FEEDING BIOLOGY AND ENERGETICS OF KING APTENODYTES PATAGONICUS AND GENTOO PYGOSCELIS PAPUA PENGUINS AT SUB-ANTARCTIC MARION ISLAND

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ABSTRACT

Adaptations of penguins for pursuit diving have resulted in reduced foraging ranges, compared to volant seabirds. However, their classification as inshore, offshore or pelagic foragers, based on rates of food provisioning to chicks, still has merit as a framework around which aspects of their feeding biology and allocation of energy within individual energy budgets may be discussed. The average rates at which seabird species supply food to chicks may influence many aspects of their biology. I defined some of the foraging parameters of the pelagic feeding King Penguin Aptenodytes patagonicus and the inshore feeding Gentoo Penguin Pygoscelis papua at sub-Antarctic Marion Island. Descriptions of the diets of these penguins were interpreted in terms of defined parameters. The generally low reproductive rates of penguins, a common feature of many seabirds, are considered to reflect energy constraints on breeding. Energy requirements for breeding and moult were assessed in this context. Given the large biomass of penguins at the Prince Edward Islands (Marion and Prince Edward islands) the impact of these birds on marine resources in the area is likely to be large. Information on diet and energy requirements of breeding and moult were combined and the magnitude of this impact was estimated.

The diet of King Penguins at Marion Island was dominated by three species of mesopelagic myctophid fish which were partly replaced by a single squid species during winter. Previously, the presumed absence of fish as an important prey for Southern Ocean pelagic predators was attributed to the paucity of obligate shoaling fish species. Consistent with the pelagic distribution of these fish, provisioning rates of King Penguins during chick rearing were low and highly variable within individuals. This was presumably a consequence of the unpredictable distribution of such prey. Such a pattern of food provisioning is typical of pelagic seabirds. In marked contrast, the diet of Gentoo Penguins contained substantial amounts of demersal fish and benthic crustaceans although pelagic crustaceans were more abundant in summer. These changes in diet appeared unrelated to interactions with sympatric penguins but, as in the case of King Penguins, were a consequence of changes in local availability that may reflect seasonal changes in productivity of especially pelagic prey. The non-pelagic prey of Gentoo Penguins were probably only available in the the relatively shallow water close to the islands. Consistent with this, Gentoo Penguins seldom ranged a maximum of more than twenty kilometres from the island while feeding chicks. Such constraints on foraging seem to have restricted the location of breeding colonies mainly to areas adjacent to relatively shallow water. Quantified comparisons of the diets of sympatric penguins at Marion Island indicated clear differences between the three penguin genera but considerable similarity between the congeneric species pair. Although the influence of other factors, including differing diving capabilities and selection based on prey size, is not denied, prey availability in the apparently distinct penguin feeding zones explained most of the differences in diets of penguins at Marion Island.

In spite of low core body temperatures, basal metabolic rates of King and Gentoo Penguins were similar and higher than those predicted from general allometric equations, respectively. Measurements of metabolic response to ambient temperatures

indicated that there were no thermal constraints on adult penguins over the normal range of ambient temperatures experienced at Marion Island. The increased rate of metabolism required by King Penguins to maintain thermal balance after immersion in water was probably met to a large extent by heat generated by swimming. Maintenance costs of King and Gentoo Penguins during moult averaged approximately one-and-a-half times basal rates. Such additional costs above basal metabolism may be related to changes in thermal conductance and feather synthesis. The apparent constraints on timing of moult, which must be fitted around breeding, may be a consequence of the high feeding rates that must be sustained during the premoult foraging period to accumulate large lipid reserves. The low incubation costs of King Penguins were not significantly different from those of resting non-incubating birds. This suggests that any potential energy constraints were also likely to arise during periods at sea between incubation shifts when accumulating lipid reserves. Costs of yolk production were less than ten percent of basal metabolism and insignificant compared to costs of other activities. Hence, energy limitations are unlikely to affect egg production. The higher hatching yolk content of hatchling King Penguins compared to Gentoo Penguin hatchlings was consistent with the longer feeding intervals of the adults. The low production efficiency of King Penguin embryos was a consequence of the small hatchling size, but relatively long incubation period.

For successful breeding, energy delivery rates by adults must match chick demands. Allocation of this intake between growth and maintenance may be understood on the basis of adult provisioning rates. A higher proportion of the energy budget of King Penguin chicks was allocated to lipid accumulation than was the case by chicks of inshore feeding Gentoo Penguins. Large lipid reserves, accumulated during the initial part of growth, were crucial for the survival of King Penguin chicks through winter when feeding visits by adults are very infrequent. The high mass proportionate energy cost of rearing King Penguin chicks, double that of Gentoo Penguins, was a consequence of the long growth period with two phases of tissue accumulation.

Comparison of the daily energy requirements of adult penguins at the nest during breeding and moult indicates these were highest during brooding. In addition, and in constrast to other activities, relatively undigested food must be delivered to terrestrial nest sites to feed chicks. There is some suggestion that limitations on the ability of inshore feeding Gentoo Penguin adults to deliver sufficent food to chicks during this period may result in brood reduction. The high feeding rates necessary to meet high foraging costs, cost of accumulation of energy reserves for the following fast and chick demands, require high prey encounter rates that may approach the physiological limits to processing such food and restrict penguins to breeding adjacent to productive marine ecosystems with resident populations of shoaling prey.

The biomass of food removed by the penguin community at the Prince Edward Islands approached one million tonnes per annum. Much of this was consumed in summer when all four species were present at the island and presumably coincided with a seasonal increase in availability of pelagic prey. Temporal separation of brooding amongst the four species of penguins at the island was the principal factor in staggering food demand within the summer period. Three-quarters of the total consumption was attributable to King Penguins. Consequently, myctophid fish were the single most important prey group consumed. This is in marked contrast to food webs in Antarctic waters where krill Euphausia superba plays a dominate role. The mean foraging ranges of penguin species at the Prince Edward Islands were positively correlated with their food requirements, presumably reflecting the increasing biomass of food available. Demersal and benthic prey exploited by the small population of inshore Gentoo Penguins may be sedentary, in contrast to the presumably more easily replenished pelagic prey utilized by offshore foraging penguins. This may explain why King Penguins are much more abundant than Gentoo Penguins at the Prince Edward Islands

CHAPTER 1

INTRODUCTION

Only two to three per cent of the world's bird species regularly obtain their food from the sea, yet this habitat covers nearly two-thirds of the earth's surface (Croxall 1987). This probably reflects the limited number of niches available in the marine environment. Seabirds show a number of specialized ecological adaptations. Amongst other features, most seabird species are large, and have small clutches with long incubation and chick rearing periods. All are constrained by the need to return to shore to breed. Many of these features may reflect the attempt to reconcile terrestrial breeding with marine feeding (Ricklefs 1983). Food or energy has been regarded as an important and potentially limiting resource for seabird populations (Lack 1954, Ashmole 1963, Birkhead & Furness 1985). Patterns of this resource use are presumably subject to natural selection and are likely to be of adaptive significance.

The most extreme marine specialization occurs among the Sphenisciformes (penguins). All species within the order have become flightless and, with the exception of the Galapagos Penguin Spheniscus mendicus are restricted to the Southern Ocean. Despite their restriction to cold relatively productive waters (Ainley & Boekelheide 1983), the often large numbers and biomass of penguins, especially in Antarctic and sub-Antarctic waters, attest to the success of their highly specialized locomotory and feeding adaptations. The ability to pursue prey underwater to depths of up to 265 m (Kooyman & Davis 1987) has more than compensated for the reduced travelling speed of penguins compared to volant seabirds.

Islands of the sub-Antarctic typically provide breeding sites for up to four species of penguins (Wilson 1983). At the Prince

Edward Islands (comprising Marion and Prince Edward islands), the breeding penguin assemblage consists of four species: the King Aptenodytes patagonicus, Macaroni Eudyptes chrysolophus, Rockhopper E. chrysocome and Gentoo Pygoscelis papua Penguins. The total biomass of penguins at the Prince Edward Islands is estimated at 10.7 X 10^6 kg or 98 % of the biomass of all surface-nesting birds. It is a recognition of their importance as consumers in some marine ecosystems (e.g. Croxall et al. 1985) that has provided stimulus for recent ecological research on penguins at the Prince Edward Islands and elsewhere.

Aspects of the energy requirements of adult Macaroni and Rockhopper Penguins and their chicks at Marion Island have been examined in detail (Brown 1984, 1985, 1987). Brown (1989) combined this information with data on diet (Brown & Klages 1987), population size, timing of breeding and moult to estimate daily food and energy requirements of their populations. In this thesis I take a similar approach. The energy requirements of the King and Gentoo Penguins during the terrestrial phase of their life cycles are quantified and integrated with information on diets and foraging parameters to examine the relationship between these predators and their marine prey. Relevant literature is reviewed briefly below.

Literature review:

King Penguins have a circumpolar breeding distribution and a latitudinal distribution from the Crozet Islands (46°S) to South Georgia (53°30′S - 55°S). Based on perceived mensural differences, Stonehouse (1960) accepted two sub-species: Aptenodytes patagonicus patagonicus which breed at sites in the

South Atlantic, and A. p. halli, which breed at sites in the South Indian Ocean (Harrison 1983). However, the validity of halli has received little critical support and was not listed as a separate subspecies by Stonehouse (1967). At present, largest numbers of King Penguins occur at islands in the South Indian Ocean (Jouventin et al. 1984, Williams 1984, Weimerskirch et al. 1989) Gentoo Penguins breed over a wider latitudinal range from the Crozet Islands in the north to the Antarctic Peninsula in the south (~65^{o}S) (Wilson 1983). Stonehouse (1970) presents more compelling evidence for two subspecies. The southern sub-species Pygoscelis papua ellsworthi is restricted to Antarctic waters. The larger P. p. papua breeds within the sub-Antarctic zone, including the Prince Edward Islands.

The breeding seasons of most seabirds at Marion Island to occur during summer, presumably reflecting a seasonal increase in food availability due to increased primary and secondary production associated with the longer summer days. However, in contrast to Macaroni and Rockhopper Penguins, King and Gentoo Penguins are present at Marion Island throughout the year. There are several biological and ecological differences between the two. Many of these differences appear to be associated with or reflect the pelagic and inshore feeding of King and Gentoo Penguins, respectively.

The King Penguin has the longest breeding cycle of any seabird, and aspects of its breeding biology have been described by Stonehouse (1960) and Barrat (1976). Typically, the breeding cycle commences with a prenuptial moult in September with chicks attaining independence about 14 months later . At

South Georgia adults were considered to be able to breed potentially successfully twice every three years (Stonehouse 1960), although biennial breeding appeared to be more likely. At the Crozet Islands there was no indication of successful breeders attempting to raise a second chick within three years, and they are almost certainly biennial breeders (Barrat 1976). Aspects of the breeding biology of Gentoo Penguins at Marion Island have been described by Williams (1980). Breeding is restricted to a period of five months, commencing in the austral winter. Accounts of the breeding cycle of Gentoo Penguins elsewhere have been presented in the context of diet studies (Croxall & Prince 1980), energy budgets (Davis et al. 1989) and interspecific comparisions of growth (Volkman & Trivelpiece 1980), at sites where breeding is restricted to the austral summer.

The long breeding and moult fasts undertaken by both King Penguin adults and chicks during breeding and moult have stimulated much research on their metabolic, biochemical and hormonal reponses to physiological stress (e.g. Cherel et al. 1987, 1988a, 1988b). In addition, metabolic response of adults (Gavrilov 1977, Barre 1980, Le Maho 1983) and chicks (Barre 1976, 1978, 1984) to varying ambient temperature and to immersion in water (Barre & Roussel 1986) have been examined. In contrast, little such work has been done on Gentoo Penguins. Taylor (1985) has studied the development of homeothermy and energy metabolism in pygoscelid chicks. Early measurements of metabolic rates of adult Gentoo Penguins (Scholander 1940 quoted in Weathers 1979) can be discounted because measurements were performed on restrained birds. These studies have investigated the metabolism of penguins from a physiological viewpoint. With the development of labelled isotope techniques which allow estimation of energy consumption of free-ranging penguins, a more ecological perspective has prevailed. Earlier studies utilized dilution rates of tritiated water to estimate at-sea energy costs and feeding rates of King (Kooyman et al. 1982) and Gentoo (Davis et al. 1983) Penguins. These studies required assumptions about the nature of the birds' diets and may be in error. More recently, this technique has been combined with rates of doubly labelled water to determine energy requirements at each main stage of the breeding cycle, including at-sea costs, to measure the energy requirements of breeding Gentoo and Macaroni Penguins (Davis et al. 1989).

Despite their large biomass, especially in the southern Indian Ocean region, descriptions of the diet of King Penguins have been limited largely to anecdotal accounts (e.g. Barrat 1976). Hindell (1988) has presented a quantitative analysis of diet of King Penguins at Macquarie Island, and a brief description of the diet at the Crozet Islands is presented by Ridoux et al. (1988). The diet of the Gentoo Penguin has been well studied, particularly at sites south of the Antarctic Polar Front, along the Antarctic Peninsula (Volkman et al. 1980, Jablonski 1985) and at South Georgia (Croxall & Prince 1980). These studies have been restricted to the austral summer during breeding. More recently, Ridoux et al. (1988) and Hindell (1989) have presented a more comprehensive account of the species' diet at the Crozet Islands and Macquarie Island, respectively. The recent development and deployment of remote-sensing depth gauges and new radio-tracking techniques have begun to provide important new insights into the foraging behaviour and performance of penguins at sea. The diving capabilities of King Penguins (Kooyman et al. 1982) and of Gentoo Penguins (Adams & Brown 1983, Trivelpiece et al. 1986, Croxall et al. 1988) are well known.

Study area:

The main climatic features of the Prince Edward Islands are the predominately strong westerly winds, often of gale force, high relative humidity, low mean temperature showing little annual and diel variation, and abundant precipitation. Annual average air temperature is 5.5°C with monthly average temperatures ranging from 3.6°C to 7.8°c. Extreme temperatures have ranged from -6.8°C to 22.3°C. The annual average sea surface temperature is 5.0°C with monthly averages from 4°C to 6.1°C (Schulze 1971). King Penguins generally breed in sheltered sites (Barrat 1976). This coupled with crecheing behaviour of the chicks during severe weather (pers. obs.) may ameliorate the effects of wind and cold.

The Prince Edward Islands lie between the sub-Tropical Convergence and Antarctic Polar Front (APF) in an area of great circulatory complexity. In fact, Benon & Murail (1979) have suggested that the APF lies to the north of the islands (46°S) instead of its usually plotted position of some 200 to 250 km south of the islands. The major ocean current that flows past the Prince Edward Islands is the West Wind Drift. This current is deflected northward by the Marion Ridge carrying with it a component of the cold Weddell Current. The Agulhas Current may also exert some influence on the water circulation pattern around the islands (Boden & Parker 1986) and there appears to be interchange between Antarctic and sub-Antarctic waters reflected in the composition of zooplankton community (Boden 1988, Boden & Parker 1986). Seas in the immediate vicinity of the islands are more productive than the surrounding ocean (Allanson et al. 1985). Grindley & Lane (1979) suggest that upwelling of deep Antarctic water under the stress of strong predominately north-west winds were the primary mechanism in introducing nutrients to the ecosystem, although this has been disputed (Boden 1988, Boden & Parker 1988). Frontal regions between current systems may also form areas of biological enhancement (Lutjeharms et al. 1985). Whether or not such features are also favoured feeding areas for penguins breeding at the Prince Edward Islands, remains to be assessed.

Thesis presentation:

This thesis is divided broadly into two parts. The first section examines the diet and aspects of the feeding biology of King and Gentoo Penguins. This information is fundamental to an understanding of the relationships between these seabird predators and their marine prey. The section is concluded with a review and synthesis of these data from all four species of the penguin assemblage at the Prince Edward Islands. The importance of foraging performance in determining diet is assessed and the trophic relationships between all four penguin species are examined. The second part of the thesis examines the energy requirements of adults and chicks during their period ashore. Energy costs of moult, incubation and chick growth and maintenance are assessed. The concluding chapter utilizes data from most of the preceding chapters and additional information on activity budgets, population sizes and at-sea energy costs to consider overall food consumption of the King and Gentoo Penguin populations. Information from Macaroni and Rockhopper Penguins is incorporated in this model and the timing, nature and extent of the impact on the marine resources is assessed and compared.

The thesis has been prepared as a series of separate papers. This approach results in some repetition and differences in style. Chapters 2 to 6, Chapter 8 (in part) and Appendices 2 and 3 have already been published. Co-authored papers are indicated. In all such papers I was the senior author, having been responsible for both the data collection in the field and for the major part of manuscript preparation.

