penguins breed sympatrically at Marion Island (Williams *et al.* 1979, Watkins, in press). There is considerable overlap in their breeding periods and, especially, in their chick rearing. Feeding rates of chicks (Williams 1982) and the diets fed to chicks (Williams and Laycock 1981, Horne 1985, Chapter 7) are broadly similar. Williams (1982) suggested, however, that potential interspecific competition for food could be reduced during chick rearing by differences in type or size of prey, foraging depth, or speed at which the parents travel. Travelling speed in part determines foraging range, which

for both species at Marion Island has been estimated to be about 95 km (Williams and Siegfried 1980). At South Georgia, the potential foraging range of Macaroni Penguins has been estimated to be up to 115 km, although the birds may in fact forage on the edge of the continental shelf only 50 km away (Croxall and Prince 1980). These figures are generally based on estimated travelling speed and time spent away from the nest between chick feedings. Travelling speeds reported for penguins in general range from 7 to 12 km/h (Kooyman 1975, Clark and Bemis 1979). More specifically, Macaroni and Rockhopper Penguins reportedly swim at 8.2 and 7.8 km/h respectively (Clark and Bemis 1979). These are maximum speeds measured for penguins swimming in a tank and may not represent speeds attained at sea. Furthermore, it is now apparent that penguins do not swim all the time they are at sea and neither do they necessarily swim a straight course. The ratio of time spent swimming to time at sea in Gentoo (*Pygoscelis papua*), Chinstrap (*P.antarctica*) and Adélie Penguins (*P.adeliae*) is highly variable (Wilson *et al.* 1986, Adams and Wilson, 1987). Consequently, large overestimates may occur when estimating foraging range from chick feeding rates if the parents are assumed to be travelling for the entire time they are away from the nest.

METHODS

The study was carried out at Marion Island (46°52'S, 37°51'E) between 7 January and 24 February 1985. A colony of

Rockhopper Penguins breeds near the research station and a small colony of Macaroni Penguins breeds about 1 km away. Both species were rearing chicks during the course of the study. Ages of Rockhopper chicks ranged from about 7 to 30 d, whereas Macaroni chicks ranged from 26 to 62 d.

Twenty-six speed meters (Wilson and Bain 1984b) were attached to Rockhoppers and 16 to Macaronis. Each meter consisted of a spring-mounted, polyurethane bung enclosed in a tube. A radioactive, phosphorus-32 bead was inserted into the bung and a sachet of X-ray sensitive film was taped to the outside of the tube (see Wilson and Bain 1984b for illustrations and operation details). In contrast to Wilson and Bain (1984b), who attached their devices to the front of their penguins using harnesses, the devices in the present study were attached with hose-clamps to the feathers on the dorsal midline of the penguins. The mass of each device in air was about 2.5 g.

Penguins were caught at their respective colonies, weighed, and, after attachment of meters, were released. The Rockhopper colony was checked frequently each day for metered birds departing and returning: the Macaroni colony was checked once or twice daily. When next observed, birds with meters were recaptured, weighed, and the meters removed. Because of low isotope activity in some beads and the short feeding interval of Rockhopper Penguins during early chick rearing, some birds were allowed to make two or

more foraging trips before recapture to ensure sufficient film exposure time.

The film (Kodak Direct Exposure Film) was processed for 3 min at 24°C in Kodak GBX developer and fixed for 3 min in Kodak GBX fixer. Optical density of the developed film was measured with a transmission densitometer. Traces typically showed two discrete blackened patches corresponding to the travelling speed and the zero position when the bung was stationary. The travelling speed and total distance travelled were calculated from the traces (see Wilson and Bain 1984b). Wilson *et al.* (1986) report that devices attached to free-ranging Jackass Penguins (*Spheniscus demersus*) affect travelling speed. The magnitude of the effect was related to the cross-sectional area of the device as a percentage of penguin cross-sectional area. Meters attached to Macaroni and Rockhopper Penguins had cross-sectional areas less than 2.0% that of the birds, and the reduction in travelling speed was estimated to be less than 5%.

Foraging range was estimated from total distance travelled and number of foraging trips made between release and recapture. A number of assumptions was necessary. For Rockhopper Penguins, when devices were left on for more than one foraging trip, the birds were assumed to have travelled the same distance on each trip. If the durations of two or more foraging trips differed, distance travelled was assumed

to be proportional to duration of each trip (i.e. if a bird made one 12 h trip followed by one of 36 h before recapture, that bird travelled three times farther during the longer trip than the shorter one). Because visits to the Macaroni colony were less frequent and adults did not remain long at the colony when feeding older chicks (pers obs.), the birds usually completed several foraging trips before recapture. The number of foraging trips made was estimated from the approximate age of chicks in the colony and the known feeding frequency of chicks of this age (Williams 1982). The birds were assumed to have travelled the same distance each trip and in all cases were assumed to have travelled directly to and from the feeding grounds on a constant heading. Consequently, foraging range was overestimated.

RESULTS AND DISCUSSION

Thirteen of 16 devices on Macaroni Penguins and 19 of 26 on Rockhopper Penguins were recovered, but only five films from Macaroni and seven from Rockhopper Penguins had useable traces. Water or light leaks in the sachets were the major cause of ruined traces, and some films showed no traces because the bung twisted about its axis as the spring was compressed so that the radio-isotope no longer exposed the film.

Three meters from Macaroni Penguins were recovered 9 to 16 d after deployment, whereas all those from Rockhopper

Penguins were recovered within seven days. A further two devices were recovered from Macaroni Penguins 53 days after release and included the pre-moult foraging trip which lasts between four and five weeks. Results obtained from the developed traces from Macaroni and Rockhopper Penguins are presented in Tables 8.1 and 8.2, respectively.

Travelling speed.--The mean ($\pm$ 1 S.D.) measured travelling speed of Macaroni Penguins was 7.5 $\pm$ 0.5 km/h (range 7.0 - 8.2 km/h) and that of Rockhopper Penguins was 7.4 $\pm$ 0.5 km/h (range 6.9 - 8.1 km/h), both within the range recorded for several other penguin species (Kooyman 1975, Clark and Bemis 1979, Wilson and Bain 1984b, Adams and Wilson, 1987). The travelling speeds obtained from free-ranging Macaroni and Rockhopper Penguins in the present study are only slightly lower than the maximum speeds measured by Clark and Bemis (1979) and, presumably, represent the most economical speeds.

There was no perceptible variation in individual travelling speed, each bird showing typically only one discrete travelling trace even when devices were carried for several foraging trips and, in the case of two Macaroni Penguins, for the extended pre-moult foraging trip. Adams (1987) and Adams and Wilson (1987) observed the same for King Penguins (*Aptenodytes patagonicus*) and Gentoo Penguins and concluded that they forage solitarily since, if birds foraged in groups, travelling speed would have to vary to

Table 8.1. Time spent travelling, travelling speed, distance travelled and estimated foraging ranges of Macaroni Penguins.

Meter #		Time at sea (h)[a]	Time spent travelling (h)	% time spent travelling	Speed km/h	Total distance travelled (km)	No. foraging trips	Estimated foraging range (km)
VM99		218.0	47.2	21.7	7.5	354	3	59
VM10		310.0	242.0	78.0	7.5	1,815	3	303
VM78		386.3	125.0	32.4	8.2	1,025	3	171
VM72	1	269.0	306.0	24.1	7.0	2,142	2 + PM	180; 711[b]
VM57	1	269.0	428.0	33.7	7.2	3,082	2 + PM	180; 1,180[b]

[a] Assuming time spent ashore feeding chicks is negligable in relation to time spent at sea.

[b] Assuming an average foraging range of about 180 km, calculated from the three foraging ranges estimated above.