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CHAPTER 2

SEASONAL VARIATION IN THE DIET OF THE KING PENGUIN *APTENODYTES PATAGONICUS* AT SUB-ANTARCTIC MARION ISLAND

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The diet of the King Penguin *Aptenodytes patagonicus* at Marion Island was examined throughout the year by analysis of stomach samples. Fish accounted for 87 % by wet mass, 75 % by numbers and 69 % by reconstituted mass. Their proportional importance by wet mass increased from 68 % during winter to almost 100 % in summer and probably reflects a real increase in their local availability. Squid comprised most of the remainder with crustaceans forming less than 1 % of the diet by numbers. Prey items were generally small, the most abundant being three species of myctophid fish, *Krefftichthys anderssoni* and *Protomyctophum tenisoni* and *Electrona carlsbergi*, and a squid *Kondakovia longimana*. King Penguins took both juvenile and adult *Krefftichthys anderssoni* and *P. tenisoni*, but only adult *E. carlsbergi*. The juvenile and adult modal size classes of *K. anderssoni* and *P. tenisoni* increased from March through to February and the proportion of juvenile to adult fish increased in winter. The increase in the modal size class of the *K. anderssoni*/*P. tenisoni* complex during the year probably reflects growth of the fish, rather than movement of different populations in and out of the area exploited by King Penguins. All squid consumed were probably juveniles. The modal size class of *Kondakovia longimana* increased from March to August, but in September - October smaller squid again formed a large proportion of the squid component of the diet. Numbers of measureable squid beaks recovered from November to February were low. This study was the first to show mesopelagic myctophid fish as a major component of the diet of a vertebrate predator in the Southern Ocean.

INTRODUCTION

Approximately 31 % of the King Penguin's (Aptenodytes patagonicus) world population occurs at the Prince Edward Islands, incorporating Marion and Prince Edward Island, in the southern Indian Ocean, accounting for about 54 % of the total seabird biomass at these islands (calculated from data in Williams et al. 1979). The King Penguin is unique among penguins breeding in the Southern Ocean in that a pair takes more than a year to raise a chick (Stonehouse 1960, Barrat 1976). Moreover, breeding is not as highly synchronized as in other Southern Ocean species of penguins (Croxall 1984). A significant proportion of the adult King Penguin population is therefore engaged in feeding chicks throughout the year. During winter when most of the summer-breeding birds are not present, the proportional importance of King Penguins thus increases still further. Consequently, when considered on a year-round basis, the species is the most important avian consumer of marine resources at the Prince Edward Islands (Chapter 12). This may also be the case at other islands with large breeding populations of King Penguins. However, in spite of its importance as a consumer in the sub-Antarctic, published accounts of the King Penguin's diet are largely restricted to gross estimates of the proportional representation of principal prey classes (Barrat 1976, Croxall & Prince 1980, 1982, Ridoux et al. 1988). More recently, however, a detailed description of the diet of the King Penguin at Macquarie Island has been published (Hindell 1988). This report describes the diet of the King Penguin at Marion Island, highlighting seasonal differences in the relative proportions and sizes of prey classes and species consumed.

METHODS

Stomach samples were collected at Archway Bay, Marion Island ($46^{o}53'S$, $37^{o}54'E$) from March 1984 to March 1985. Archway Bay has a breeding colony of 700 - 1000 pairs of King Penguins at the beginning of the season in November - December, decreasing to approximately 400 chicks by the end of October.

Meal sizes were determined from the mass of stomach samples collected for diet analysis (see below), daily weighings of chicks and reconstitution of meal sizes from diet analysis.

Fifteen chicks captured at the beginning of October 1984 were individually marked with soft plastic bands tied to the upper part of the flipper. At this stage chicks were approximately 10 months old and large (generally > 6 kg). Chicks were weighed daily (to ± 0.1 kg) on a Pesola spring balance, for at least 72 d. To minimize disturbance in the colony, all chicks to be weighed were caught and placed in a temporary holding pen until processed. Due to mass loss between a feed and the subsequent weighing, meal sizes calculated from daily weighings are underestimates of actual meal sizes. Meal sizes were corrected for mass loss of $265\ g.d^{-1}$, calculated from daily weighings of 16 chicks not fed for at least four days. I assumed chicks were fed approximately halfway between weighings. Reconstituted meal sizes were calculated by summing the estimated mass of individual prey items in the stomach samples (calculated from regressions given in Appendix I). Mass of prey items not measured was assumed to have the same individual average mass as measured prey items of the same species. Unidentified myctophids (Pisces: Myctophidae) were considered to comprise the same proportion and mean mass as identified myctophid species. Squid beaks too eroded for measurement were presumed to have been in the stomach for long periods (see discussion) and were considered not to have formed part of the sampled meal. In spite of this precaution, it is likely we overestimated both the numbers and reconstituted mass of squid in the sampled meals (see discussion).

Collection of food samples:

A total of 120 stomach samples of King Penguin adults and chicks was collected non-destructively by stomach pumping, using the water off-loading technique (Wilson 1984). The technique has been validated for penguins and recovery mass of 90 - 100 % in stomachs containing soft part remains can be expected (Gales 1987). King Penguins invariably had to be pumped twice (see Ryan & Jackson 1986). Confirmation of complete or almost complete emptying of the stomach could be gauged by the flushing of small pebbles which presumably collect in the bottom of the stomach.

On average, 10 adults or chicks were sampled each month. Adults arriving at the colony to feed chicks or recently fed chicks were stomach pumped. Samples were then immediately drained through a 0.5 mm sieve. Some very fine highly digested material was lost through the sieve during the draining procedure.

Handling time per bird from capture to draining of food samples did not exceed 45 minutes.

Analysis of food samples:

The drained food samples were weighed to the nearest gram in the laboratory. Samples were then stored in a refrigerator at 4oC until sorting, which was usually performed within 24 h of sampling and invariably within 48 h. Repeated washing separated the highly digested unidentifiable material from the remaining identifiable material and loose hard-part remains. Soft identifiable material, usually consisting of compacted fish pieces and squid tentacles and mantles, was sorted into fish, cephalopod and crustacean components and weighed. If present, whole prey items were preserved to confirm identifications made from hard-part remains. The generally advanced state of digestion of soft prey in the stomachs of both adult and chick King Penguins meant identification of prey items was almost exclusively based on the analysis of hard-part remains, namely, fish otoliths and cephalopod lower beaks.

Analysis of fish remains:

All loose otoliths and those removed from fish skulls were cleaned, dried and counted. I measured otolith diameter (OD) of otoliths that showed little or no signs of digestion (see North et al. 1983, Gales 1988) using a binocular microscope fitted with a graticule.

Identification of otoliths was made by direct comparison with a reference collection held at the Port Elizabeth Museum and from the literature (Karrer 1973, Schwarzhans 1978, Hecht & Hecht

1981, North et al. 1984). Additional otolith reference specimens and unpublished biometric data for the fishes were made available by T. Hecht (Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa) and T. B. Linkowski (Sea Fisheries Institute, Gdynia, Poland). I then estimated standard length and mass of fish from regressions linking OD to these parameters (Appendix 1). Insuffcent data precluded us estimating length and mass of some fish species of minor numerical importance.

Analysis of cephalopod remains:

Cephalopod beaks (mandibles) were collected loose from the stomach contents or removed from the buccal mass using the procedure described by Wolff (1982). Alternatively, the buccal mass was left in an open dish with tap water where bacterial action freed the beaks from adhering flesh in about two weeks. Beaks were stored subsequently in 50 % isopropyl alcohol.

I estimated the number of squid present from the number of lower beaks. These beaks were then identified to species by comparison with material held in the Port Elizabeth Museum reference collection and from the literature (Clarke 1962, Voss 1969, Filipova 1972, Imber 1978, Clarke 1980, 1986). The identification of very small beaks (lower rostral length (LRL) < 2 mm) was problematic, since beaks of this size usually do not show sufficient specific characters to permit determination to species or even genus. It was, however, usually possible to establish the family. In several cases intact or partially digested squid were recovered and identified by reference to the literature (Roper et al. 1969, Filipova 1972, Clarke 1980, Voss 1980).

LRL (Clarke 1962) was measured with Vernier calipers or under a microscope. Regressions (Appendix 1) were used to estimate dorsal mantle length (DML) and mass (W) of the cephalopods from LRL. Intact squid found in King Penguin stomach samples were used to improve these regressions.

Analysis of crustaceans:

When present, crustaceans were removed from samples and identified using published keys (Bowman & Gruner 1973, Kirkwood 1982, 1984). Their advanced stage of digestion precluded measurement of body size.

RESULTS

Meal size:

The average wet mass of stomach contents from chicks and adults combined was 1 107 ± 734 g (range: 1 - 3 030 g, n = 120). Samples under 10 g consisted almost entirely of hard parts and were from penguins that had not fed recently. Average mass of samples excluding these small samples was 1 153 ± 714 g (n = 115). Mean meal size determined for 15 large chicks from daily weighings and corrected for mass loss was 1 650 ± 325 g (range: 1 170 - 2 190 g). Average meal size of reconstituted meals was 1 403 ± 1 235 g (range: 11 - 6 012 g, n = 120). There was no significant difference in mean meal sizes determined by the three different methods (P's > 0.05). The mean mass of adults feeding chicks was 13.1 ± 1.3 kg (n = 33). Meals varied from

8.5 - 12.6 % of adult body mass, depending on the method of determining meal mass.

General diet composition:

A total of 70 427 prey items was recovered. Forty-three items were crustaceans, 6 573 lower squid beaks and 63 811 fish otoliths (equivalent to a minimum of 31 906 fish since each fish has two otoliths), representing 0.1 %, 17.1 % and 82.8 % of the total number of individuals of the different prey classes respectively. Thirty species or species groups were identified (Table 1).

Twelve species or species groups of fish were identified. Special problems were encounted with the identification of _Krefftichthys_ _anderssoni_ and _Protomyctophum_ _tenisoni_. The otoliths of these two species span the same size range and are very similar in general appearance. In well-preserved specimens the microstructure of the inner face of the otolith is species specific. However, in a large proportion of the samples, digestion had destroyed these features and the otoliths were inseparable. I treated the two species as a species complex. I consider this justifed because available data indicate that both species grow to similar body size and show similar relationships between otolith diameter and fish length or mass. Significant numbers of otoliths (1 113) from an unidentified species (Myctophid A) were recovered. Broken and highly digested otoliths could only be identified to family and were classified as myctophids. It is very likely that a large proportion of these remains originated from the myctophid fishes _K_.

TABLE 1

Numbers and frequency of ocurrence of prey items identified from King Penguin stomach samples from Marion Island

Prey item	Numbers	% of total	Frequency of ocurrence %
Fish			
Myctophidae	13 385	34.75	83.3
Krefftichthys anderssoni/ *Protomyctophum tenisoni*	12 234	31.76	85.0
Electrona carlsbergi	5 068	13.16	70.0
Myctophid A	557	1.45	70.8
Protomyctophum normani	379	0.98	28.3
Gymnoscopelus sp. (?*bolini*)	90	0.23	3.3
Paralepis coregonoides	64	0.17	30.0
Protomyctophum bolini	46	0.12	9.2
Protomyctophum sp.	45	0.12	6.7
Unidentified fish	24	0.06	10.0
Notothenia squamifrons	8	0.02	2.5
Notothenia magellanica	6	0.02	1.7
Squid			
Kondakovia longimana	4 609	11.96	86.7
Onychoteuthidae < 2 mm LRL	750	1.95	60.8
Onychoteuthidae > 2 mm LRL	637	1.65	29.2
Unidentified decapod squids <1 mm LRL	253	0.66	35.0
Unidentified decapod squids >1 mm LRL	198	0.51	34.2
Oegopsid A	36	0.09	14.2
Histioteuthis sp.	30	0.08	10.0
Alluroteuthis sp.	20	0.05	11.7

Moroteuthis sp.	19	0.05	5.0
Martialia hyadesi*	9	0.02	7.5
Gonatus antarcticus	8	0.02	1.7
Galiteuthis glacialis	3	0.01	0.8
Brachioteuthis sp.	1	<0.01	0.8
Crustaceans			
Amphipoda	25	0.06	6.7
Nauticarus marionis	9	0.02	4.2
Euphausiacea	3	0.01	1.7
Decapoda, Natantia	3	0.01	1.7
Unidentified crustaceans	3	0.01	1.7
Total	38 522	100.00	

*Martialia hyadesi has been much confused with Todorodes aff. sagittatus. However, our identification has been confirmed by G.J.B Ross (pers. comm.) and tentatively confirmed by M.R. Clarke (in litt.)

andderssoni, *P.* *tenisoni* and *Electrona carlsbergi*. Forty-eight otoliths could not be identified.

Thirteen species or species groups of squid were identified. Two species of the genus *Moroteuthis*, *M. robsoni* and *M. knipovitchi*, could not be separated with confidence. In addition, several isolated lower beaks and two partially digested bodies from an unknown oegopsid species (Oegopsid A) were recovered. A few species clearly different from the species listed in Table 1 were too eroded to be identified with confidence, and were listed as "unidentified". Some onychoteuthid beaks of less than 2 mm LRL could only be identified to family. Other, still smaller, beaks were identified no further than "Decapoda, Oegopsida", although in both cases general appearance and circumstantial evidence suggests that they belong to the species *Kondakovia longimana*.

Five species or species groups of crustaceans were found in the stomach samples. Items too digested to permit a positive identification were listed under "Decapoda, Natantia" or "unidentified crustaceans". It is not clear whether crustaceans recovered from King Penguins were actually taken by the birds or orginally occurred in the fish and squid stomachs and were subsequently released by digestion.

The relative proportions of the main prey classes for all samples (Table 2) indicate the importance of fish in the diet of the King Penguin at Marion Island. Crustaceans comprise a

TABLE 2

Composition by wet mass of identifiable material, numbers of prey items and reconstituted mass of King Penguin stomach samples from Marion Island

		Fish	Squid	Crustaceans
Wet mass (%)	Mean	86.5	13.5	trace
	SD	24.4	24.3	
	Range	(3.2-100)	(0.0-97.3)	
Numbers (%)	Mean	75.2	24.5	0.3
	SD	32.3	32.5	1.4
	Range	(0.0-100)	(0.0-100)	(0.0-11.7)
Reconstituted mass (%)	Mean	68.7	31.3	trace
	SD	36.1	31.1	
	Range	(0.0-100)	(0-100)	

measureable proportion of the diet only when expressed as per cent numbers.

The proportion of fish relative to squid and crustaceans showed a distinct seasonal pattern (Fig. 1). During July - August the proportion of diet comprised by fish reached a minimum, rising to a maximum during November - December. Since the proportion of crustaceans remained low throughout the year, the relative abundance of squid mirrors that of the fish.

Fish:

Fig. 2 demonstrates a winter minimum (July - August) in the relative abundance of E. carlsbergi, whereas Krefftichthys anderssoni/P. tenisoni shows a distinct peak from September-October to November - December. The relative proportions of the other species of fish are generally low except for a peak in the abundance of Myctophid A in July - August.

5 192 otoliths were measured, comprising 8.14 % of all otoliths counted. The modal mass of K. anderssoni/P. tenisoni was estimated at between 1.9 and 2.8 g (range: 0.02 - 12 g) and standard length (SL): 51.1 to 58.4 mm (range: 10.6 - 92.0 mm) (Fig 3). Plotted on a two-month basis, the size-frequency distribution is bimodal with the two modal peaks shifting from a March - April low of 25.2 mm and 47.5 mm SL, respectively, to a January - February maximum of 40.2 mm and 58.4 mm SL respectively (Fig 4). From March - April through to July - August the proportion of smaller fish in the diet increased in comparison to the larger fish. From September - October to March

FIGURE 1

Per cent composition of the diet of the King Penguin at Marion Island made up by fish expressed as wet mass (■----■), number (●——●) and reconstituted mass (▲—·—▲) at two-month intervals.