PM = Pre-moult foraging trip.

Table 8.2. Time spent travelling, travelling speed, distance travelled and estimated foraging ranges of Rockhopper Penguins

Meter #	Time at[a] sea (h)	Time spent travelling (h)	% time spent travelling	Speed km/h	Total distance travelled (km)	No. & duration of foraging trips	Estimated foraging range (km)
VM87	15.0	0.9	6.0	7.6	7.1	1	3.5
VM30	43.0	6.5	15.1	7.2	46.8	3x12h	7.8
VM87	40.0	18.0	45.0	7.8	140.4	3x12h	23.4
VM29	53.9	15.1	28.2	6.9	104.2	1x12h 1x36h	17.4; 34.8
VM48	54.5	17.1	31.4	7.0	119.7	2x12h 1x24h	15.0; 30.0
VM87	70.5	16.6	23.6	8.1	134.5	1x12h 1x36h	16.8, 50.4
VM57	148.0	88.2	59.6	7.1	626.2	2	156.6

[a] Estimated from observations of the approximate arrival and departure times of the birds at the colony.

maintain group cohesion. Macaroni and Rockhopper Penguins both leave and return to their colonies in groups (pers. obs.), but these may only be maintained while they pass through the inshore area where predators, in particular Killer Whales (*Orcinus orca*), are likely to be encountered. Individuals of both species, returning ashore in conspecific groups, frequently have totally different food in their stomachs (pers. obs.), further suggesting that they forage individually.

Time spent travelling.-- Macaroni and Rockhopper Penguins feeding older chicks spend little time ashore. Consequently, the time between release and recapture of the Macaronis was a reasonable estimate of the time spent at sea. The amount of time Rockhoppers spent at sea was estimated from their presence at the colony during the frequent checks for returning birds. Macaroni Penguins spent 38.0 $\pm$ 23.0% of their estimated time at sea swimming at speed, whereas Rockhopper Penguins spent 29.8 $\pm$ 18.0%. The difference is not significant ($P > 0.5$).

The amount of time at sea spent travelling, calculated from the density of the travelling trace, included time spent commuting to and from the feeding area plus time spent feeding underwater, but did not include time spent swimming on the surface or porpoising, when the meters are out of the water and not recording. However, Adélie Penguins spend less than 6% of their total swimming time porpoising (Wilson *et*

al., in press), and penguins probably travel only short distances by surface swimming (Adams and Wilson 1987, Trivelpiece *et al.* 1986), so errors in time spent travelling and, consequently, in distance travelled are probably small.

Rockhopper chicks during the present study were seven to 30 d old. Chicks of this age are fed only by the females and are guarded by the males (Warham 1963). The feeding interval is short, usually less than 36 h in the first two weeks and less than 60 h for chicks between 16 and 30 d of age (Williams 1982). Females spend the night ashore and forage during the day, usually leaving just before first light (about 04:00) and returning in the late afternoon or soon after dark at about 19:00 (pers. obs.). Macaroni chicks during the study were older than Rockhopper chicks and were fed at longer intervals by both parents. Consequently, the breeding adult Macaroni Penguins spent more time at sea, foraged farther afield and spent a relatively greater proportion of their time travelling than did Rockhopper Penguins. Similarly, King Penguins feeding large chicks spend about 36% of their time at sea travelling, whereas those with small chicks requiring brooding spend only 19% of their time at sea travelling (Adams 1987). Gentoo Penguins, which are diurnal foragers that usually return ashore each evening, spend about 19% of their time at sea swimming and feeding (Adams and Wilson 1987).

Foraging range.-- Estimated foraging ranges of Macaroni Penguins feeding chicks vary between 59 and 303 km (Table 8.1), although the latter estimate was from a bird which spent an unusually large proportion of its time swimming. Rockhopper Penguins ranged from about 4 to 157 km away (Table 8.2). Since the travelling speeds and chick feeding rates of the two species are almost identical, it seems likely that Rockhoppers forage at distances similar to Macaroni Penguins later in the season when the chicks are older. Indirect evidence for this comes both from the species composition of the Rockhopper Penguins' diet, which becomes increasingly similar to that of Macaroni Penguins later in the season, as well as from the increasing degree of digestion of the stomach contents as the season progresses (Chapter 7). Similarly, Macaroni Penguins almost certainly forage closer to shore when their chicks are small and the feeding interval shorter. Stomach contents of Macaroni Penguins are less well digested with many intact prey items during early chick rearing (pers obs.).

The relatively short foraging range of 95 km estimated by Williams and Siegfried (1980) is explained by their underestimate (4.5 km/h) of travelling speed. Croxall and Prince (1980) estimated a potential foraging range of 115 km for Macaronis at South Georgia but this was based on a chick feeding rate of once every two days, more typically associated with younger chicks (Williams 1982).

Two Macaroni Penguins made pre-moult foraging trips before being recaptured. These birds covered 2,142 and 3,082 km respectively in a period of 53 days. Both were estimated to have made two foraging trips before their pre-moult trip and these were assumed to have averaged 180 km in range (Table 8.1). Consequently, the estimated distances covered during the pre-moult trips were 1,422 and 2,362 km, with potential maximum ranges from their colony of 711 and 1,181 km, respectively.

Weight changes.-- Four of five recaptured Macaroni Penguins lost weight while at sea, the maximum weight loss being 850 g over a period of 16 days. One bird gained 1,200 g over a 13-day period. Mean weight change was -20 g. Ten Rockhopper Penguins lost and seven gained weight during foraging trips. The mean weight change was -111 g. Maximum weight lost was 520 g and maximum weight gained 260 g. Five of the Rockhoppers that lost weight were observed feeding chicks, and had obviously been foraging. Since adult penguins are capable of undergoing prolonged fasts, it may be that they do not always feed for themselves but may collect food only for their chicks during some foraging trips, as suggested by Adams (1987).

Both Macaroni and Rockhopper Penguins feed predominantly on euphausiids and juvenile shrimp *Nauticaris marionis* (Chapter 7). These are abundant in the immediate vicinity of Marion Island (Boden and Parker 1986). A Rockhopper Penguin

that had travelled less than 8 km from its colony was observed feeding crustaceans to its chick and also had several crustaceans caught in the hose clamps attaching the meter to its feathers. Fish species found in the diets of Macaroni and Rockhopper Penguins were all oceanic myctophids with a broad sub-Antarctic and Antarctic distribution, as is true of the cephalopods consumed (Chapter 7).

Macaroni and Rockhopper Penguins have broadly similar diets and very similar chick feeding rates, travelling speeds and probably foraging ranges. There is, as yet, no information on the depths to which they can dive, but several penguins of similar size appear to have similar diving capabilities (Adams and Brown 1983, Lishman and Croxall 1983, Wilson and Bain 1984a). Furthermore, the similarity of the prey of Macaroni and Rockhopper Penguins make it unlikely that they forage at different depths.

The principal factor segregating the two species appears to be the timing of the breeding cycle. Macaronis begin breeding three to four weeks before Rockhoppers and, consequently, chicks hatch earlier. Initially, Macaroni Penguins feed their chicks almost entirely crustaceans. The feeding intervals are short and the birds probably feed relatively close to their breeding sites. As the chicks age they are fed less frequently and the diet includes a large proportion of pelagic fish and cephalopods with relatively few crustaceans. Consequently, at a time when the Rockhopper

chicks are hatching and are being fed frequent meals of crustaceans, the Macaroni Penguins are foraging farther afield on slightly different prey. Nevertheless, there is a period of several weeks when both species are feeding large chicks at similar intervals on similar diets. As there is probably an overlap in foraging range during this period, segregation of the two species is incomplete.

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CHAPTER 9

ENERGY REQUIREMENTS AND FOOD CONSUMPTION OF MACARONI AND ROCKHOPPER PENGUINS AT THE PRINCE EDWARD ISLANDS

ABSTRACT

Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*) account for a substantial proportion of the avian biomass at sub-Antarctic Marion Island in summer, when both species are breeding at the island. Information on breeding population sizes and breeding and moulting activities were combined with measurements of the penguins' energy requirements and diets, to construct a bioenergetic model of their energy requirements and food consumption at Marion and Prince Edward islands. Total energy requirements of adults and chicks amounted to 460 X 10^9 kJ and 80 X 10^9 kJ for Macaroni and Rockhopper Penguins, respectively. Food consumption was estimated to amount to 145 000 tonnes during the seven-month breeding and moulting cycle, of which Macaroni Penguins consumed 87 %. Most, if not all, of this food is taken within a 200-km radius of the islands. Available information suggests that potential primary production in the immediate vicinity of the islands is sufficient to support the Macaroni and Rockhopper Penguin populations. However, the importance of several more typically Antarctic and sub-tropical prey species in the diets of Macaroni and Rockhopper Penguins at the Prince Edward Islands suggests that the penguins rely to a large extent on the importation of prey populations from other areas.

INTRODUCTION

Seabirds play important roles in the functioning of marine ecosystems where they frequently constitute a major class of predator (Croxall 1987). As a result of this, several bioenergetic models have been constructed for seabird assemblages (e.g. Wiens and Scott 1975, Furness 1978, Furness and Cooper 1982, Pettit *et al.* 1984, Briggs and Chu 1987). Such quantitative assessments of energy and food requirements of seabirds are of interest because they provide information on energy flow through marine ecosystems (e.g. Wiens and Scott 1975), and allow assessment of the demands of seabirds on marine resources, of particular interest where these may conflict with commercially exploitable, or potentially exploitable, prey stocks (e.g. Furness 1978, 1981, Furness and Cooper 1982).

Bioenergetic models usually integrate counts, or estimates, of population sizes with estimates of individual metabolism. Basic information required includes population sizes, diet, activity budgets and energy requirements of the species concerned (Wiens 1984). A fundamental problem associated with modelling seabird energy requirements is that of estimating energetic costs associated with various activities. To date, most models have assessed existence metabolism (EM) from allometric equations and have subsequently assigned multiples of EM to other activities.

However, estimates of population energy requirements are especially sensitive to the use of these equations and generate results with 95 % confidence intervals of up to 50 % of the mean (Furness 1978), although the use of more recent, improved equations (Kendeigh *et al.* 1977) has reduced this to 30 % (Furness 1981). Despite evidence that Kendeigh's equations result in large imprecisions in estimates of population energy requirements, they continue to be used in modelling seabird energetics, usually because of lack of empirical data on individual energy expenditures of seabirds. Furthermore, for reasons discussed by Croxall *et al.* (1984), most estimates of seabird energy and food requirements to date have focused on northern hemisphere, or low-latitude southern hemisphere, seabirds and few assessments have been made for Antarctic and sub-Antarctic seabird communities.

Mougin and Prevost (1980) made crude estimates of seabird consumption for the whole Antarctic and sub-Antarctic region. Although based on the early Kendeigh (1970) equations and, in some instances, inappropriate methods, their results nevertheless emphasize the pre-eminent role of penguins in the region. A reassessment of data by Croxall (1984) suggests that, in terms of biomass and food consumption, 80 % of the birds in the sub-Antarctic can be considered to be penguins and of these 50 % are Macaroni Penguins (*Eudyptes chrysolophus*). More recently, Croxall and Prince (1982) and Croxall *et al.* (1984) assessed the impact

of seabirds on marine resources in the vicinity of South Georgia (54°00'S, 37°00'W) and later extended this to include the Scotia Sea (Croxall *et al.* 1985). Although these studies also based existence metabolism of the birds on the equations of Kendeigh *et al.* (1977), a significant departure from most models of seabird energetics was the use of empirical data for energetic requirements of the birds during incubation and moult (based on mass loss data during the fasts), for penguins swimming at sea (based on isotope dilution rates), and for chick-rearing (from meal sizes and feeding frequency).

Preceding chapters in this thesis have considered aspects of the energetic requirements of Macaroni Penguins and Rockhopper Penguins (*E. chrysocome*) at Marion Island during their breeding and moulting cycles, including measurements of their resting metabolic rates and energy expenditures during incubation and moult (from measurements of oxygen consumption) and energy requirements for growth and maintenance of chicks (from measurements of oxygen consumption and body composition). In this chapter, results from the preceding chapters are combined with information on the penguins' population sizes, activity patterns and diets to construct a bioenergetic model of the timing and magnitude of the food requirements of Macaroni and Rockhopper Penguins around Marion Island (46°52'S, 37°51'E). Total energy and food requirements of the two species during

their 6 to 7-month breeding cycle at the Prince Edward Islands are estimated from the model.

METHODS AND DATA BASE

Breeding cycle

Macaroni and Rockhopper Penguins are absent from their breeding grounds at the Prince Edward Islands for about five months of the year. Although their whereabouts during the winter months is unknown, at least two groups of Rockhopper Penguins were observed 400 nautical miles (740 km) WNW of the Prince Edward Islands in September 1979, about two months before their normal arrival at the islands to breed (Enticott 1986). There have been no reported sightings of Macaroni Penguins in the Prince Edward sector of the Southern Ocean outside the breeding period, but a number of records of moulting individuals of both species on the southern African coast indicates that they are capable of long-distance dispersal (see Cooper 1987 and references therein). Consequently, the birds are assumed to be dispersed away from the islands outside their breeding seasons.

The breeding cycles (here taken to include the post-breeding moult) of Macaroni and Rockhopper Penguins at the Prince Edward Islands have not been well documented. However, those of Royal Penguins (*Eudyptes chrysolophus*

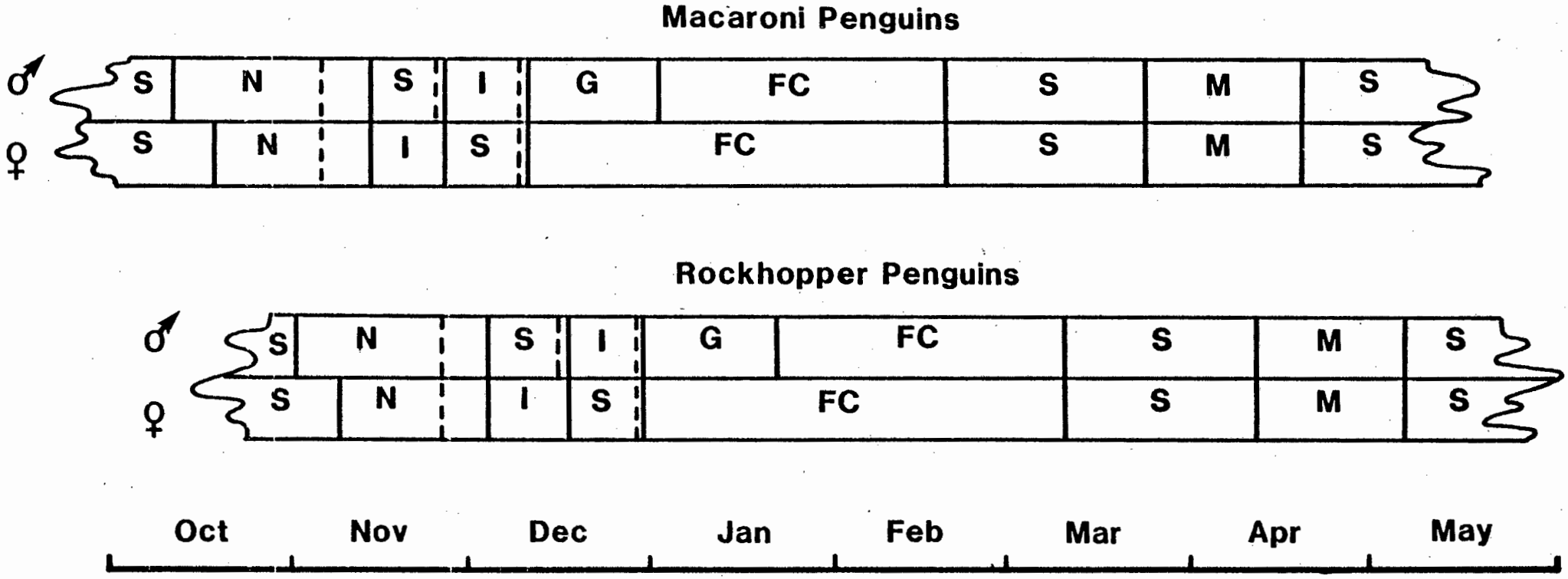
schlegeli) and Rockhopper Penguins at Macquarie Island (54° 30'S, 159°00'E) have been described in detail by Warham (1963, 1971) and are, presumably, similar to those at the Prince Edward Islands. The breeding cycles of the two species are similar, although Macaroni Penguins begin breeding earlier than do Rockhopper Penguins. However, the activity patterns of the sexes differ during at least a part of the breeding cycle. The activity patterns of each sex during the breeding cycles, based on Warham (1963, 1971) and using the timing of breeding events at Marion Island from unpublished reports of the FitzPatrick Institute and personal observation, are presented in Figure 9.1.