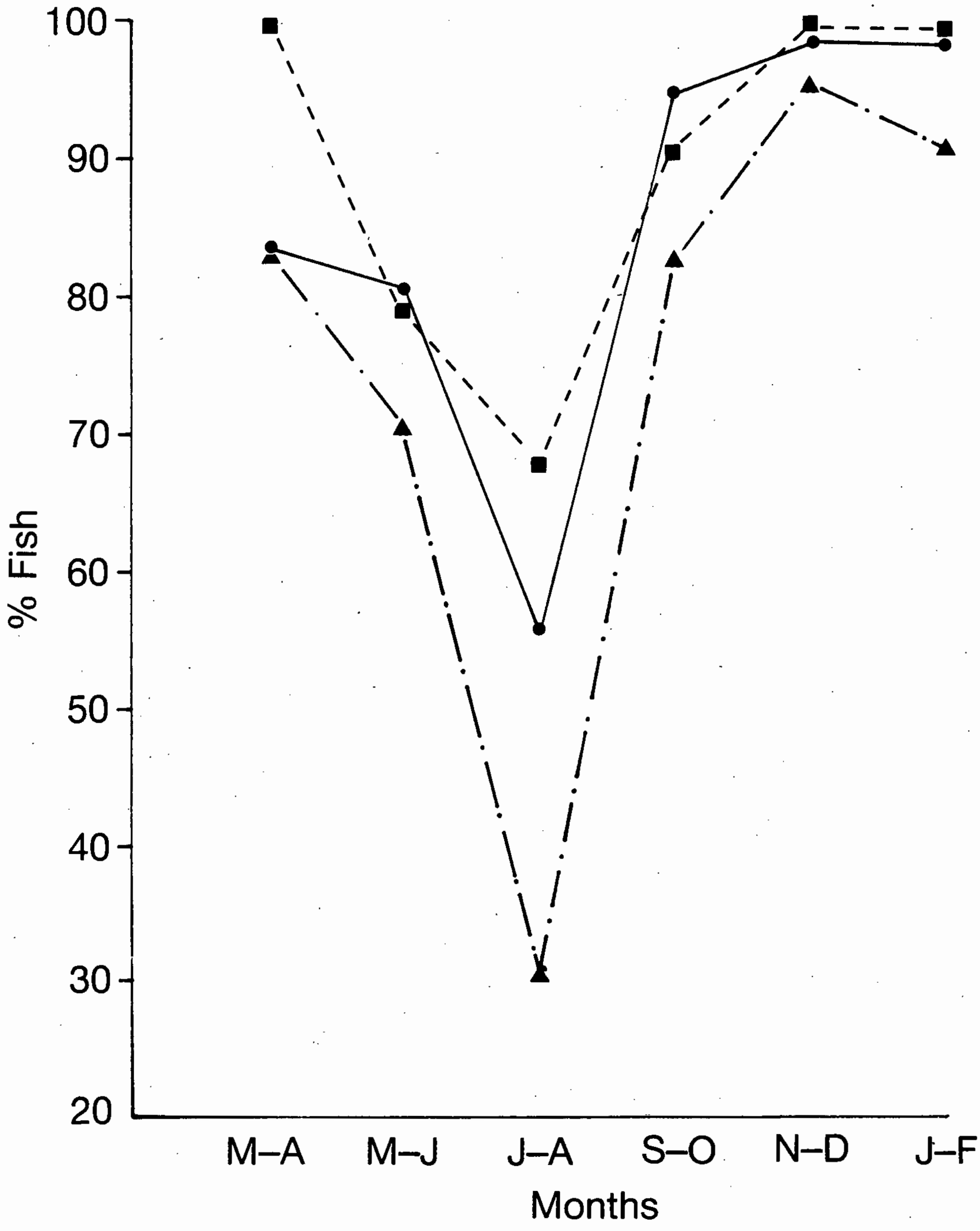

100
90
80
70
60
50
40
30
20
% Fish
M–A
M–J
J–A
S–O
N–D
J–F
Months

FIGURE 2

Per cent composition by numbers of the fish component of the diet of the King Penguin at Marion Island at two-month intervals. Numbers are mean number of otoliths per stomach sample. Figure legend: ▲——▲ ,Unidentified myctophids; ○——○,*Krefftichthyes anderssoni*/*Protomytophum tenisoni*;●—·—●, *Electrona carlsbergi*; ◆--·-◆ Myctophid A;◇——◇,*Protomyctophum normani*.

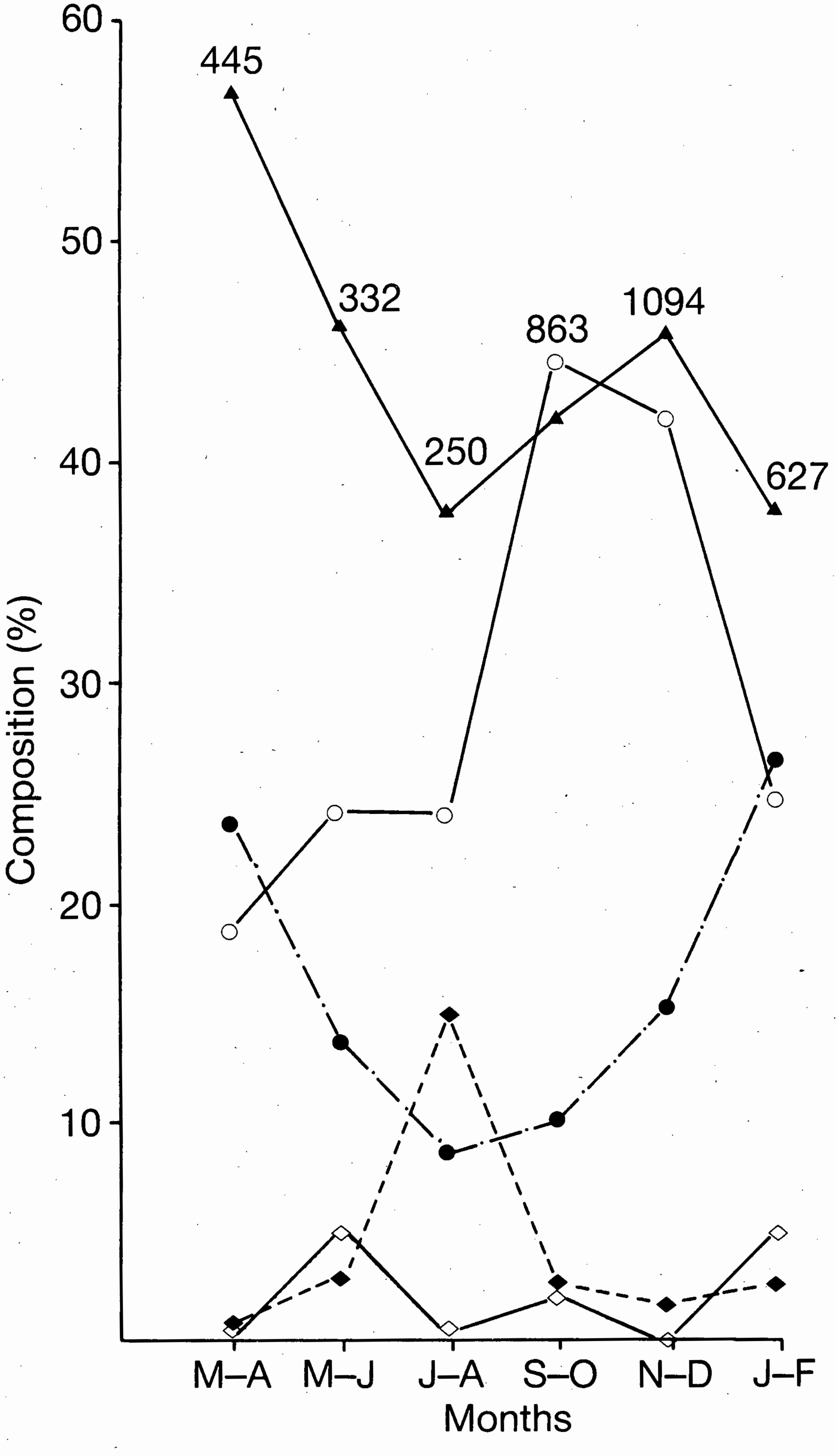

60
50
40
30
20
10
Composition (%)
445
332
250
863
1094
627
M–A
M–J
J–A
S–O
N–D
J–F
Months

FIGURE 3

Length-frequency distribution of otoliths of *Krefftichthys anderssoni*/*Protomyctophum tenisoni* species complex consumed by King Penguins at Marion Island. Estimated standard length and mass of whole fish is given on a separate scale.

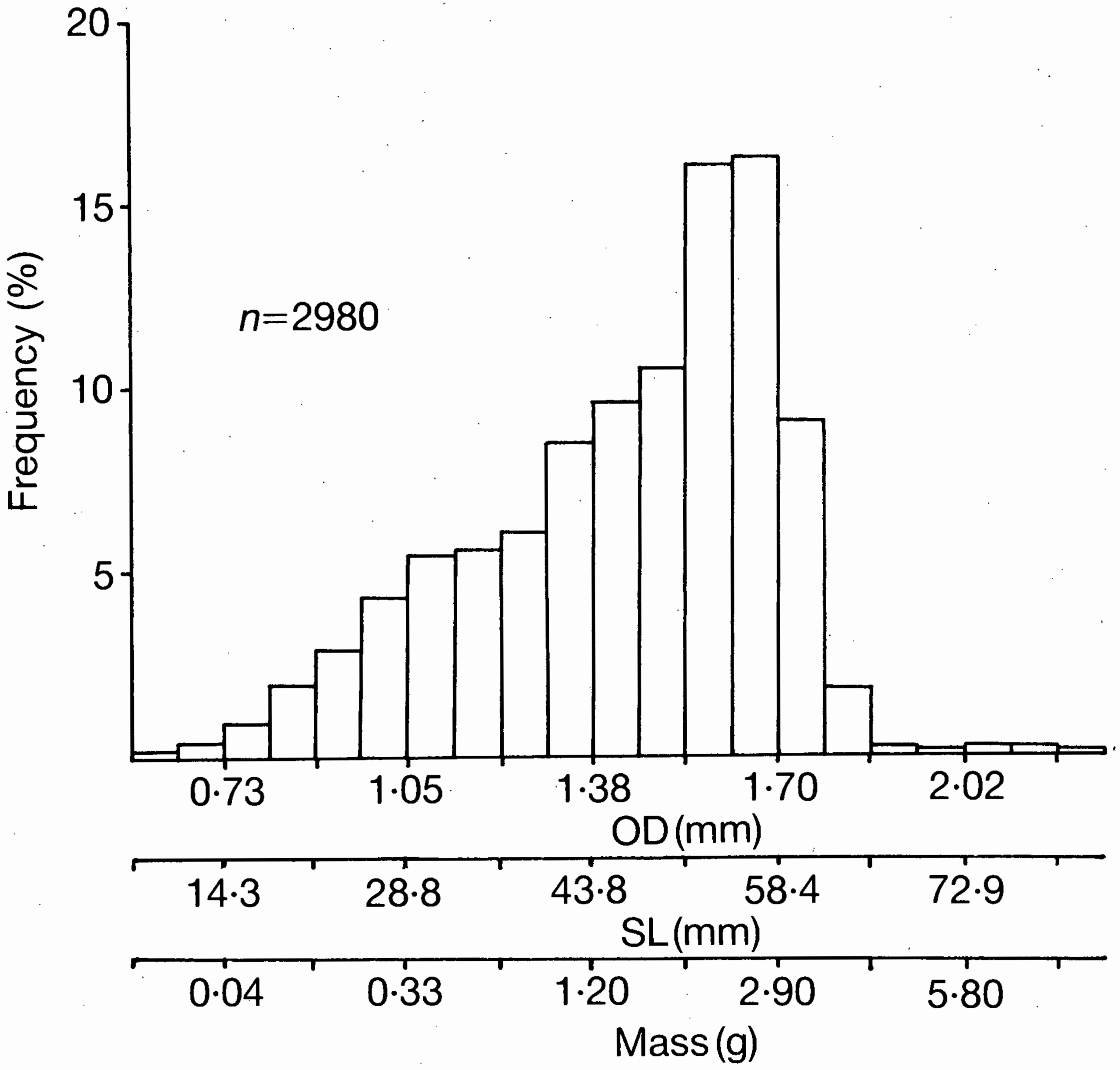
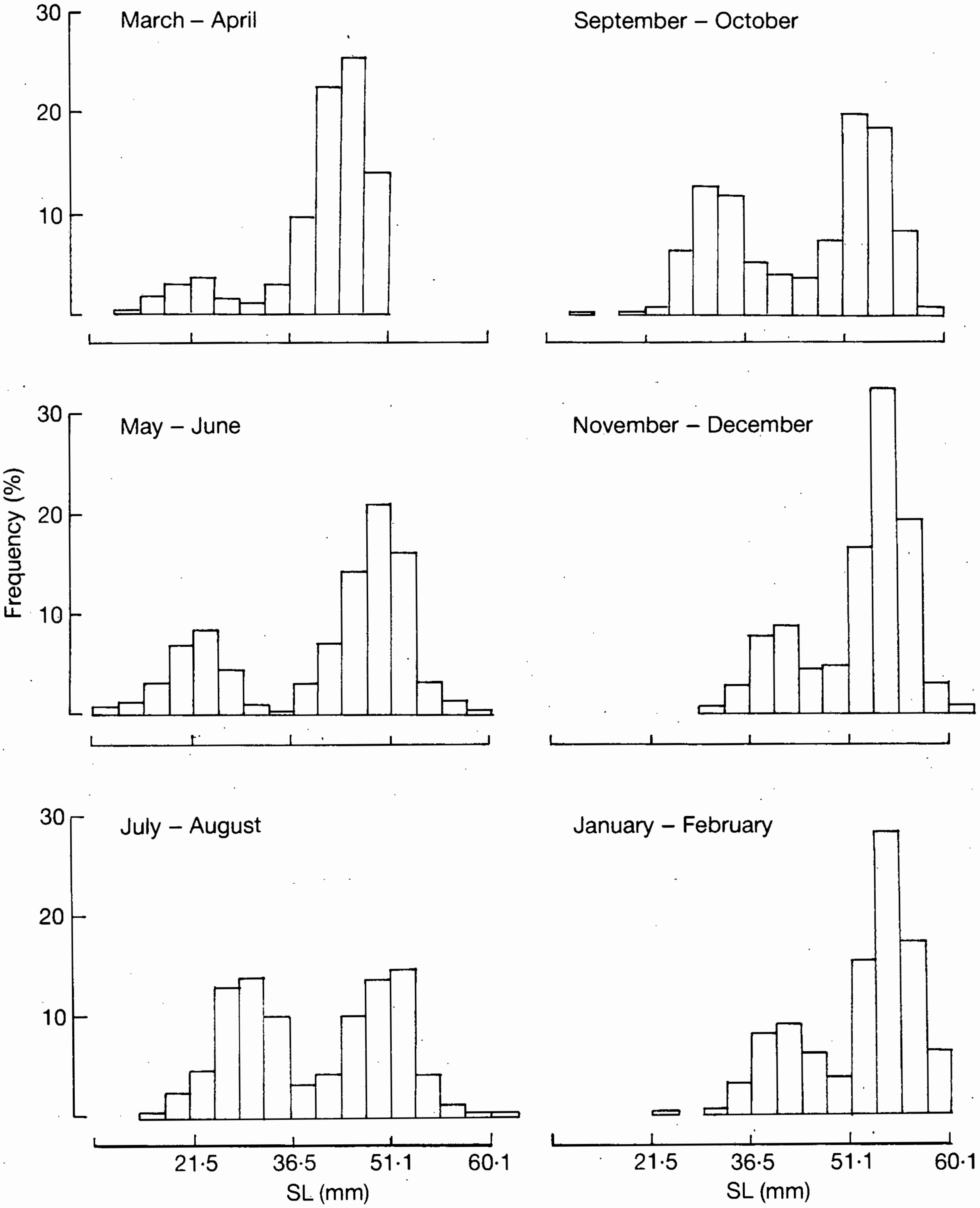

20
15
10
5
Frequency (%)
n=2980
0·73
1·05
1·38
1·70
2·02
OD (mm)
14·3
28·8
43·8
58·4
72·9
SL (mm)
0·04
0·33
1·20
2·90
5·80
Mass (g)

FIGURE 4

Length-frequency distribution of otoliths of _Krefftichthys anderssoni_/_Protomyctophum tenisoni_ complex consumed by King Penguins at Marion Island at two-month intervals.


March – April
September – October
May – June
November – December
July – August
January – February
Frequency (%)
30
20
10
21·5
36·5
51·1
60·1
SL (mm)

- April the larger size classes once again became relatively more important in the diet (Fig 4).

Ninety per cent of all E. carlsbergi taken by King Penguins were within the size range 5.1 - 11.8 g (70.6 - 98 mm: SL) (Fig. 5), with no evidence of a change in size-class distribution through the year.

A summary of the relevant parameters of the less common fish is included in Table 3.

Squid:

Kondakovia longimana was the dominant identified squid species in the diet of the King Penguin at Marion Island throughout the year (Fig. 6); relative abundance of other identified squid species remaining below 1 %.

Forty-five per cent of squid beaks removed could not be measured due to excessive wear. The percentage of non-measureable beaks recovered from chick stomach samples was significantly higher than from adults ($P < 0.01$). However, there was no significant difference in absolute numbers of measureable beaks recovered from chick and adult stomach samples ($P > 0.05$). 1 070 lower beaks were measured, of which K. longimana comprised 933 (87.2 %). Specimens of this species ranged from 5 g (DML: 45 mm) to 481 g (DML: 273 mm). However, about 90 % of all specimens were less than 61 g (DML: 131 mm), with a modal size of 11 to 15 g (DML: 67 to 75 mm) (Fig 7). Plotted on a two-month basis the size-frequency distributions show a gradual increase from March - April (modal size class: 2.2 - 2.5 mm LRL) to July

FIGURE 5

Length-frequency distribution of otoliths of <u>Electrona carlsbergi</u> consumed by King Penguins at Marion Island. Estimated standard length and mass of whole fish is given on a separate scale.

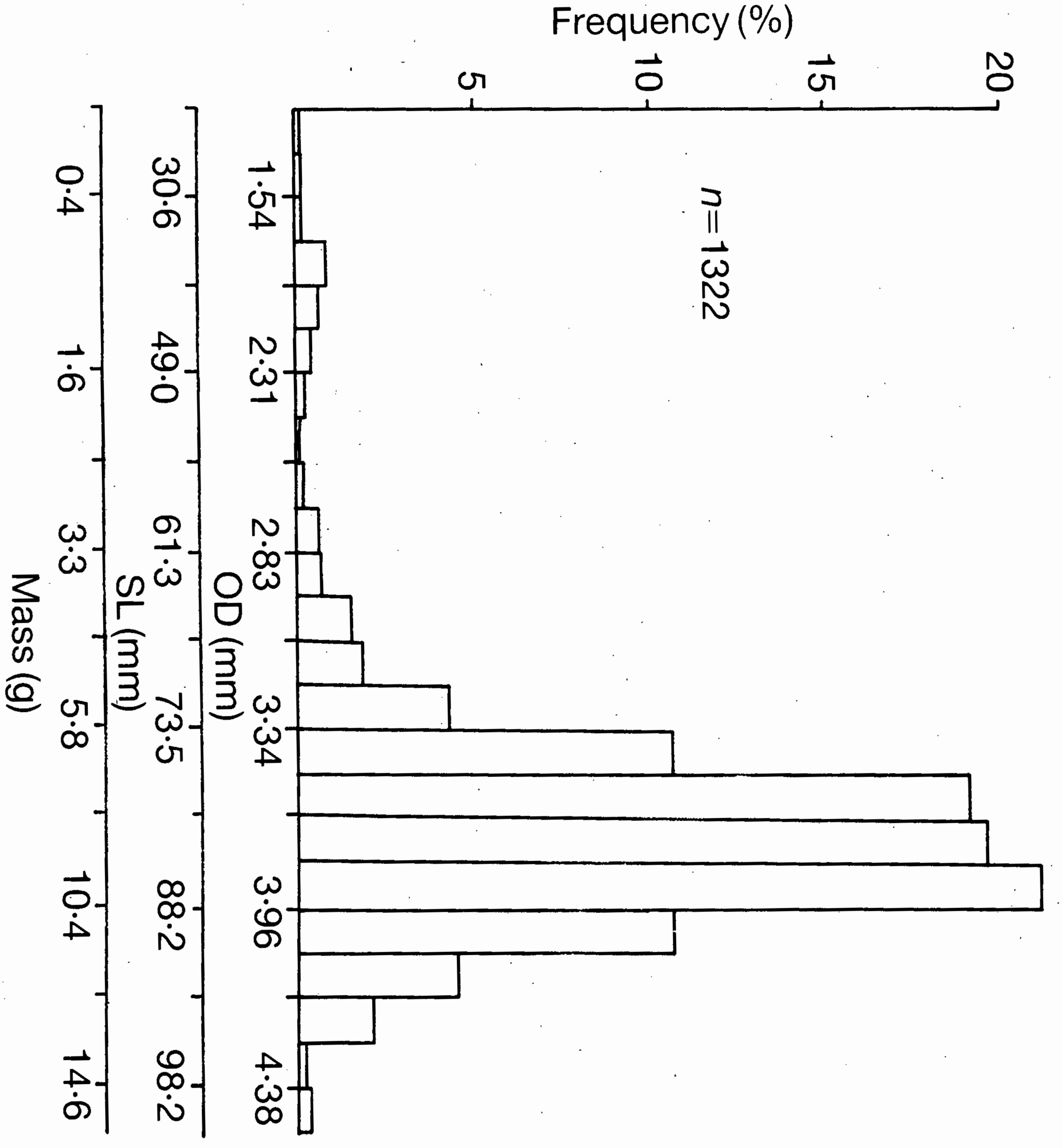

Frequency (%)
5
10
15
20
n=1322
1·54
2·31
2·83
3·34
3·96
4·38
OD (mm)
30·6
49·0
61·3
73·5
88·2
98·2
SL (mm)
0·4
1·6
3·3
5·8
10·4
14·6
Mass (g)

TABLE 3

Summary of otolith diameter (OD), standard length (SL) and mass of fish removed from King Penguin stomach samples from Marion Island

Species		OD (mm)			SL (mm)			Mass (g)		
	N	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
<u>Krefftichthys andersoni</u>	2 980	1.5	0.2	0.7-2.4	48.3	10.1	10.6-92.0	1.9	1.0	0.02-12.0
<u>Protomyctophum tenisoni</u>										
<u>Electrona carlsbergi</u>	1 332	3.7	0.4	1.0-4.5	82.3	6.2	17.3-101.1	8.7	2.1	0.1-16.0
Myctophid A	381	2.2	0.4	0.9-3.1						
<u>Protomyctophum normani</u>	214	2.4	0.2	1.5-2.8	79.7	8.0	43.5-124.8	6.4	1.8	0.7-11.0
<u>Gymnoscopelus</u> sp.	46	4.1	1.5	2.1-6.4						
<u>Paralepis coregonoides</u>	86	4.2	1.2	3.6-6.3						
<u>Protomyctophum bolini</u>	82	2.3	0.1	1.8-2.6						
<u>Notothenia squamifrons</u>	1	2.0			50.7			2.6		
<u>Notothenia magellanica</u>	11	2.1	0.2	2.0-2.5	115.6	16.7	103.1-162.4	34.1	22.0	24.0-93.8

FIGURE 6

Per cent composition by numbers of the squid component of the diet of the King Penguin at two-month intervals. Numbers are mean number of lower beaks per stomach sample. Figure legend: ●——● *Kondokovia longimana*; ○——○, Onychoteuthidae > 2mm LRL; ▲—·—▲ Onychoteuthidae < 2mm LRL; △······△ , Decapoda squid > 1mm LRL; ■- - -■, Decapoda squid < 1mm LRL.

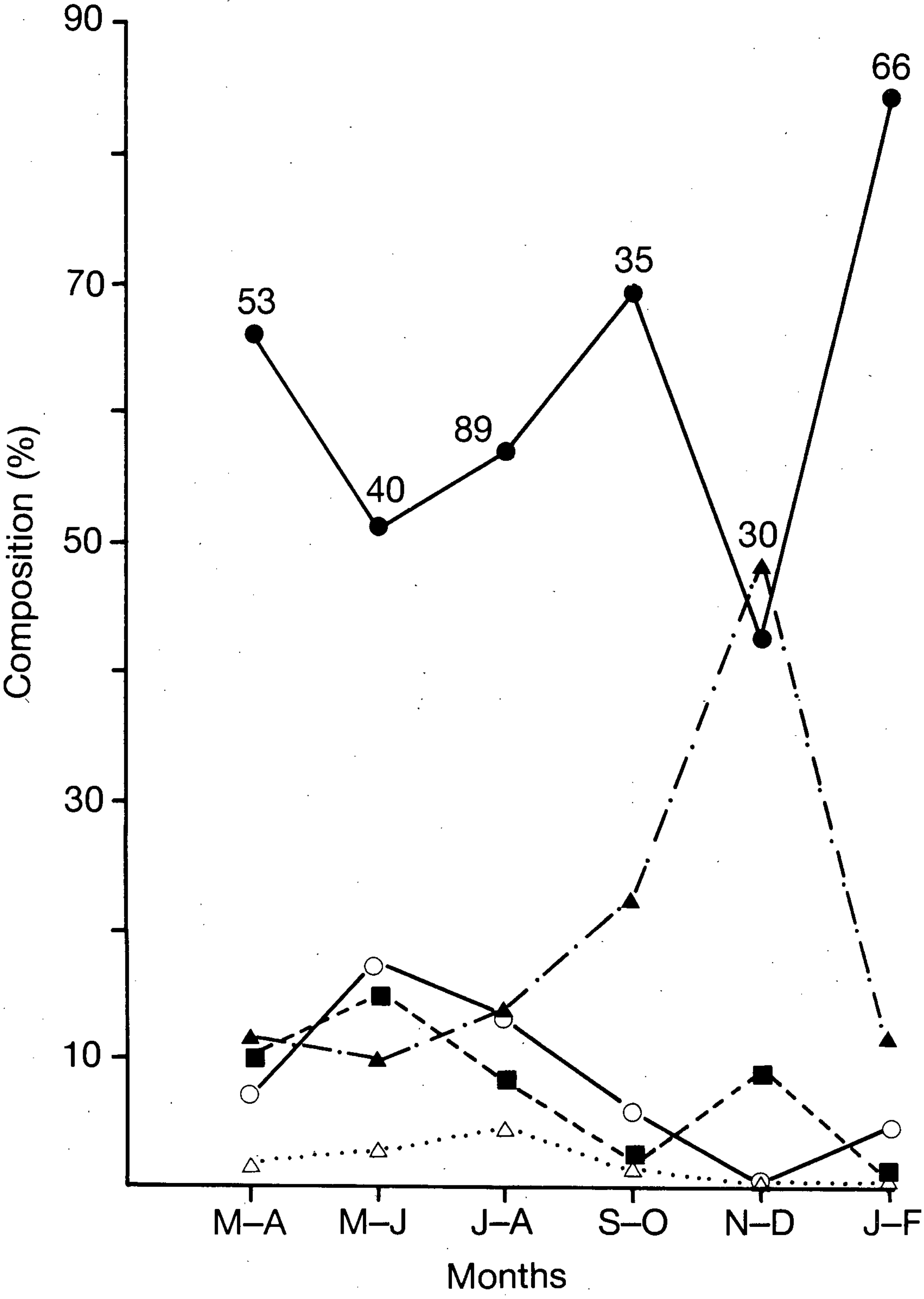
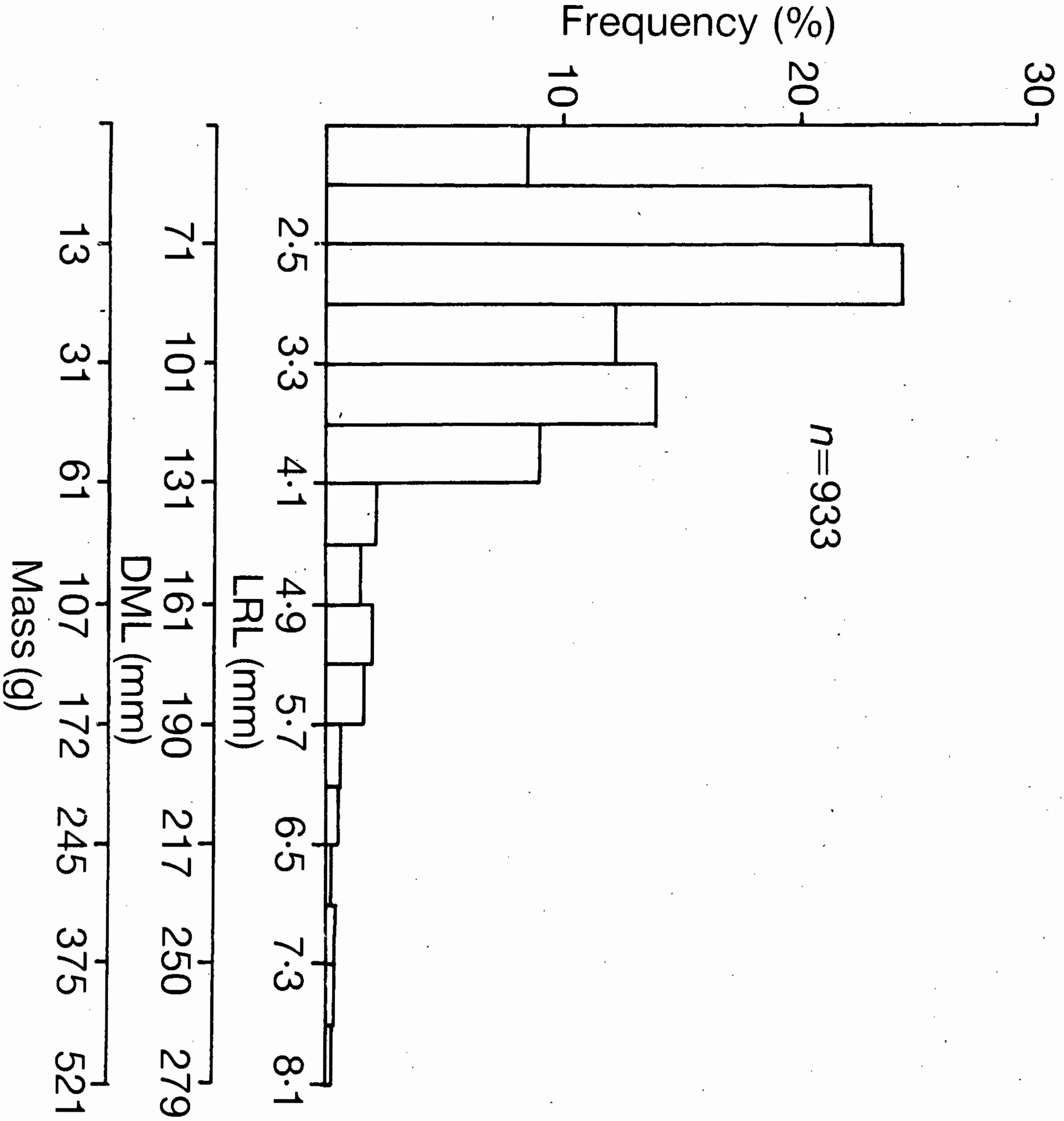

90
70
50
30
10
Composition (%)
53
40
89
35
30
66
M–A
M–J
J–A
S–O
N–D
J–F
Months

FIGURE 7

Length-frequency distribution of lower rostral length of beaks of *Kondokovia longimana* consumed by King Penguins at Marion Island. Estimated dorsal mantle length and mass of whole squid is given on a separate scale.



Frequency (%)
10
20
30
n=933
2·5
3·3
4·1
4·9
5·7
6·5
7·3
8·1
LRL (mm)
71
101
131
161
190
217
250
279
DML (mm)
13
31
61
107
172
245
375
521
Mass (g)

- August (modal size class: 3.4 - 3.7 mm LRL), with small squid again appearing in the diet in September - October (Fig. 8). This was followed by another progressive increase in the modal size class of K. longimana from 2.2 - 2.6 mm LRL in September - October to 5.3 - 5.7 mm LRL in January - February. However, sample sizes of measured beaks in November - December and January - February were low (< 25 per two-month interval) and the results may not reflect real trends. Sample sizes of measured beaks from other identified species of squid were also low (< 15), and a summary of the results is presented in Table 4. The largest squid, Moroteuthis sp., taken by a King Penguin was estimated at 807 g.

DISCUSSION

Biases in analysis:

Analysis of the highly digested stomach samples recovered from King Penguins introduces a number of biases due to differential digestion rates of both hard and soft part remains. Squid fed to captive seabirds take longer to be evacuated from the stomach than do fish (Wilson et al. 1985, Jackson & Ryan 1986). Chitinous squid beaks are also more resistant to digestion than the calcium carbonate of fish otoliths. A Shy Albatross Diomedea cauta and Whitechinned Petrels Procellaria aequinoctialis retained large squid beaks for 38 d and 24 d, respectively, at which time they were still relatively uneroded (Furness et al. 1984, Jackson & Ryan 1986). The generally small and unpigmented beaks that occur in King Penguin stomachs may, however, be digested considerably faster (see Imber 1973, Imber & Berruti 1981). In contrast to the long retention time of squid beaks, Duffy and Laurensen (1983) estimated a 25 % reduction in

FIGURE 8

Length-frequency distribution of lower rostral length of beaks of *Kondakovia longimana* consumed by King Penguins at Marion Island at two-month intervals.