Population sizes

Population numbers (breeding pairs) of Macaroni Penguins at Marion Island, based on a census conducted in 1983, were obtained from Watkins (in press). The number of breeding Rockhopper Penguins at Marion Island, and breeding Macaroni and Rockhopper Penguins at Prince Edward Island, were based on earlier estimates (Siegfried *et al.* 1978).

The number of pairs breeding, from incubation until chicks fledged, was calculated on a weekly basis from mortality data of eggs during incubation and of chicks during brooding and guarding and subsequently until fledging (Williams 1980). Rates of mortality from week to week during each stage were assumed to be linear and failed breeders

Figure 9.1. Approximate breeding and moulting schedules of Macaroni and Rockhopper Penguins at Marion Island. Based on data from Warham (1963, 1971), FitzPatrick Institute (unpubl. data) and personal observation. N = pre-laying nest and courtship activities, S = at sea, I = incubation, G = brooding and guarding chicks, FC = feeding chicks, and M = moulting.


Macaroni Penguins
♂
S
N
S
I
G
FC
S
M
S
♀
S
N
I
S
FC
S
M
S
Rockhopper Penguins
♂
S
N
S
I
G
FC
S
M
S
♀
S
N
I
S
FC
S
M
S
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May

were assumed to remain at sea feeding in the vicinity of the islands and to return ashore to moult with successful breeders. For simplicity, it was assumed that all activities of breeding birds were synchronous (i.e. all birds of each sex were involved in the same activity at the same time).

Energetic costs

Males of both Macaroni and Rockhopper Penguins have a slightly greater lean body mass than do females. However, where testable, metabolic rates of the two sexes were not significantly different so slight weight differences between the sexes were ignored. Body mass of both sexes varies considerably during the breeding season as a result of periods of fasting (c.f. Richdale 1947). The effects of differences in body mass on energy expenditures during different breeding activities were taken into account during measurement of energy expenditure.

Daily energetic costs of breeding activities were, with the exception of at-sea and brooding costs, calculated from data presented in preceding chapters. Energy expenditure of adults during pre-laying activities at the nest were considered to be equivalent to average daily metabolic rates, about 15 % higher than measured resting levels and 25 % higher than predicted basal metabolic rate (Chapter 1).

The energetic cost of forming the two eggs was not measured. However, Grau (1982) estimated that peak energy

requirements for egg formation in the Fjordland-crested Penguin (*E. pachyrhynchus*) amounted to about 27 kcal day^{-1} (113 kJ day^{-1}). Based on Grau's estimate and the size of Macaroni and Rockhopper Penguin eggs, peak energy costs of egg formation in Macaroni and Rockhopper Penguins were estimated to amount to 126 and 92 kJ day^{-1}, respectively, less than 10 % of their daily energy expenditure during pre-laying activities. Consequently, the cost of egg formation was regarded as negligible and was not taken into account when calculating energy requirements.

Energetic costs of incubation were taken from rates of energy expenditure measured over 24 h during incubation (Chapter 2).

Energy expenditures of five species of penguins, while feeding at sea, have been measured using dilution rates of either tritium (Kooyman *et al.* 1982, Davis *et al.* 1983) or doubly-labelled water (Nagy *et al.* 1984, Costa *et al.* 1986). Log energy expenditure of birds in the above studies was plotted against log body mass, and energy expenditure of Macaroni and Rockhopper Penguins at sea were estimated from the resulting regression equation using a lean body mass of 4 800 g for Macaroni Penguins and 2 500 g for Rockhopper Penguins. Estimated energy expenditures were 2 764 and 1 405 kJ day^{-1} for Macaroni and Rockhopper Penguins, respectively. These values integrate time spent swimming (between 30 and 40 % of their time at sea in Macaroni and Rockhopper

Penguins; Chapter 8), time spent resting on the water and, in some instances, time spent ashore feeding chicks.

During the first three weeks of chick-rearing, males remain at the nest brooding and guarding the chicks. Energy expenditure during this period has been measured for Macaroni Penguins by Davis *et al.* (1983) using dilution rates of tritiated water. Energy expenditure of Rockhopper Penguins was calculated from this on a mass-specific basis. During the guard period, chicks are fed by the females who spend about two-thirds of their time at sea foraging and one-third (usually at night) at the nest (Chapter 8). Daily energy requirements of females during this period were calculated from their at-sea and at-nest energy expenditures using the above proportions.

Penguins undergo a rapid moult lasting, in the case of Macaroni and Rockhopper Penguins, about four weeks, of which about 25 d is spent ashore fasting (Chapter 4). Energy expenditure during this period comprises maintenance energy expenditure, cost of new feather synthesis and cost of thermoregulation during a period of reduced feather insulation. Average energy expenditure during moult was assessed in Chapter 3.

Energetic cost of chick-rearing comprises the cost of the adults at sea (assuming that time spent ashore feeding chicks after initial brooding is negligible) plus the cost of growth and maintenance of surviving chicks. Energetic

cost of the latter was calculated from energy budgets presented in Chapter 6.

Food requirements

Diets of Macaroni and Rockhopper Penguins were studied quantitatively over two successive chick-rearing periods (Chapter 7). Energy content of crustaceans and cephalopods in the diet, measured by bomb calorimetry, averaged 4.68 and 3.25 kJ g^{-1} wet mass, respectively (C.R. Brown, unpublished data). Energy content of fish in the diet was not measured and a value of 3.97 kJ g^{-1} wet mass (Clarke and Prince 1980) was used. Mean energy content of the diet was calculated from the energy content of each prey type and its proportional representation in the diet based on the reconstituted biomass from 1985 samples. These were 62 % crustaceans, 25 % fish and 13 % cephalopods for Macaroni Penguins and 81 % crustaceans, 14 % fish and 5 % cephalopods for Rockhopper Penguins (Chapter 7).