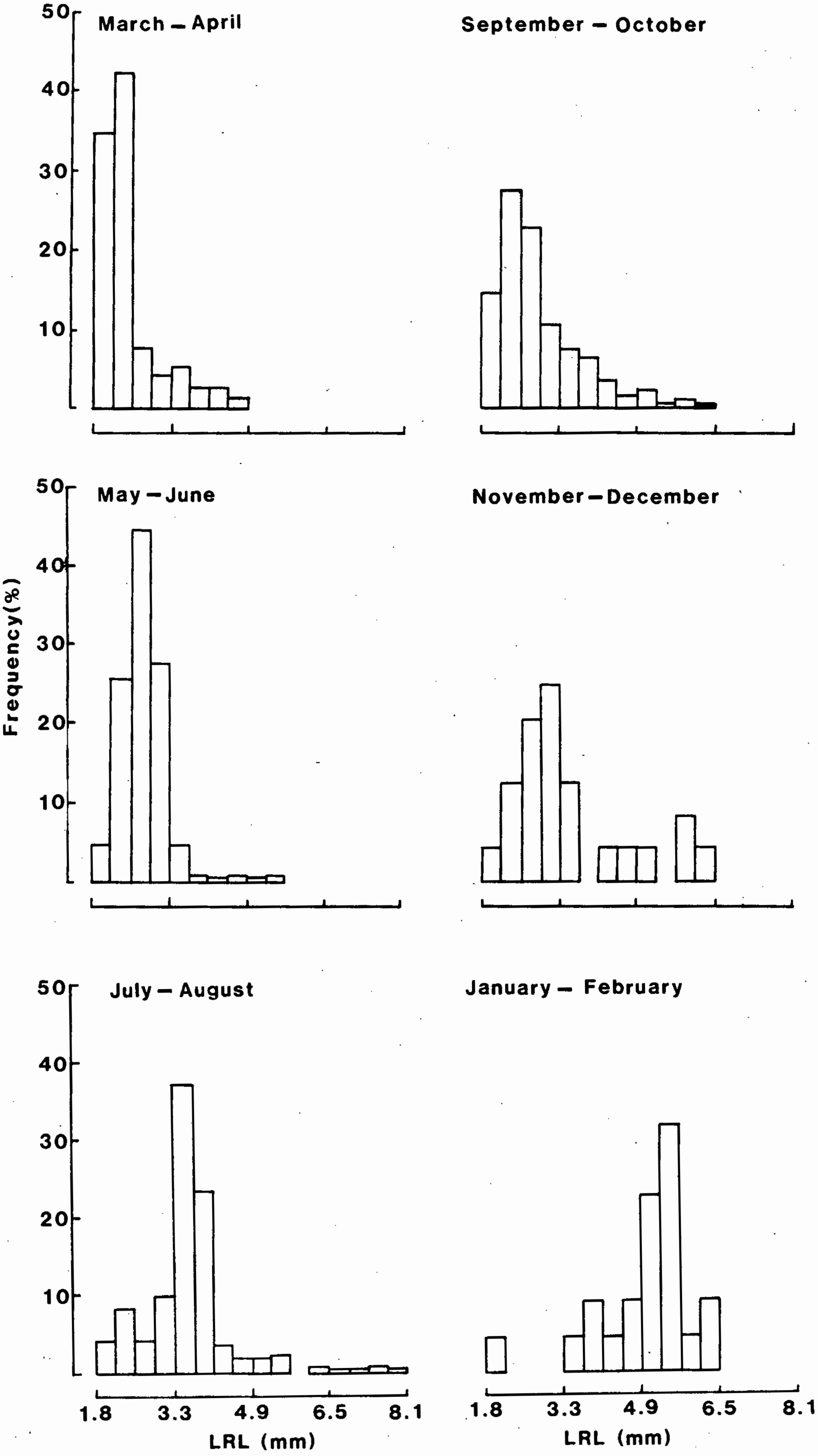

March – April
September – October
May – June
November – December
July – August
January – February
Frequency(%)
50
40
30
20
10
1.8
3.3
4.9
6.5
8.1
LRL (mm)

TABLE 4

Summary of lower rostral length (LRL), estimated dorsal mantle length (DML) and mass of squid recovered from King Penguin stomach samples from Marion Island

Species	N	LRL (mm)			DML (mm)			Mass (g)		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Kondakovia longimana	933	3.1	0.7	1.8-7.9	73.0	26.0	45.0-273.0	34.0	23.0	5.0-481.0
Oegopsid A	36	1.9	0.7	1.5-3.3						
Histioteuthis sp.	12	2.4	1.3	2.6-3.6	55.7	6.1	44.1-66.4	68.7	13.6	44.7-94.9
Alluroteuthis sp.	16	3.6	0.5	2.6-4.6						
Moroteuthis sp.	19	4.6	1.2	2.8-6.9	146.6	95.3	12.3-324.1	257.0	258.4	23.4-807.2
Martialia hyadesi	5	5.4	1.0	3.9-6.4						
Gonatus antarcticus	8	2.5	0.7	2.0-4.0	6.4	2.8	4.2-12.8	13.4	16.3	5.2-52.5
Galiteuthis glacialis	3	4.1	0.5	3.7-4.6	178.0	19.2	163.1-199.8	55.9	15.6	44.2-73.6
Brachioteuthis sp.	1	2.0								

otolith length from ingestion of whole fish by Cape Cormorants Phalacrocorax capensis to production of regurgitation pellets between half and one day later. Jackson and Ryan (1986) noted that whole fish fed to Whitechinned Petrels were completely digested, including otoliths, within 12 h of ingestion. Therefore, otoliths present in the stomach of King Penguins probably represent the accumulation of fish caught on one foraging trip only, although accumulation over more than one day is presumably possible in some circumstances, as evidenced by some very large reconstituted meal sizes (e.g. 6 012 g) consisting largely of fish. Studies of the diets of seabirds based on analyses of highly digested stomach contents and accumulated hard parts will therefore overestimate the importance of squid, and in particular large squid in relation to fish.

The effect of these biases is well illustrated when diet composition is compared using different methods of analyses (Table 2, Fig. 1, J-A). The smaller proportion of the diet made up by fish in terms of % numbers relative to % mass reflects the long residence time of squid beaks compared with that of otoliths. The even smaller % fish by reconstituted mass reflects the longer residence time of large squid beaks compared with that of small beaks. The significantly higher percentage of non-measureable beaks in chick samples compared to adult samples is then not surprising, because adults are presumably offloading accumulated squid beaks to chicks when regurgitating food.

In spite of these biases favouring overestimation of the relative importance of squid, our results indicate that the diet of the King Penguin at Marion Island is predominantly fish. Irrespective of the method of calculation, fish account for more than 70 % of the diet for at least 10 months of the year and nearly 100 % of the diet from November - December to January - February. Previously it had been implicit in the literature that King Penguins were largely squid feeders (Biomass Working Party on Bird Ecology 1980, Croxall 1984), although the observations underlying this assumption were made at localities farther south than the Prince Edward Islands and were based on poorly documented evidence. Other studies of the diets of Southern Ocean predators based on identification of accumulated hard parts may have underestimated the importance of fish.

Fish:

At Marion Island the fish component of the diet of the King Penguin is accounted for almost entirely by pelagic myctophids. The three most abundant species of fish in its diet have a wide distribution throughout the Southern Ocean. Krefftichthys anderssoni and Protomytophum tenisoni can be regarded as broadly Antarctic species (Hulley 1981). Electrona carlsbergi occurs in waters close to the Antarctic continent (Linkowski 1983) northwards to the Subtropical Convergence (Krefft 1974). The only non-myctophiform species recovered, Notothenia squamifrons and N. magellanica, rarely occurred in the diet of the King Penguin.

The decrease in relative proportion of fish in the diet from March - April to July - August corresponds with a decrease in the numbers of King Penguins and in the growth rate of the chicks at Marion Island (Chapter 11). The subsequent increase in the relative proportion of fish to nearly 100 % from November - December to January - February corresponds with an increase in the chick growth rate and increase in numbers of King Penguins, and hence population energy demand. This suggests that the increase in the abundance of fish, relative to squid, over these months may represent a real increase in the availability of fish around the Prince Edward Islands. A similar pattern of fluctuation in penguin numbers and chick growth rate occurs at South Georgia (54^{o}S,37^{o}W) (Stonehouse 1960) and Crozet Islands (46^{o}30'S,52^{o}30'E) (Barrat 1976), suggesting a similar seasonal variation in prey availability.

The bimodal size-frequency distribution of the _K. anderssoni_/_P. tenisoni_ complex indicates that two age classes are being exploited by King Penguins. _Krefftichthys anderssoni_ is probably sexually mature at about 54 mm SL, and _P. tenisoni_ at about 45 mm SL (Hulley 1981). The smaller size classes therefore represent juvenile fish, whereas the larger size class may be considered adult from at least May to February. The increase in the modal size of the small size class from a minimum in March - April to a maximum in January - February is paralleled by an increase in the modal size class of the larger size class over the same period. The bimonthly increases in the modal size classes may represent growth of a relatively stationary and homogeneous population or the migration of populations of different size classes in and out of the area exploited by King Penguins at Marion Island. The progressive increase in the modal size class throughout the year suggests the former explanation to be the most likely.

Sixty per cent of all E. carlsbergi consumed by King Penguins at Marion Island fall within the size range 73.5 - 88.2 mm SL (Fig. 5). Electrona carlsbergi is probably sexually mature at about 83 mm SL (Hulley, 1981). Therefore, King Penguins at Marion Island take largely adult or near adult E. carlsbergi.

Everson (1977) in part attributed the presumed absence of fish as an important prey item for Southern Ocean pelagic predators to the paucity in the region of obligate shoaling fish. However, the occurrence of a large number of these generally small fish in the diet of the King Penguin suggests that myctophids may frequently occur in dense shoals around the Prince Edward Islands. Given the wide distribution of myctophid fish and their probable tendency to occur in shoals these fish may prove to be an important dietary component of other Southern Ocean vertebrate, pelagic predators. Recent studies of King Penguins at the Crozet Islands (Ridoux et al. 1988) and Macquarie Island (Hindell 1988) have confirmed the importance of myctophid fish in the diets of these birds at sites distant from Marion island.

Squid:

The total number of species or species groups of squid recovered from the stomachs of King Penguins is low in comparison to the number recovered from albatross regurgitations (Imber & Russ 1975, Berruti & Harcus 1978, Clarke et al. 1981). The limited foraging range (Adams 1987a), and the non-scavenging feeding behaviour of the King Penguin compared to that of the albatrosses are probable explanations of the low species richness.

Clarke (1980) suggests that the onset of spawning in Kondakovia longimana occurs around a DML of 500 - 580 mm, therefore the K. longimana taken by King Penguins at Marion Island are all immature. Although some larger individuals are consumed by King Penguins at Marion Island most squid taken are less than 61 g (131 mm DML). This may reflect: (i) the upper size limit of this squid that a King Penguin can comfortably handle; and (ii) differences in the vertical distribution of large and small squid. Larger squid may be generally restricted to water deeper than the King Penguin is able to exploit (cf Nemoto et al. 1985). Although these differences in vertical distribution of large and small squid are well established, the presence of large K. longimana beaks in regurgitation casts of five species of surface-feeding albatross occurring at Marion Island (Berruti & Harcus 1978, Imber & Berruti 1981, Brooke & Klages 1986) indicates that large squid do occur at shallow depths. Consequently, I consider the first explanation more likely.

Kondakovia longimana has been regarded as a cold water Antarctic species restricted to the distributional range of Antarctic krill Euphausia superba (Filipova 1972, Clarke 1980). However, the regular occurrence of juveniles in King Penguin stomach samples, and beaks of adults in regurgitation casts of albatrosses at Marion Island, suggest that K. longimana is the most abundant squid in the waters around the Prince Edward Islands.

Interpretation of trends in seasonal size-frequency distribution of K. longimana are made difficult by our current inability to identify beaks of < 1.8 mm LRL. However, the continued increase in the modal size of K. longimana from March - April to July - August suggests growth of an age cohort.

Foraging parameters and diet:

Myctophid fish are generally regarded as mesopelagic, occurring between depths of 50 - 2 500 m (Hulley 1981). In particular, Krefftichthys anderssoni forms a large proportion of the catch of krill nets trawled between 50 - 150 m south of the Antarctic Polar Front (APF) (Hulley 1981). Onychoteuthid squid, and in particular Kondakovia longimana, have been recovered from trawls between 10 and 200 m conducted north of the South Shetland Islands (60^{o}S) (Nemoto et al. 1985). The generally deep dives of the King Penguin, 50 % of which exceed 50 m (Kooyman et al. 1982), relative to those of other species of penguin (see Croxall & Lishman 1987) have been interpreted as reflecting the generally deeper distribution of its large squid prey at South Georgia (Lishman & Croxall 1983). Since concentrations of juveniles of otherwise deep-water squid may occur in shallow water (Tarasevich 1968, Clarke & Lu 1975, Nemoto et al. 1985) and the same may be true of fish, King Penguins at Marion Island, feeding on small squid and fish, may not need to dive deeply around Marion Island to encounter their prey.

Based on the average prey item of a 420 g squid, Croxall and Lishman (1987) calculated that a King Penguin need only be successful on 5 % of its dives during an average foraging trip in order to meet the energy requirements of both chick and adult. At Marion Island, the most abundantly taken prey items comprised 2.4 - 2.9 g Krefftichthys anderssoni or P. tenisoni, 8.5 - 10.5 g E. carlsbergi and 13 - 20 g Kondakovia longimana. King Penguins at Marion Island must encounter prey far more frequently than calculations suggest they do at South Georgia. The highly digested nature of King Penguin stomach samples, and the almost total absence in the bird's diet of fish species which form the largest part of the diet of the inshore foraging Gentoo Penguin (La Cock et al. 1984, Adams 1987b) indicate that King Penguins do not feed in the immediate vicinity of the islands. During spring and early summer, while feeding large chicks prior to fledging, the average maximum foraging trip of adult King Penguins is 600 km (Adams 1987a). Most of the prey during summer must therefore be taken within 300 km of the island. During winter , adult birds feeding chicks are away from the colony for longer periods than in summer (pers. obs) but it is not clear if adult penguins extend their foraging range or if they merely spend longer searching for prey within approximately the same distance from the island as during summer.

Comparison with other studies:

Gross descriptions of the diet of the King Penguin at South Georgia are given by Croxall and Prince (1980, 1982) in which squid account for 70 % by mass and 90 % by numbers. Todarodes aff. sagittatus, of average size 420 g, was the most common squid species recovered at South Georgia (Croxall & Lishman 1987). This is considerably heavier than the modal mass of approximately 13 g of K. longimana at Marion Island. King Penguins at Marion Island do take large squid comparable in size to those found in samples from South Georgia but only rarely. Larger squid may come closer to the surface in the generally colder surface waters around South Georgia and therefore be available to King Penguins. Kondakovia longimana was the only squid species common to King Penguins sampled at both Marion Island and South Georgia. Moroteuthis spp of mean mass 32.4 g were the most important species in the squid component of the diet of King Penguins at Macquarie Island. The low recovery by frequency of occurrence of fish from King Penguins (9.8 %) compared to cephalopods at the Crozet Islands (Barrat 1976), is in marked contrast to a more recent study. Ridoux et al. (1988) indicates that greater than 90 % by mass of diet was accounted for by myctophid fish. Similarly 92 % by mass of the diet of King Penguins at Macquarie Island was accounted for by two species of myctophid fish Krefftichthys anderssoni and Electrona carlsbergi (Hindell 1988). Given the wide distribution of some species of myctophid fish their occurrence in the diets of King Penguins elsewhere is not surprising.

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APPENDIX 1

Conversion formulas for fish species. Unless otherwise stated all dimensions are in mm and g.

The general relationship used to convert standard length (SL) of myctophids to total length (TL) was:

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

This regression is based on data from 19 individuals of 19 species of myctophids from the South Atlantic (P.A. Hulley, South African Museum, Cape Town; pers. comm.).

The relationships used to convert otolith diameter (OD) to SL or TL and SL or TL to mass (W) for individual species of fish are given below.

Protomyctophum normani

$$OD = 0.760 + 0.020 . SL \ (r^2 = 0.78, n = 18)$$

$$W = 3.93 \times 10^{-5} . TL^{2.599} \ (r^2 = 0.78, n = 11)$$

Krefftichthys anderssoni/Protomyctophum tenisoni

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

$$W = 5.36 \times 10^{-6} . TL^{3.082} \ (r^2 = 0.90, n = 16)$$

Electrona carlsbergi

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

$$W = 7.43 \times 10^{-6} . SL3.159 \ (r2 = 0.90, n = 60)$$

Notothenia magellanica (Hecht & Cooper, 1986)

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

$$W = 2.19 \times 10^{-5} . TL^{3.0} \ (r^2 = 0.99, n = 133)$$

Notothenia squamifrons

$$OD = 0.3298 + SL . 0.0335 \ (r^2 = 0.79, N = 63)$$

$$W = 6.4790 \times 10^{-4} . SL^{2.11}$$

Conversion formulas for cephalopod species are given below.

Abbreviations are dorsal mantle length (DML) and lower rostral lengths (LRL).