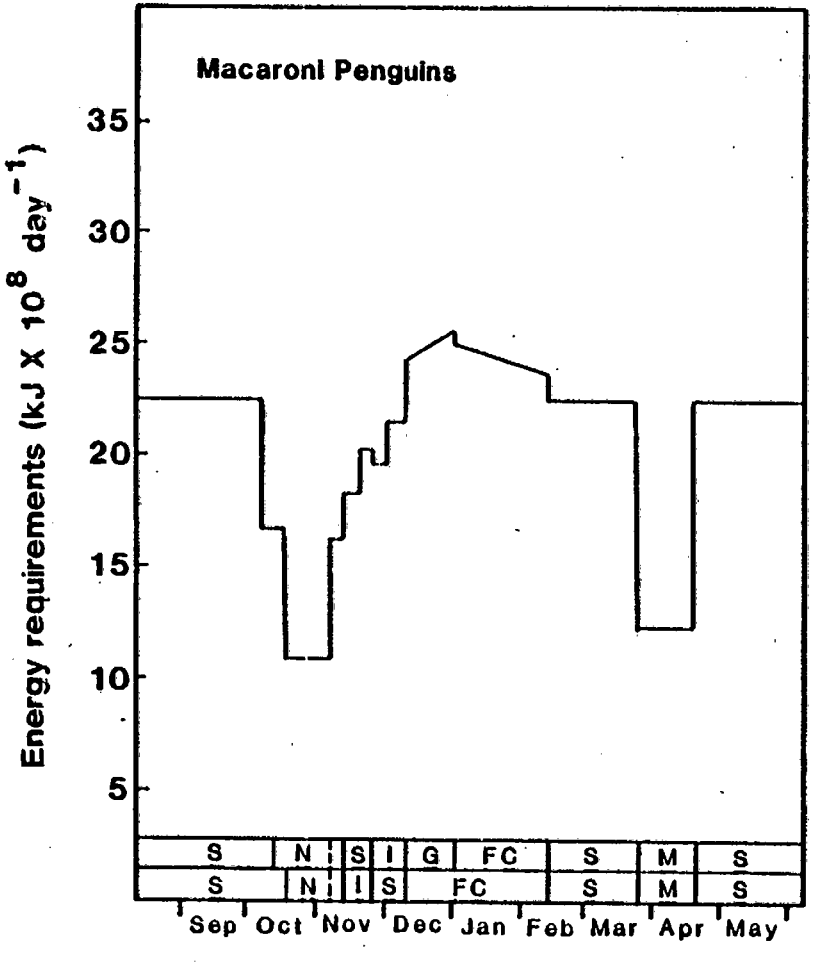
Measured assimilation efficiencies of penguins are 74 % for Jackass Penguins (*Spheniscus demersus*) fed on fish (Cooper 1977) and 81 % for King Penguins (*Aptenodytes patagonicus*) fed on squid (Adams 1984). Whitechinned Petrels (*Procellaria aequinoctialis*) fed on crustaceans, fish and squid had assimilation efficiencies averaging 76 % (Jackson 1986). Consequently, an assimilation efficiency of 76 % was used for Macaroni and Rockhopper Penguins.

Macaroni and Rockhopper Penguins undergo fasts during the breeding season, notably during incubation, brooding and moulting. Energy reserves (lipid and protein) to sustain them through the fast must be accumulated in the period at sea prior to the fast and are in addition to normal at-sea maintenance and activity energy requirements. Synthesis of energy reserves may require an energy intake equivalent to 1.2 - 2.1 times that available to the birds through oxidation of the reserves (Kendeigh *et al.* 1977). For present purposes, production efficiency of energy storage was assumed to be 75 % (Ricklefs 1974). Consequently, daily food requirements prior to fasts were calculated as normal maintenance and activity requirements while at sea, plus total energy requirements for the fasting activity, multiplied by the reciprocal of production efficiency (1.33) and divided by the number of days spent at sea before the fast. This correction was not applied to food requirements prior to the pre-laying fast because it was assumed that energy reserves for this period were accumulated before the birds' arrival in the immediate vicinity of the islands.

RESULTS AND DISCUSSION

Daily energy requirements of Macaroni and Rockhopper Penguins during their respective breeding seasons at Marion Island are illustrated in Figure 9.2. Peak energy demands occur during chick-rearing when all breeding adults are at

Figure 9.2. Seasonal changes in energy requirements of Macaroni and Rockhopper Penguins at Marion Island. Conventions for breeding schedule as for figure 9.1.


Macaroni Penguins
Energy requirements (kJ X 10^8 day^{-1})
35
30
25
20
15
10
5
S
N
S
I
G
FC
S
M
S
S
N
I
S
FC
S
M
S
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May