Kondakovia longimana

$$DML = -22.348 + 37.318 \,.\, LRL \ (r^2 = 0.95, n = 13)$$

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

Moroteuthis sp.

$$DML = -200.58 + 76.04 \,.\, LRL \ (r^2 = 0.8, n = 10)$$

$$\log W = 3.471 + 3.50 \,.\, \log LRL \ (\text{units : g, cm})$$

Histioteuthidae

$$DML = -1.36 + 22.21 \,.\, LRL \ (\text{units : cm, } n = 54)$$

$$\log W = 3.002 + 2.31 \,.\, \log LRL \ (\text{units : g, cm; } n = 53)$$

Gonatus antarcticus

$$DML = -4.34 + 42.87 \,.\, LRL \ (\text{units : cm, } n = 17)$$

$$\log W = 3.046 + 3.33 \,.\, \log LRL \ (\text{units : g, cm; } n = 20)$$

Galiteuthis sp.

$$DML = 12.2 + 40.78 \,.\, LRL \ (n = 39)$$

$$\ln W = 0.728 + 2.34 \,.\, \ln LRL \ (n = 38)$$

Ommastrephidae

$$W = 1737.8 \,.\, LRL2.93 \ (\text{units : g, cm; } n = 156)$$

A regression of LRL versus DML for _Martialia hyadesi_ is not available.

CHAPTER 3

FORAGING RANGE OF KING PENGUINS *APTENODYTES PATAGONICUS* DURING SUMMER AT MARION ISLAND

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Foraging ranges of King Penguins Aptenodytes patagonicus were estimated by combining information on the feeding rates to chicks and brood shift lengths of adults (assessed by daily weighings of large chicks and daily checks of marked birds brooding small chicks) with measurements of travelling speeds and activity budgets at sea (assessed using remote recording devices). Adults brooding small chicks were relieved on average every 13 days and large chicks were fed every 4 days. Adults with large chicks spent 36 % of their time between attachment of device and recapture travelling at an average speed of 8.7 km.h-1. This gives an estimated mean maximum foraging range of about 300 km. Adults attending small chicks spent 19 % of their time away swimming, giving an estimated maximum foraging range of 225 km. Extreme foraging ranges for all birds were 75 and 902 km for penguins returning between 2 and 24 days at sea, respectively. Total distance travelled was highly correlated with time away from the colony.

INTRODUCTION

Until recently, only indirect estimates of the distances travelled by pelagic foraging seabirds were available. In particular, the length of time between successive visits to feed chicks combined with estimates of travelling speed have been used to give an indication of potential foraging distances (e.g. Croxall & Prince 1980, Williams & Siegfried 1980, Lishman 1985). However, Trivelpiece et al. (1986) have shown that the total time away from the colony may be a poor indicator of time spent travelling. The development of shore-based radio-telemetry techniques (Trivelpiece et al. 1986) has allowed foraging movements of breeding seabirds to be monitored directly, but application of this technique is at present restricted to inshore foragers because of range limitations of equipment. The foraging trips of King Penguins Aptenodytes patagonicus at South Georgia are 5.6 days (Croxall, Ricketts & Prince 1984), and the birds cover large distances out of range of shore-based telemetry. I present here estimates of the foraging ranges of King Penguins derived by combining measurements of travelling speeds and activity budgets at sea, obtained using remote recording devices.

MATERIALS AND METHODS

The study was conducted at a breeding colony of 700 - 1 000 pairs of King Penguins at Archway Bay, Marion Island ($47^{o}52'$S, $37^{o}51'$E) from September to December 1984 and March to April 1985. From September to December adult birds were feeding large chicks (8 - 10 months old) prior to fledging, and during March and April adults were brooding small chicks (2 - 5 weeks old).

Travelling speed and travelling time:

Travelling speed and travelling time were measured using speedmeters (Wilson & Bain 1984) attached with adjustable hose clamps to feathers along the dorsal midline of the penguins (Lishman & Croxall 1983). The meters consist of a compression spring with terminal bung mounted inside a cylindrical tube. The speed of travel through the water determines the amount of compression of the spring. Meters recorded speeds within the range 3.4 to 10 km.h-1. A sealed radioactive bead in the bung exposes an X-ray sensitive film sealed inside a light-tight, waterproof, plastic sachet taped to the outside of the tube. The type of film can be selected on the basis of bead activity. For high activity beads I used Kodak X-omat K, a film with a slow response to ionising radiation. For low activity beads I used a fast film, Kodak Direct Exposure Film (D.E.F.). The faster the film, the more sensitive is its response to radiation from the bead.

Twenty speedmeters, containing X-omat K as the X-ray sensitive film, were attached to adult King Penguins captured while feeding chicks on 29 and 30 September. Each adult was individually marked on its chest using picric acid and weighed to 0.1 kg on a Pesola spring balance. The colony was subsequently searched daily any time between 13h00 and 17h00 for 85 d for returning adults. Meters were recovered from adults on the first occasion they were observed back at the colony. Recaptured adults were weighed, speedmeters removed, and the date and time noted. An additional 11 speedmeters were attached to adults captured on 19 and 20 December, following the procedure described above. From 3 - 15 March 1985, 36 meters, using D.E.F. as the X-ray sensitive film, were attached to King Penguins brooding chicks. To minimize disturbance and reduce the risk of desertion, these adults were not weighed. The departure dates of penguins with meters were noted. On their arrival back at the colony, the meters were removed and the dates noted.

Speedmeter analysis:

All films were processed at Marion Island (to avoid the problem of latent image fading) using Kodak GBX developer and fixer. The radioactive bead typically exposes the film in two places, the zero position representing the penguin at rest and another representing the normal travelling speed of the penguin in question. All meters had previously been calibrated for bung movement against speed through the water on a model of a penguin. The distance between the exposed positions is therefore a measure of the travelling speed. The meters have an insignificant effect on travelling speed because the cross-sectional area of the speedmeter is small compared to that of the penguin at its broadest section (< 2 %) (see Wilson et al. 1986).

The time spent travelling is determined by reading the density of the exposure of the travelling trace. Normal procedure is initially to calibrate the exposure density against exposure time (Wilson & Bain 1984). This is different for every bead, since each has its own specific activity. The duration of travelling at any particular speed can therefore be determined by comparing the exposure density with calibration exposures. This procedure is only valid if measurements and calibration are determined over a small fraction of the half life of the radioisotope used. In this study ^{32}P was used as the radioactive source. Since ^{32}P has a half life of only 14.3 d and meters were attached to birds for up to 65 d, I used a modified method for determining travelling time from the film. The density of the travelling trace was divided by the density of the travelling trace plus the zero trace. This fraction was then multiplied by the total time the meter was attached to the bird. This gives the total amount of time the bird was travelling within the period the meter was attached. This method assumes that exposure density is linearly related to exposure time. To test this, I determined the relationship between exposure density and exposure time for X-omat K and DEF. The relationship was linear up to an optical density of 2.30 and 2.00 respectively. The highest density measurements for films retrieved from the King Penguins were 2.89 for X-omat K and 1.28 for DEF. I therefore discarded four X-omat K traces with optical densities > 2.30. A second assumption is that King Penguins distribute their activity equally throughout the period the meter is attached. I have no data to test this, but a systematic bias would seem unlikely.

Feeding frequency and brooding shifts:

Fifteen chicks were captured at the beginning of October and individually marked with soft plastic strips tied around the upper part of their flippers. These chicks were weighed to ± 0.1 kg every day for 72 - 77 d during the period speedmeters were attached to adult penguins. To minimize the period of disturbance to the colony, all chicks to be weighed were captured and placed in a temporary holding pen until processed. A feed was considered to have taken place if a mass increase of > 200 g between two consecutive weighings was detected; increases of < 200 g were attributed to weighing error and were not considered to imply a feed. The maximum frequency at which a meal could be detected was 1 d and it is possible that I underestimated feeding frequency as a result. However, Lishman (1985) found no significant differences between feeding frequencies of chicks of Chinstrap Penguins _Pygoscelis antarctica_ and Adelie Penguins _P. adeliae_ calculated from daily or 3 h weighings, although both these species feed their chicks more frequently than do King Penguins (see below). Brooding shifts of adults attending small chicks were determined by individually marking adult penguins brooding chicks and then making daily checks to record arrivals and departures.

RESULTS

Eighteen of the 20 meters attached in September were recovered at a mean of 36.9 ± 10.9 d (range 18.2-65.0 d) after attachment. Eight of the film traces could be analysed for travelling speed and only four of these for time, but these included the two birds recaptured after the minimum and maximum recorded periods away. Six of the 11 meters attached in December were recovered at a mean of 13.0 ± 7.5 d (range 1-19 d) after attachment. Only three traces were suitable for speed analysis and only two for time. Ten of 21 adults recovered with speedmeters had gained mass whereas 11 were lighter. Average mass change was negligible, at 0.12 ± 2.04 kg. The remaining three birds were recovered in premoult condition and were on average 3.1 kg heavier. Twenty eight of the 36 meters attached in March were recovered at a mean of 12.8 ± 5.4 d (range 4 - 21 d). Only four meters could be analysed for travelling speed and three of these for travelling distance.

The high number of unreadable films was due mainly to leaking sachets and was largely attributable to the long period of attachment and consequent wear of tape and plastic. In addition, by March, the activity of the radioactive beads was generally too low to expose even the fast film. I could not replace low activity beads as supply trips to Marion Island are restricted to the austral autumn and spring.

Travelling speed:

Average travelling speed for adult King Penguins was 8.7 ± 1.2 $km.h^{-1}$ (range 7.0 - 10.8 $km.h^{-1}$, n = 15). In all cases the travelling trace occurred as a single exposure indicating that the normal travelling speed of an individual does not vary significantly even over a period as long as 65 d. Within the size range of King Penguins measured there was no relationship between size (body mass) and travelling speed (r = 0.337, n = 12, P > 0.1).

Activity budget:

Adult penguins feeding large chicks spent 36.0 ± 5.5 % (range 28 - 44 %, n = 6) of their time, between attachment of the speedmeter and its retrieval, swimming. Adults feeding small chicks spent 19.0 ± 16.5 % (range 8 - 38 %, n = 3) of their time swimming.

Travelling distance:

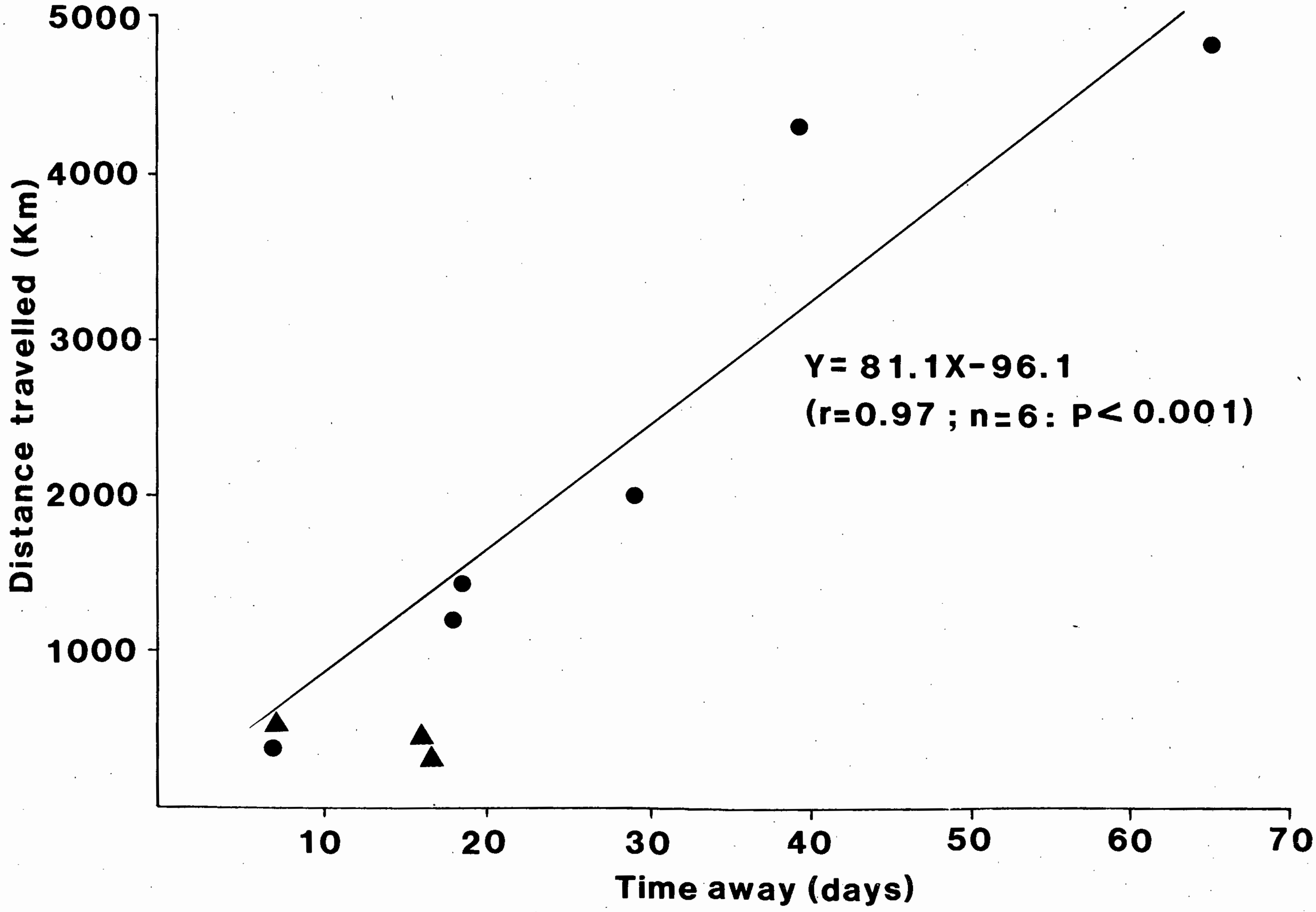
Travelling distance was highly correlated with the time that adult birds were away from the colony. For adults feeding large chicks:

$$y = 81.1x - 96.1 \quad (r = 0.97,\ P<0.001,\ n = 6)\ \text{(Fig. 1)}$$

Adults feeding large chicks travelled 73.8 ± 18.3 $km.d^{-1}$ (range 52 - 107 $km.d^{-1}$, n = 6), whereas those feeding small chicks travelled 38.3 ± 30.3 $km.d^{-1}$ (range 17 - 73 $km.h^{-1}$, n = 3). The difference is significant (t = 2.37, d.f. = 7, P < 0.05).

FIGURE 1

Relationship between distance travelled by King Penguin adults feeding large chicks at Marion Island and time between attachment and retrieval of speedmeter (●). Distance travelled by adults feeding small chicks at Marion Island are included for comparison (▲).