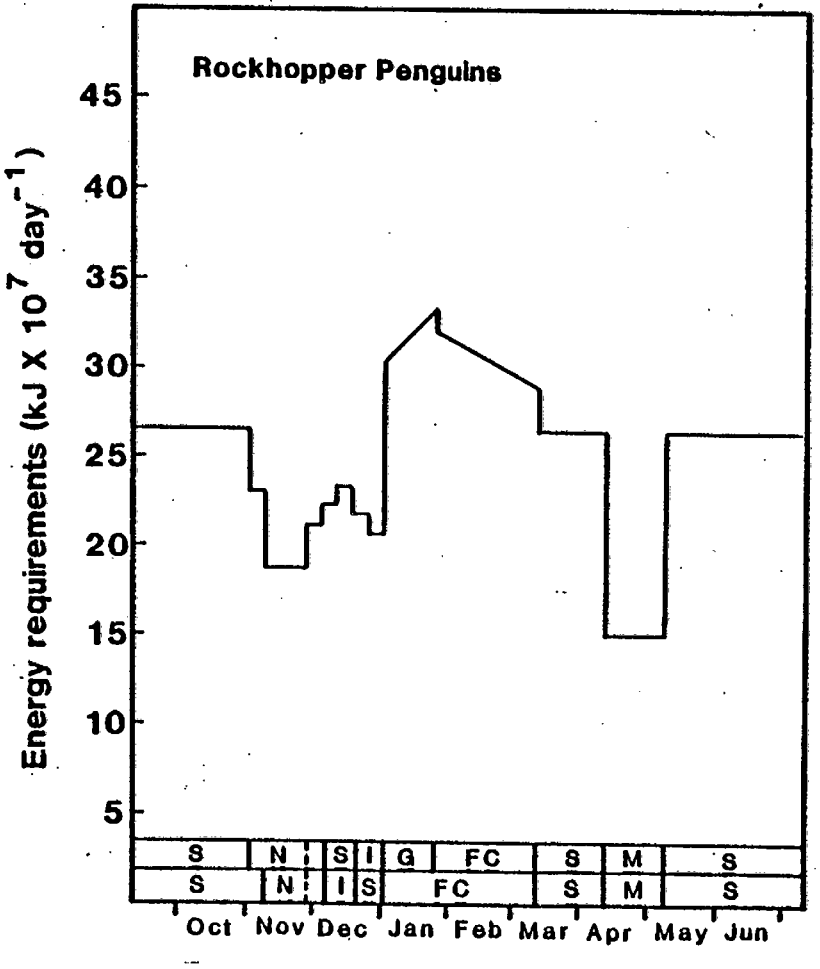
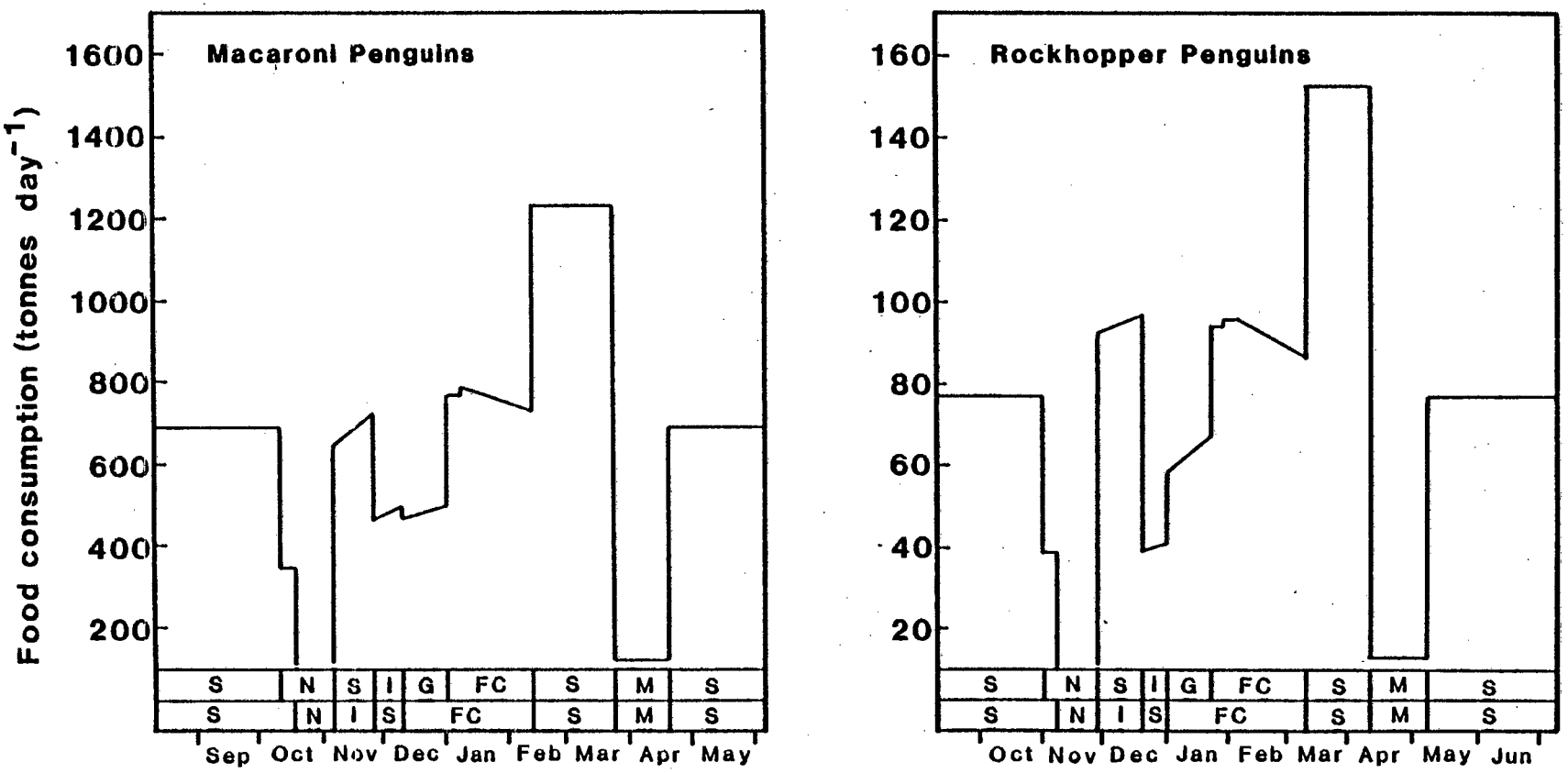

Rockhopper Penguins
Energy requirements (kJ X 10^7 day^{-1})
45
40
35
30
25
20
15
10
5
S
N
S
I
G
FC
S
M
S
S
N
I
S
FC
S
M
S
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun

TABLE 9.1. Energy requirements (kJ X 10^9) of breeding Macaroni and Rockhopper Penguins at the Prince Edward Islands during the breeding and moulting seasons.

	Males	Females	Failed breeders	Chicks	Total
Macaroni Penguins					
Marion Island	138.1	141.4	125.2	29.0	433.7
Prince Edward Island	5.8	5.9	5.3	9.3	26.3
Rockhopper Penguins					
Marion Island	19.2	19.3	14.0	5.5	58.0
Prince Edward Island	7.2	7.2	5.3	2.5	22.2
Grand total					540.2

Figure 9.3. Seasonal changes in food consumption of Macaroni and Rockhopper Penguins at Marion Island. Conventions for breeding schedule as for Figure 9.1.


Macaroni Penguins
Food consumption (tonnes day^{-1})
1600
1400
1200
1000
800
600
400
200
S N S I G FC S M S
S N I S FC S M S
Sep Oct Nov Dec Jan Feb Mar Apr May
Rockhopper Penguins
160
140
120
100
80
60
40
20
S N S I G FC S M S
S N I S FC S M S
Oct Nov Dec Jan Feb Mar Apr May Jun

both species, 93 700 tonnes comprised crustaceans, 34 050 tonnes fish and 17 250 tonnes cephalopods. Most, if not all, this food is removed from within a 300 km, and probably closer to 200 km, radius of the islands (see Chapter 8). In contrast to energy requirements, food consumption was highest during the pre-moult foraging trip when the entire breeding population and their surviving, newly fledged chicks were assumed to be at sea. In addition to normal at-sea food requirements, breeding adults were also laying down energy reserves to sustain them for their four-week moult fast ashore. Although pre-moulting birds may travel considerable distances during this period (see Chapter 8), there is no evidence to suggest that they travel outside their normal foraging ranges so their food demand is assumed to be met by prey stocks in the vicinity of the islands.

Potential primary production in the immediate vicinity of the Prince Edward islands ranges from about 140 mg C m^{-2} d^{-1} to as much as 4 200 mg C m^{-2} d^{-1} (Mitchel-Innes 1967, El-Sayed *et al.* 1979, Parker 1984, Allanson *et al.* 1985, D.G.M. Miller, pers. comm.). Assuming 0.4 g C g^{-1} dry weight of prey (Curl 1962), Macaroni and Rockhopper Penguins feeding within 200 km of the islands require an estimated 0.5 mg C m^{-2} d^{-1} (0.4 % of the primary production) during their seven-month breeding and moulting cycles, and King Penguins probably require as much again during this period.

Penguins feed at the third and fourth trophic level. Assuming a 10 % efficiency of trophic transfer, a potential 1.5 - 46.0 mg C m^{-2} d^{-1} of primary and secondary carnivores (crustaceans, fish and cephalopods) would be produced. However, primary production at the Prince Edward islands has only been measured during austral spring and autumn, when phytoplankton production levels are generally high. Furthermore, all measurements were made within about 50 km of the islands where primary production is enhanced by an island mass effect (Allanson *et al.* 1985), the influence of which is unlikely to extend to ranges at which the penguins forage when food requirements are highest. Nevertheless, even the lowest estimate of primary production suggests that there is potentially sufficient food in the vicinity of the islands to support the large breeding populations of breeding Macaroni and Rockhopper Penguins, and probably King Penguins as well, although pre- and non-breeders have not been taken into account. However, net-hauls in the vicinity of the Prince Edward islands frequently contain several species of crustaceans more typical of sub-tropical and Antarctic waters than of sub-Antarctic waters. The presence of these is thought to occur through advection and eddying of foreign water masses past the islands (Boden and Parker 1986). Despite the apparent high productivity in the vicinity of the islands, the importance of sub-tropical and Antarctic prey species in the diets of Macaroni and Rockhopper Penguins suggests that these birds rely, to a

large extent, on importation of prey-stocks from other areas. Apart from qualitative data from net hauls, little information is available on the abundance, distribution and movements of these important prey species in the vicinity of the Prince Edward Islands and quantitative data should be considered a priority for future marine-orientated research in the area.

Despite refinements, the model still suffers several limitations. The population estimate for breeding Macaroni Penguins at Marion Island is good, but that of Rockhopper Penguins less so because of difficulties associated with counting this species. An up-to-date census of both Macaroni and Rockhopper Penguins at Prince Edward Island is overdue.

Data on energetics of the species are considered good, although measurements of incubation costs in the field using doubly-labelled water are desirable to validate those made in metabolic chambers. However, substantial refinements of energy expenditures are probably not warranted until better information is available on individual activity budgets, and foraging distribution, especially outside the breeding season.

Dietary information for the two species is good during the chick-rearing period but, as at other localities, little is known of the diets outside this period. Also, seasonal and year-to-year changes in diets (Chapter 7), and

consequently energy intake, have not been considered in the model.

Probably the largest, single limitation of the present model, and also that of Croxall *et al.* (1984), is the lack of information on numbers of birds too young to breed (pre-breeders) and non-breeding penguins. As pointed out by Croxall *et al.* (1984), demographic data are, at present, inadequate to assess the size of these populations, although Croxall and Prince (1982) estimated the pre-breeding population of Macaroni Penguins to be 40 % of the breeding population. Extrapolating this figure for the Prince Edward islands, and assuming that pre-breeding birds spend half the breeding period ashore and half at sea, their food requirements could amount to an additional 106 400 tonnes and 18 300 tonnes for pre-breeding Macaroni and Rockhopper Penguins, respectively.

In most respects, the model of food consumption presented for Macaroni Penguins corresponds very closely with that of Croxall *et al.* (1984) for the same species at South Georgia with the notable exception of food requirements of pre-moulting birds at sea. However, the authors point out that they did not include additional food required to establish energy reserves for moult and they recognized that food consumption during this period was an underestimate. Overall, Croxall *et al.* (1984) estimated that 8×10^6 breeding pairs of Macaroni Penguins in the vicinity of South

Georgia consumed 4.0 million tonnes of food, chiefly krill. This amounted to 51 % of the total annual food consumption of all seabirds at South Georgia, although Croxall *et al.* (1984) assumed that the penguins were feeding in the vicinity of the island throughout the year. Nevertheless, Macaroni Penguins are an important consumer at South Georgia and seasonal patterns of food consumption largely reflect the consumption of this species. In contrast, although Macaroni and Rockhopper Penguins account for a substantial proportion of the avian biomass at the Prince Edward islands, the King Penguin is probably the most important single consumer of marine resources in the area. A preliminary estimate suggests that the 220 000 breeding pairs of King Penguins, which are resident at the islands throughout the year, consume about 280 000 tonnes of food per year, most of which is removed from within a 300-km radius of the islands (Adams 1987, N.J. Adams, unpubl. data).

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SUMMARY AND CONCLUSIONS

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Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*) are widely distributed in the sub-Antarctic. Macaroni Penguins, in particular, account for an appreciable proportion of the avian biomass in the region. Both species breed at Marion Island (46°52'S, 37°51'E), the larger of two islands which make up the Prince Edward islands group. Breeding populations at Marion Island are estimated to number 405 100 and 93 300 pairs of Macaroni and Rockhopper Penguins, respectively. An additional 17 000 and 35 000 pairs breed at nearby Prince Edward Island.

The energy requirements of adult Macaroni and Rockhopper Penguins and their chicks were assessed during the seven-month breeding cycle at Marion Island. Resting metabolic rates (RMR) of adults, calculated from the lowest, stable, periods of oxygen consumption measured over 24 h, averaged 1 161 kJ day^{-1} (307 kJ kg^{-1} day^{-1}) for Macaroni Penguins and 863 kJ day^{-1} (344 kJ kg^{-1} day^{-1} for Rockhopper Penguins, about 15 % lower than the birds' metabolic rates measured over the full 24-h period. Nevertheless, RMRs were 25 % greater than basal metabolic rates (BMR) predicted for birds of equivalent mass from allometric equations. A review of metabolic rates of penguins showed that metabolic rates measured on long-term captive penguins were close to, or lower, than predicted BMR, possibly because of less stress

to these birds during experiments than to wild birds in temporary captivity. If metabolic rates of long-term captive birds are regarded as more representative of BMR, then BMR of penguins can best be predicted from the relationship $BMR = 3.01\ W^{0.68}$ where BMR is in kJ day^{-1} and W is the body mass in grams. Measurements of metabolic rates of wild birds in temporary captivity should then at best be regarded as RMR and can be predicted by the equation $RMR = 4.94\ W^{0.66}$, where conventions are as described above.

Measurements of metabolic rates of Rockhopper Penguins at temperatures between $-10^{o}C$ and $25^{o}C$ suggest that the thermoneutral zone of this species lies between $0^{o}C$ and $5^{o}C$. Metabolic rates of Macaroni Penguins increased generally over the full range of temperatures and their thermoneutral zone could not be clearly ascertained. It is probable, however, that it is similar, if not slightly lower than that of the Rockhopper Penguin because of the Macaroni Penguin's larger size. Body temperatures of resting birds averaged 38.5 and $39.0^{o}C$ for Macaroni and Rockhopper Penguins, respectively.

The incubation period of Macaroni and Rockhopper Penguins is about 35 days. Although both parents may take turns incubating the eggs in the first few days after laying, each adult undergoes one long incubation shift, during which it fasts. Incubation shifts may last up to 19 days for females,

which take the first shift, and 16 days for males. Energy expenditures of incubating Macaroni and Rockhopper Penguins, calculated from rates of oxygen consumption, averaged 224 and 267 kJ kg^{-1} day^{-1}, respectively, and were significantly lower thanthose of resting, non-incubating birds when compared on a mass-specific basis. However, incubating Macaroni and Rockhopper Penguins were appreciably heavier than non-incubating individuals because of fat deposits laid down to sustain them through the incubation fast. This tends to result in proportionately lower mass-specific energy expenditures compared to non-incubating individuals. Nevertheless, absolute energy expenditures of incubating birds were similar, or slightly lower, than those of resting, non-incubating birds, averaging 1 095 kJ day^{-1} for Macaroni Penguins and 740 kJ day^{-1} for Rockhopper Penguins. Hence, it is concluded that incubation is not energetically expensive for small penguins. Furthermore, metabolic rates during incubation may be a better indication of BMR than are resting metabolic rates.

Penguins undergo an annual moult during which they renew their entire plumage. Because they cannot go to sea to feed during this period, they must subsist on fat reserves laid down during a pre-moult foraging trip. Moult in penguins is regarded as an energetically expensive process because of the cost of new feather synthesis and an increased cost for thermoregulation associated with the decrease in feather

insulation. Energy expenditures of adult Macaroni and Rockhopper Penguins, estimated from rates of oxygen consumption, decreased during moult as the birds lost mass. Peak moult costs were 386 kJ kg^{-1} day^{-1} for Macaroni Penguins and 378 kJ kg^{-1} day^{-1} for Rockhopper Penguins, or 1.81 and 1.50 times estimated BMR. Overall, however, energy expenditures averaged 1 519 kJ day^{-1} for Macaroni Penguins and 1 056 kJ day^{-1} for Rockhopper Penguins; 30 % and 20 % greater, respectively, than those of resting, non-moulting birds and 40 % and 34 % greater than estimated BMR.