Distance travelled (Km)
5000
4000
3000
2000
1000
10
20
30
40
50
60
70
Time away (days)
Y= 81.1X-96.1
(r=0.97 ; n=6 : P< 0.001)

Feeding frequency and brood shifts:

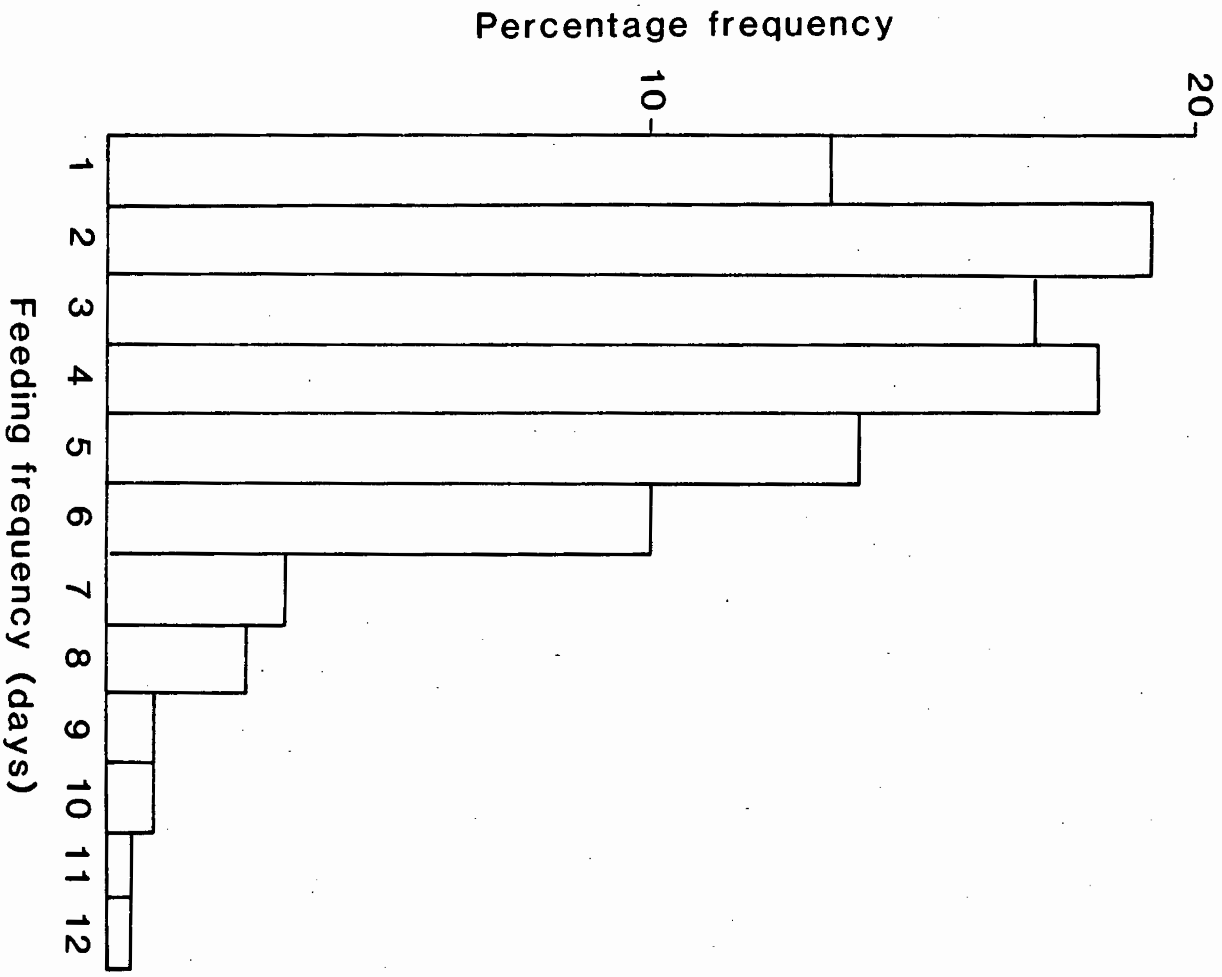
Two hundred and thirty eight feeds were recorded, spanning 1076 bird days. The average feeding frequency for 15 chicks was 4.0 ± 0.6 d (range 3.2 - 5.1 d) during the period October to December 1984. Average feeding frequency for individual chicks ranged from 3.2 ± 1.1 d (range 1 - 4 d) to 5.1 ± 3.2 d (range 1 - 12 d). Variability within individuals was greater than between individuals. Ninety five per cent of all feeds were delivered within seven days of the previous feed (Fig. 2). Assuming that parents take an equal share in feeding their chick, and that they feed it alternately , the mean interval between feeds by the same parent was 8.0 d (range 2 - 24 d). For King Penguins attending small chicks the period at sea between brood shifts lasted a mean of 12.8 ± 5.4 d (range 4 - 21 d, n = 28). Brood shifts progressively shorten through the brooding period (Stonehouse 1960) but I did not assess what stage of the brooding period individual chicks were at.

Foraging range:

Evidence from daily checks of the colony indicates that King Penguins spend < 24 h ashore at the colony when returning to feed large chicks. Logistical considerations meant that the colony could only be checked once daily, therefore I did not necessarily recapture metered birds after only one foraging trip except in the case of adults attending brooded chicks. To estimate foraging range I assumed that adult King Penguins fed chicks at the same intervals that I determined for individual adults from daily weighings of chicks. For adults feeding large chicks I assumed all birds travelled at 8.7 $km.h^{-1}$, returned to feed chicks every 8.0 d, and spent 36.0 % of their time at sea,

FIGURE 2

Feeding interval of King Penguin chicks' October - December 1984 at Marion Island.


Percentage frequency
10
20
Feeding frequency (days)
1
2
3
4
5
6
7
8
9
10
11
12

swimming. The estimated average travelling distance is then 602 km, giving a mean maximum foraging range of 301 km. Ninety five per cent of all foraging trips during this period could not have exceeded 526 km from Marion Island, and 68 % could not have exceeded 301 km. The minimum foraging range assuming a 2 d feeding interval (see above) is 75 km, and maximum foraging range assuming a 24 d interval (see above) is 902 km. For adults feeding small chicks I assumed all birds travelled at 8.7 km h^{-1}, returned to relieve brooding partners every 12.8 d and spent 19 % of their time at sea, swimming. The estimated average travelling distance is then 510 km giving a mean maximum foraging range of 255 km and a range of 80 - 418 km assuming minimum and maximum relief periods of 4 and 21 d (see above) respectively.

DISCUSSION

Travelling speed:

Mean normal travelling speed of the King Penguin is higher than that measured using the same technique for other Pygoscelid, Eudyptes or Spheniscid Penguins (Adams & Wilson 1987; Brown 1987, Wilson 1985, Wilson et al. 1989). The only previous measurement of King Penguin swimming speed is 12.1 $km.h^{-1}$, timed over a short measured course using a stop watch on captive individuals (Clarke & Bemis 1979). This value falls outside the range measured using speedmeters. However, this is a maximum swimming speed and it is not surprising that it is higher than the normal travelling speed recorded by the speedmeters. Maximum swimming speeds are probably only attained when avoiding predators or perhaps at prey capture. Because predators concentrate mainly in the inshore area during summer

(Condy et al. 1978), only a small proportion of the total swimming time is likely to be spent at maximum speed.

Travelling speeds of King Penguins varied from 7.0 - 10.8 $km.h^{-1}$, but individual penguins showed no detectable variation (< 0.5 $km.h^{-1}$) in travelling speed. This is the case for other species of penguins and continues to support the concept of an energetically optimum travelling speed. There is a threshold value below which meter response is minimal, however, this is low (approximately 3.0 $km.h^{-1}$) and evidence from other penguin species suggests they do not swim at low speeds for sustained periods (see Adams & Wilson 1987). Meters do not record swimming on the surface but we consider the distance covered in this manner to be negligible (see Adams & Wilson, 1987).

Activity budget:

Assuming that birds spent an insignificant time ashore when feeding chicks (maximum average error is 12 %), King Penguins swam underwater 9 h of every 24 h at sea when feeding large chicks. If birds spent longer ashore then the proportion of time spent swimming while at sea would increase. King Penguins feeding small chicks spent only 4.5 h of every 24 h swimming underwater. Travelling time as measured by the speedmeter will include time swimming underwater searching for prey. This indicates King Penguins feeding large chicks spend more time foraging than do adults feeding small chicks. The obvious inference that adults with large chicks need to forage for longer than do adults with small chicks may not necessarily be correct (see later).

Variability in time spent swimming per day (and consequently in distance travelled per day), expressed as a fraction of the mean daily travelling distance, is considerably less for the long-ranging King Penguin than for the short-ranging Gentoo, Adelie, Chinstrap and Jackass Penguins (Adams & Wilson 1987, Wilson 1985, Wilson et al. 1989). Variability is particularly low for King Penguin adults feeding large chicks. Although measurement of travelling distances over a long period of time will have the effect of smoothing out day to day variations, the low variability may be a direct consequence of the need to travel considerable distances to and from foraging areas well offshore. As travelling time increases relative to foraging time, so, total variability in time away should decrease.

Foraging range:

Feeding frequency is more variable within individuals than between individuals and presumably reflects large variations in foraging distance due to changes in prey distribution from foraging trip to foraging trip. Based on a feeding frequency of 5.6 d for an individual adult King Penguin (Croxall, Ricketts & Prince 1984) the maximum potential foraging at South Georgia is an estimated 424 km. At Marion Island, nearly 70 % of all foraging trips undertaken by adult King Penguins feeding large chicks during summer were estimated to be within 301 km of their breeding colonies. I recognise that defining maximum potential foraging range as total distance travelled divided by two is simplistic and that actual foraging range from the island may be considerably less. Wilson et al. (1989) have developed a simple model which attempts to correct for horizontal deviation from straight line travel and for vertical diving. Based on data presented in this chapter they estimated average potential foraging range at 175 km. The data of Stahl et al. (1985) lends support to this. In February when most penguins were feeding small chicks, weighted mean distance of King Penguins observed at sea to the nearest breeding island was about 120 km. This increased to 300 km in September, when most adults were feeding large chicks. (Stahl et al. 1985).

Although adults attending small chicks travel significantly less per day than do adults attending large chicks their foraging trips last longer. The absolute energy requirements and meal sizes of small chicks are lower than those of larger chicks; however, small rapidly growing chicks need to be fed more frequently (or at least more regularly) (see Williams 1982; Lishman 1985). Adult King Penguins are able to collect large meals (up to 3 kg, Adams & Klages 1987) greater than the stomach capacity of small chicks. Daily weighings of brooded chicks show increases in mass up to 7 d into the shift (N.J. Adams unpublished data) suggesting adults feed small chicks well into the brood shift. The ability to transfer these large meals to chicks at regular intervals during the brood shift and for large chicks to withstand fasts allows King Penguin adults to utilize favourable offshore feeding areas not available to penguins foraging closer to land.

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CHAPTER 4

TEMPORAL VARIATION IN THE DIET OF THE GENTOO PENGUIN _PYGOSCELIS_ _PAPUA_ AT MARION ISLAND

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The diet of the Gentoo Penguin Pygoscelis papua at sub-Antarctic Marion Island was sampled by stomach pumping at monthly intervals from March 1984 to March 1985. Overall, fish accounted for 53 % of the diet by mass, crustaceans 44 % and cephalopods 2 %. Crustaceans predominated between March and June 1984; a marked increase in the proportion of fish in July coincided with the start of egg laying by Gentoo Penguins. Fish accounted for almost all of the diet in January and March 1985. Juvenile nototheniid fish, in particular Notothenia squamifrons, formed the bulk of the fish component; myctophids and Channichthys rhinoceratus were less common. The pelagic euphausiid Euphausia vallentini accounted for about 50 % by mass of the overall crustacean component lumped over the entire study period. The decapod shrimp Nauticaris marionis was the most important crustacean species consumed during the period June to September 1984. Cephalopods were predominantly octopods which were taken in February and March 1985. The hypothesis that seasonal changes in diet occur in direct response to the arrival of crested penguins (Eudyptes spp) early in summer is not supported by the data. Changes in diet appear rather to reflect local changes in the availability of prey species within the inshore waters exploited by Gentoo Penguins.

INTRODUCTION

Studies of the diets of both migrant and resident penguins in the Southern Ocean region have concentrated on birds during the chick-rearing period (Croxall & Lishman 1987), with little information for the non-breeding season (but see Hindell 1989). The Gentoo Penguin Pygoscelis papua is a year-round resident at sub-Antarctic Marion Island (van Zinderen Bakker 1971), and at some other breeding sites in the Southern Ocean (Watson 1975), affording opportunities for sampling its diet throughout the year.

Williams (1981) suggested that seasonal changes in the diet and early breeding by Gentoo Penguins at Marion Island, compared to populations at higher latitudes, ensured a crustacean diet during incubation and early chick rearing. He suggested that a switch to a fish diet later in the season, deduced from a change in colour of the excreta, was a response to the arrival of large numbers of two species of potentially competing, summer-resident crested penguins, the Macaroni *Eudyptes chrysolophus* and the Rockhopper *E. chrysocome*. Recent data from Gentoo Penguins at the Crozet Islands, which have the same penguin assemblage on an equivalent breeding schedule, support this view (Ridoux et al. 1988). However, food samples collected at Marion Island in September 1982 showed that fish are common in the diet of Gentoo Penguins before the arrival of the other penguin species La Cock et al. (1984). I report here on a more comprehensive set of samples collected throughout a single year at Marion Island. My principal objective was to investigate temporal changes in diet.

METHODS

A total of 144 stomach samples was collected from Gentoo Penguins at three colonies distributed along a nine kilometre stretch of the east coast of Marion Island ($46^{o}53'$ S, $37^{o}54'$ E) from March 1984 to March 1985 inclusive. Using the technique of Wilson (1984), I stomach pumped an average of 11 birds a month as they returned to their landing beaches in the evening. Recently the use of this technique for obtaining stomach samples has been validated (Ryan & Jackson 1986, Gales 1987). I did not attempt to distinguish the breeding status of the birds. Gentoo Penguins tend chicks from late July to December. Consequently, during this period, we probably sampled both breeding and non-breeding birds.

Immediately after collection, samples were drained through a 0.5 mm sieve. Subsequently, drained samples were weighed to the nearest gram and then stored at $4^{o}C$ until sorting, generally completed within 24 h of collection. Soft identifiable material was sorted into fish, cephalopod and crustacean components (further separated into shrimps, euphausiids and amphipods) and weighed. I appreciate biases in diet analyses due to differential digestion of the soft parts of different prey will occur (Jackson et al. 1987). Readers are referred to Chapter 2 for a fuller discussion of potential biases in analysis of stomach samples. However, most stomach samples from Gentoo Penguins contain one prey type only (see below) reducing potential biases due to differential digestion of different prey.

Most fish were recovered with heads separated from the remainder of the body. Consequently, analyses were based on identification and measurement of otoliths (Adams & Klages, 1987). I estimated standard length (SL) and mass of fish from regressions relating otolith diameter to these parameters. Regressions not available in Adams & Klages (1987) and Brown & Klages (1987) are given in Duhamel (1981), Hecht & Cooper (1986), and Hecht (1987). Since, otoliths were removed from intact fish crania digestion and hence measurement error was minimal.

Crustacean species were identified with the aid of published keys (Bowman & Gruner 1973, Kirkwood 1982, 1984). Total length of intact individuals was measured from the anterior margin of an eye to the tip of the telson. Numbers of crustaceans in each sample were estimated by dividing total mass by the average mass of an individual crustacean of each respective species. Actual numbers and fresh mass of prey ingested will be underestimated in well-digested samples.

Most of the small cephalopods were recovered intact, and numbers were counted directly. The identification of squid beaks was facilitated by a reference collection at the Port Elizabeth Museum, and confirmed by comparison with the literature (Clarke 1986). We estimated dorsal mantle length (DML) and mass of squid from regressions relating lower rostrum length (LRL) to these parameters (Adams and Klages 1987). Juvenile octopods were not identified.

RESULTS

Mean mass of food samples was 139.2 ± 130.5 g (range: 8 - 650 g, n = 144), similar to the 147 g recorded by La Cock et al. (1984). Mean monthly sample mass was highest in December at 332 g.

General composition of the diet:

Thirty species or species groups were identified (Table 1), with fish comprising the largest single group (11 species). However, samples from individual penguins were largely homogeneous. Fifty-eight percent of stomach samples contained only a single prey taxon, 26 % contained two taxa and 10 % contained three taxa (analysis based on taxon comprising at least 5 % by mass of individual prey species). Mean number of taxa recovered from individual penguins during October 1984 to March 1985 was greater than during March to September 1984, because of increased numbers of fish species.

Fish and crustaceans accounted for 53.5 and 44.4 % respectively of the total annual diet by mass (Table 2). However, considerable changes in proportions of fish, crustaceans and cephalopods occurred over the year (Table 3, Fig. 1). Crustaceans accounted for over 75 % of the diet by mass from March to June 1984 but decreased to 0 % by March 1985. Cephalopods accounted for more than 10 % of the diet only in February and March 1985.

Fish:

The fish component of the diet was dominated by the family Nototheniidae, represented in particular, by _Notothenia squamifrons_. It is likely that most of the unidentified juvenile nototheniids were also this species (Table 1). Nototheniids accounted for over 90 % of the fish component during June to October 1984. Myctophids and the channichthyid _Channichthys rhinoceratus_ appeared more commonly in the diet from October and accounted for most of the food items in March 1985 (Table 3).