Macaroni and Rockhopper Penguins lost an average of 45 % of their initial body mass during moult at a rate of 132 and 78 g day^{-1}, respectively. Energy expenditures, estimated from rates of loss of body mass and changes in body composition, were 2 012 kJ day^{-1} for Macaroni Penguins and 1 337 kJ day^{-1} for Rockhopper Penguins, 32 % and 27 % greater, respectively, than energy expenditures estimated from rates of oxygen consumption. This suggests that estimates of the amount of fat oxidized during the moult fast were too high. The relatively high energetic cost of moult in these penguins is probably offset to a large degree by their reduced activity during the moult. Nevertheless, birds which come ashore with insufficient fat reserves may approach terminal starvation before completing feather replacement.

Macaroni and Rockhopper Penguins remained ashore during moult for 20 - 30 days, averaging 25 days. However, new

feathers began developing under the skin an estimated 3 - 5 days before the birds returned ashore, and by the time they began emerging through the skin 5 days later, they were already over half their final length. Active feather synthesis decreased between 13 and 18 days after the penguins returned ashore and was completed by 21 days, although new feathers had not yet emerged to their full length. Total duration of moult thus averaged 29 days, with a range of 25 - 35 days.

Macaroni and Rockhopper Penguins lay two eggs which are markedly dimorphic in size, the first laid A-egg being smaller than the second laid B-egg. Although laid three to four days before the B-egg, when retained, the A-egg always hatches last. Because only one chick is ever reared to independence, this has implications for brood reduction. Measurements of egg temperatures and embryonic oxygen consumption of A-eggs incubated singly, in different positions in the nest, or pre-incubated in a hot-room for several days were slightly, but not significantly, different. However, all A-eggs had rates of embryonic oxygen consumption lower than that of B-eggs. Notably, A-eggs of Macaroni Penguins, which are the same size as B-eggs of Rockhopper Penguins, are incubated singly in the posterior position in the brood pouch. These A-eggs, which produce similar sized hatchlings to Rockhopper Penguin B-eggs, had rates of embryonic metabolism significantly lower than that

of Rockhopper Penguin B-eggs at equivalent stages of incubation. These observations suggest that egg temperature alone does not account for the difference in incubation periods which result in chicks from B-eggs always hatching first. Consequently, it is concluded that embryos from A-eggs have an inherently slower rate of development than do those from B-eggs. This may be related to the different proportions of albumen in the eggs; A-eggs have proportionately less albumen than B-eggs.

Energy requirements for growth and maintenance of Macaroni and Rockhopper Penguin chicks were measured from rates of oxygen consumption and body-composition analysis. Energy expenditures were correlated with body mass, but mass-specific energy expenditures increased to peaks between 14 and 21 days of age and subsequently decreased. Homeothermy in Macaroni and Rockhopper Penguin chicks was thus inferred to be attained between two and three weeks of age. Accumulation of body lipid increased markedly after 30 days of age, corresponding to the time when the male joins the female in feeding the chick, but decreased after 45 days of age and was presumably metabolized. Protein was laid down throughout growth. An energy budget was constructed for Macaroni and Rockhopper Penguin chicks. Energy requirements of both species reached a peak about halfway through the 70 day growth period and subsequently decreased. Total energy requirements for growth and maintenance were

estimated to amount to 76 200 kJ for Macaroni Penguin chicks and 59 400 kJ for Rockhopper Penguin chicks, of which 38 % and 28 %, respectively, was allocated to growth.

Macaroni and Rockhopper Penguins at Marion Island fed predominantly on crustaceans, with fish and cephalopods generally being of lesser importance. The proportion, by reconstituted mass, of each prey type was different in each of two successive years but averaged, overall, 75 % crustaceans, 15 % fish and 10 % cephalopods in Macaroni Penguins, and 87 % crustaceans, 9 % fish and 4 % cephalopods in Rockhopper Penguins. *Nauticaris marionis* and *Euphausia vallentini* were important crustaceans in the diets of both species and *Themisto gaudichaudi* and *Thysanoessa vicina* were found in substantial numbers in the diets of Macaroni Penguins, but not Rockhopper Penguins. Over 95 % of the fish consumed by Macaroni and Rockhopper Penguins belonged to the family Myctophidae (lantern-fishes), of which three species, *Krefftichthys anderssoni, Protomyctophum normani* and *P. tenisoni* were the most important. Macaroni Penguins also took appreciable numbers of *Electrona carlsbergi*. However, species composition of crustaceans and fishes in the diets of Macaroni and Rockhopper Penguins were different in each of two successive years. Cephalopods in the diets were *Kondokovia longimana* and *Moroteuthis knipovitchi* (squid) and an unidentified octopod.

The composition of the diet changed during chick-rearing. During early chick-rearing, both Macaroni and Rockhopper Penguins fed predominantly on crustaceans. The proportionate importance of fish and cephalopods increased as chicks grew and by the end of chick-rearing in Macaroni Penguins fish and cephalopods comprised 100 % of the diet. However, in the last two weeks of chick-rearing in Rockhopper Penguins, crustaceans again made up the bulk of the diet. Crustaceans in the diets of Macaroni and Rockhopper Penguins, and in net hauls from the vicinity of the island, included species regarded as being more typical of Antarctic and sub-Tropical waters as well as those normally associated with sub-Antarctic waters. These are presumably present as a result of periodic eddies and intrusions of foreign water masses past the island and may account for some of the year-to-year changes in prey species composition.

Macaroni and Rockhopper Penguins swim at an average speed of 7.5 and 7.4 km hr^{-1}, respectively. Rockhopper Penguins feeding small chicks spent only 30 % of their time at sea swimming at speed and Macaroni Penguins feeding large chicks 38 %. Foraging ranges of Rockhopper Penguins feeding small chicks ranged from 4 to 157 km and those of Macaroni Penguins feeding large chicks from 60 to 300 km. Because chick-feeding frequencies of both species are very similar, it is probable that both species forage relatively close to shore when their chicks are small and farther offshore when

chicks grow larger. This accounts for the absence of pelagic fish and cephalopods in the diets of the penguins early in chick-rearing and their increased proportion in the diets as chicks get older.

Diets, chick-feeding rates, travelling speed and probably foraging range of Macaroni and Rockhopper Penguins at Marion island are very similar. Consequently, the principal factor resulting in dietary segregation of the two species is the three to four week difference in the timing of the breeding cycle. Rockhopper Penguins begin breeding later than Macaroni Penguins and by the time their chicks hatch and are being fed frequent meals of crustaceans, Macaroni Penguins are foraging farther afield on slightly different prey.

Total energy requirements of the breeding adult populations of Macaroni and Rockhopper Penguins and their chicks over the seven-month breeding and moulting cycle at the Prince Edward Islands amounted to 460 X 10^9 kJ for Macaroni Penguins and 80 X 10^9 kJ for Rockhopper Penguins. Food consumption was estimated to amount to 145 000 tonnes, of which 93 700 tonnes comprised crustaceans, 34 050 tonnes fish and 17 250 tonnes cephalopods. Macaroni penguins acounted for 87 % of the total consumption. Peak food demand occurred during the pre-moult foraging trip when, in addition to normal at-sea food requirements, adults were

laying down fat reserves for the moult and surviving, newly-fledged, chicks were assumed to be still in the area.

Food consumption by Macaroni and Rockhopper Penguins takes place within 200 - 300 km of the islands. Available information suggests that potential primary production in the vicinity of the islands is sufficient to support the breeding populations of breeding Macaroni and Rockhopper Penguins, and probably the large breeding population of King Penguins (*Aptenodytes patagonicus*) as well. However, the food requirements of non-breeding Macaroni and Rockhopper Penguins and those too young to breed were not included in the model. Furthermore, the importance in the diets of the penguins of several species of crustaceans and fish more typically associated with Antarctic and sub-Tropical waters suggests that the penguins rely to a large extent on prey stocks imported from other areas. However, there is no information of the distribution, movement and abundance of these in the vicinity of the Prince Edward Islands.

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