Fish of 78.8 - 84.1 mm (5.9 - 7.3 g) were the most frequently taken size class. When plotted on a monthly basis, there was no evidence of any progressive change in size-class distribution throughout the year. However, during January and February smaller fish between 28.6 - 41.8 mm (0.2 - 0.7 g) accounted for

TABLE 1

Numbers and frequency of occurrence of prey items identified from Gentoo Penguin stomach samples at Marion Island

Prey species	Total number	% numbers of prey class	% frequency of occurrence
FISH			
Nototheniidae			
Notothenia _squamifrons_	1231	58.6	50.7
Unident. juv. nototheniids	442	21.1	14.6
Notothenia _acuta_	27	1.3	11.1
Dissostichus _eleginoides_	11	0.5	6.3
Channichthyidae			
Channichthys _rhinoceratus_	132	6.3	12.5
Myctophidae			
Protomyctophum _normani_	122	5.8	4.2
Gymnoscopelus _nicholsi_	32	1.5	4.2
Protomyctophum _tenisoni_	30	1.4	4.9
Krefftichthys _anderssoni_	24	1.1	3.5
Protomyctophum _bolini_	21	1.0	4.2
unid. myctophids	15	0.7	4.9
Electrona _carlsbergi_	4	0.2	1.4
Gymnoscopelus sp.	1	<0.1	0.7
Muraenolepidae			
Muraenolepis sp.	4	0.2	0.7
Unident. fish	3	0.1	1.4

CRUSTACEANS			
Euphausiacea			
Euphausia vallentini	55 496	86.4	25.7
Hippolytidae			
Nauticaris marionis	8 685	13.5	33.3
Amphipoda			
Themisto gaudichaudii	77	0.1	4.9
Hyperiella sp.	13	<0.1	2.1
Unident. amphipods	12	<0.1	2.1
Vibilia sp.	2	<0.1	1.4
Primno sp.	2	<0.1	1.4
Nematocarcinidae			
Nematocarcinus longirostris	3	<0.1	1.4
CEPHALOPODS			
Octopoda			
Unident. juv. octopods	810	94.9	18.8
Decapoda			
Unident. juv. squid	25	2.9	9.0
Kondakovia longimana	9	1.1	3.5
Onychoteuthidae LRL >2mm	5	0.6	3.5
Onychoteuthidae LRL <2mm	5	0.6	3.5
GASTROPODA			
Margarella expansa	4	100.0	2.1
ECHINODERMATA			
Ophiuroidea	1	100.0	0.7

TABLE 2

Per cent composition by wet mass and numbers of main prey classes consumed by Gentoo Penguins at Marion Island

		Fish	Crustaceans	Cephalopods
Wet mass (%)	Mean	53.5	44.4	2.1
	SD	46.9	47.4	9.8
	Range	(0-100)	(0-100)	(0-51.8)
Numbers (%)	Mean	45.4	48.9	5.6
	SD	45.2	47.6	16.1
	Range	(0-100)	(0-100)	(0-82.9)

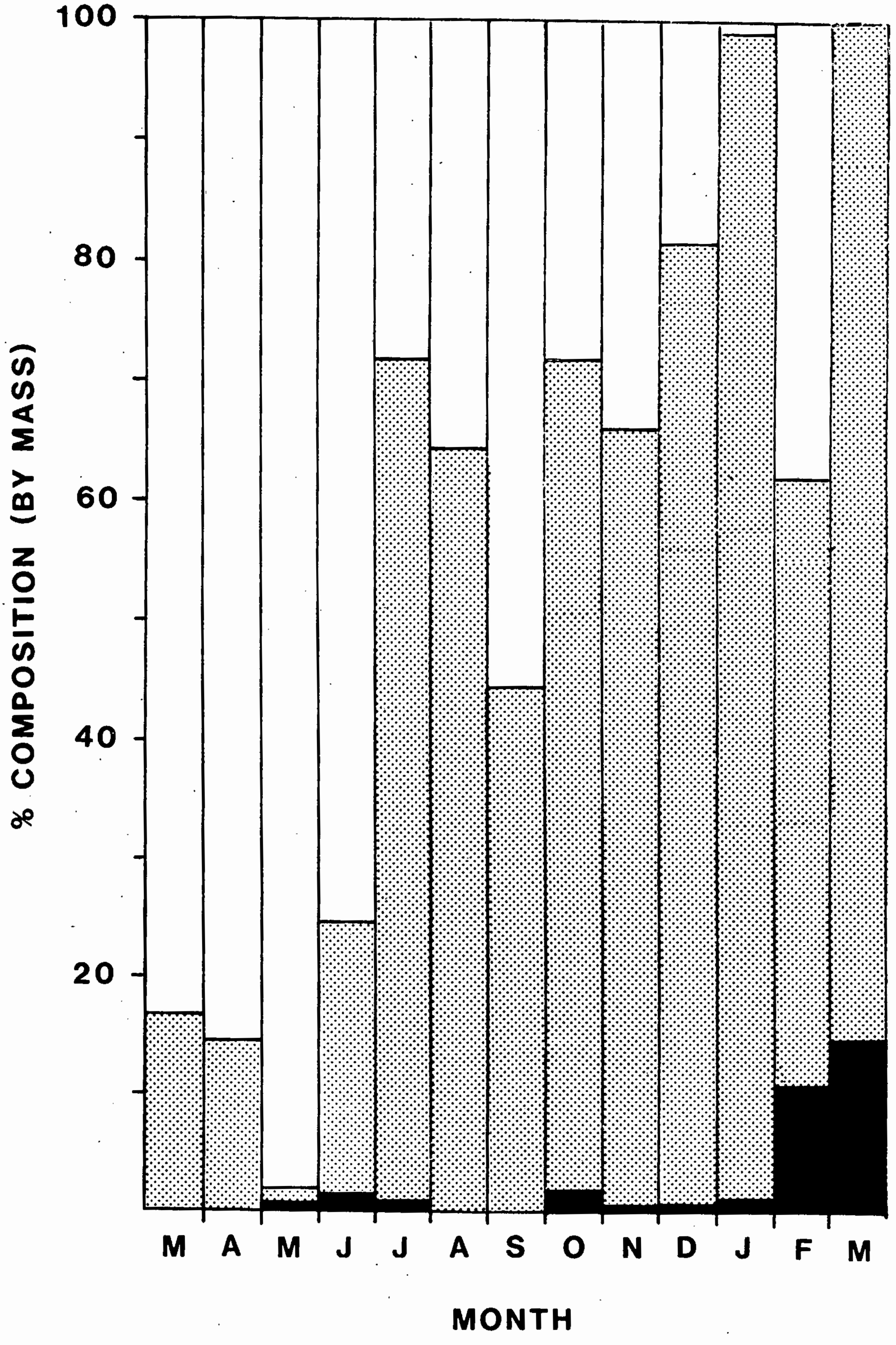
TABLE 3

Percent composition by mass of main prey types consumed by Gentoo Penguins at Marion Island by month

Species	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Crustaceans													
<u>Euphausia</u> <u>vallentini</u>	16.5	42.8	47.1	4.5	4.2	8.9	17.6	23.6	29.7	11.6	1.0	36.2	0
<u>Nauticaris</u> <u>marionis</u>	65.8	42.8	51.0	70.8	23.9	26.7	38.1	4.7	4.2	7.0	0	0	0
<u>Themisto</u> <u>gaudichaudii</u>	0	0	0	0	0	0	0	0	0	0	0	1.8	0
Fish													
Nototheniidae	0	0	0	23.5	66.4	62.5	44.3	68.4	45.1	79.1	71.4	35.2	13.5
Myctophidae	0	14.4	0	0	0.5	1.9	0	1.6	20.8	1.9	4.8	10.0	48.2
Channichythidae	0	0	0	0	0	0	0	0	0	0	21.9	6.1	23.7
Muraenolpidae	0	0	0	0	4.3	0	0	0	0	0	0	0	0
Unidentified	16.8	0	1.4	0	0	0	0	0	0	0	0	0	0
Cephalopods	0	0	0.5	1.2	0.7	0	0	1.7	0.2	0.4	0.9	10.7	14.6

FIGURE 1

Variation in the diet of the Gentoo Penguin at Marion Island throughout a single year. Unshaded segment: crustaceans, stippled segment: fish, shaded segment: cephalopods.


100
80
60
40
20
% COMPOSITION (BY MASS)
M
A
M
J
J
A
S
O
N
D
J
F
M
MONTH

the most frequently taken size class, whereas larger individuals (76.2 - 84.1 mm, 5.3 - 7.3 g) were more numerous during the remaining months. Standard parameters for all fish species are given in Table 4.

Crustaceans:

Euphausia vallentini and *Nauticaris marionis* made up nearly all of the crustacean component. During winter (March to August 1984), *N. marionis* was the largest part of the crustacean component, but *E. vallentini* subsequently increased to nearly 100 % in January and February 1985 (Table 3). Mean length of *E. vallentini* was 22.5 mm 1.74 (n = 681), considerably smaller than that of N. marionis (35.1 mm 5.18, n = 1481).

Cephalopods:

Cephalopods accounted for just over 10 % of the diet during February and March 1985 but seldom occurred in the remaining months (Table 3). Most cephalopods were small octopods (DML < 15 mm). The only squid identified were juveniles of the species *Kondakovia longimana* of estimated dorsal mantle length and mass of 58.4 ± 11.4 mm and 9.6 ± 3.8 g (n = 4) respectively.

DISCUSSION

The tendency for individual Gentoo Penguins to take either crustaceans or fish of the course of one foraging trip has previously been noted at the South Shetland Islands (Jablonski 1985) and South Georgia (Croxall et al. 1988). Fish (Ealey 1954, Volkman et al. 1980) and, in particular, Nototheniids may form a substantial of the diet of the Gentoo Penguin throughout its range. The most important prey species by mass in the diet of

TABLE 4

Summary of otolith diameter (OD), estimated standard length (SL) and estimated mass of fish recovered from Gentoo Penguin stomach samples at Marion Island

Species	OD (mm)				Estimated SL (mm)			Estimated mass (g)		
	N	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Notothenia squamifrons	1109	2.43	0.87	(0.8-5.8)	71.1	18.7	(23.3-155.5)	5.6	4.1	(0.1-56.3)
Notothenia acuta	47	3.19	0.64	(1.38-4.7)	85.0	20.3	(38.6-126.4)	9.2	6.6	(0.6-28.3)
Dissostichus eleginoides	17	3.52	0.73	(2.19-5.27)	105.7	42.6	(42.4-215.1)	10.6	16.9	(0.3-65.0)
Channichthys rhinoceratus	170	1.48	0.38	(0.97-2.45)	170.3	36.8	(127.0-238.3)	21.1	18.9	(6.8-61.9)
Protomyctophum normani	61	2.38	0.10	(2.19-2.6)	77.7	3.7	(70.0-85.2)	6.4	0.9	(4.7-8.3)
Protomyctophum tenisoni	57	1.63	0.13	(1.3-1.78)	49.2	4.9	(37.0-54.8)	1.8	0.5	(0.8-2.3)
Krefftichthys anderssoni	35	1.51	0.25	(0.97-1.87)	49.6	11.2	(25.2-66.0)	2.0	1.1	(0.2-4.3)
Gymnoscopelus nicholsi	12	6.20	0.19	(5.91-6.55)	156.2	5.7	(147.4-166.7)	44.3	4.8	(37.4-53.3)
Protomyctophum bolini	4	2.00	0.38	(1.7-2.35)	57.7	12.2	(46.1-67.3)	1.5	0.8	(0.8-2.2)
Muraenolepis sp.	7	2.7	0.58	(1.87-3.4)	141.1	46.6	(76.8-200.8)	24.9	20.8	(2.3-60.6)

Gentoo Penguins at Marion Island was Notothenia squamifrons (incorrectly identified as Harpagifer georgianus in La Cock et al. 1984, N.T. Klages pers. obs.) whereas N. rossi and N. larseni were consumed at southerly sites (Croxall & Prince 1980a, Jablonski 1985). In constrast, although inshore nototheniid fish did occur, pelagic myctophid fish constituted 92 % and 59 % respectively of the diet of Gentoo Penguins at Macquarie Island (Hindell 1989).

N. squamifrons is a widely distributed fish species occurring around the islands of the southern Indian and, less commonly, the South Atlantic Oceans (Duhamel et al. 1983). N. squamifrons taken by Gentoo Penguins at Marion Island, all in the range 28 - 134 mm, were larval or juvenile fish of 0 - 4 years (Duhamel & Ozouf-Costaz 1985). The large numbers of unidentified juvenile nototheniids in the diet in November and December precede an increase in the relative abundance of small-size class N. squamifrons in the diet in January and February and may reflect growth of these larval fish.

Juvenile Channichthys rhinoceratus, were the largest and second most abundant fish in the diet. Adults were presumably too large for consumption. The species had previously been considered a demersal species endemic to the colder waters around Kerguelen (48^{o}27′-50^{o} S, 60^{o}27′-70^{o}35′ E) and Heard Islands (53^{o}01′ S, 73o23′ E) (Kock et al. 1985). The presence of this species in the relatively warm waters around Marion Island is surprising. However, based on hydrographical evidence (Benon & Murail 1979) and samples of zooplankton (Grindley & Lane 1979, Boden & Parker 1986), the advection of foreign water masses past the island with their associated fauna may occur (Boden & Parker

1986).

The appearance of myctophids in the diet of Gentoo Penguins coincides with the increase in relative abundance of the fish in the diet of the King Penguin Aptenodytes patagonicus during summer, suggesting increased availability (Adams & Klages 1987). Small numbers of myctophids have previously been reported in the diet of Gentoo Penguins at Marion Island (La Cock et al. 1984).

Two species of crustacean Euphausia vallentini and Nauticaris marionis, were of almost equal importance by mass at Marion Island. This is in contrast to the situation at sites south of the Antarctic Polar Front, where the crustacean component of the diet of the Gentoo Penguin is dominated by a single species, E. superba. E. vallentini was the most important prey consumed by Macaroni and Rockhopper Penguins during the 1984-1985 summer, and remained abundant in the diet of Rockhopper Penguins in March 1985 (Brown & Klages 1987) when it was absent from the diet of the Gentoo Penguin. Since, both species of crested penguins probably forage farther offshore during late chick-rearing than do Gentoo Penguins (Brown 1987, Adams & Wilson 1987), this may indicate a movement of euphausiids out of the immediate inshore waters during February and March 1985. E. vallentini is also an important component of the diet of Gentoo Penguins and other seabirds at the Crozet islands (Ridoux 1988).

Due to its benthic nature, adult N. marionis is available to Gentoo Penguins only within a few kilometres of the shore (Adams & Wilson 1987). The size (average length: 35.1 mm) of N. marionis taken by Gentoo Penguins at Marion Island in 1984-1985.

is clearly greater than juveniles (maximum length : 23 mm) taken by crested penguins during December 1983 to February 1984 (Brown & Klages 1987) and by Gentoo Penguins in September 1982 (La Cock et al. 1984). The absence of juvenile N. marionis in the diet of Gentoo and crested penguins at Marion Island during January to March 1985 is difficult to explain, since at least some adult individuals recovered in this study during April to September 1984 were ovigerous (N.J. Adams pers. obs).

The occurrence of octopods in the diet of Gentoo Penguins is apparently unique to the Marion Island site. The appearance of juvenile octopods in the diet coincided with their occurence in the diet of Rockhopper Penguins late in the chick-rearing period (Brown & Klages 1987). Since adult octopods are benthic and solitary, the appearance of large numbers of juveniles in the diet suggests highly seasonal spawning, coupled with a tendency to form dense aggregations in shallower water. In contrast, the small number of juvenile squid in the diet of the inshore foraging Gentoo Penguin again emphasises the generally pelagic nature of squid (Adams & Klages 1987).

In 1984/85 Gentoo Penguins apparently switched from a largely crustacean diet during March to June 1984 to a largely fish diet during July 1984 to March 1985. This change coincided with peak egg laying and could not be considered as a direct response to the arrival, in October and November, of the largely, euphausiid consuming crested penguins (cf. Williams 1981). Moreover, the most important crustacean component by mass in the diet during March 1984 to September 1984 was adult N. marionis (not taken by Macaroni and Rockhopper Penguins) and not krill (euphausiids) as intimated by Williams (1981). The large variation in abundance and prey-species composition of crustaceans in penguin diet from year-to-year, indicated by the differences in the diet of the Macaroni and Rockhopper Penguins in two years at Marion Island (Brown & Klages 1987) and Gentoo Penguins in March 1984 and March 1985 may reflect a greater degree of unpredictability in crustacean prey than at higher latitudes. Switches in diet may merely reflect local changes in availability of particular prey within the inshore area exploited by Gentoo Penguins. Hindell (1989) came to a similar conclusion for Gentoo Penguins at Macquarie Island.

Average meal size of Gentoo Penguins at Marion Island is small (La Cock et al. 1984, this study) compared to those recovered from breeding penguins at higher latitudes (Croxall & Prince 1980a, Jablonski 1985, Volkman et al. 1980). Evaluation of the magnitude of this difference is complicated by the unknown ratio of breeders to non-breeders sampled at Marion Island. However, the difference appears real and may reflect reduced food availability compared with more southerly sites. This view is supported by the small total breeding population (Adams & Wilson 1987), low breeding success and long growth period (Williams 1980) of Gentoo Penguins at Marion Island, compared to those at more southerly localities, and suggests that the population is food limited (La Cock et al. 1984). However, in contrast to the southern populations which breed in summer (Croxall & Prince 1980b), Gentoo Penguins at Marion Island begin breeding in the austral winter (Williams 1980). The infrequent feeding of King Penguin chicks (Cherel et al. 1987) and dispersal of Eudyptes penguins away from the island during winter suggest food availability, particularly of pelagic origin, is low. The reason for winter breeding remains unclear.

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CHAPTER 5

FORAGING PARAMETERS OF GENTOO PENGUINS *PYGOSCELIS PAPUA* AT MARION ISLAND

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Williams, A.J. 1981. Factors affecting the time of breeding of Gentoo Penguins at Marion Island. In: Proceedings of the symposium on birds of the sea and shore, 1979. Cooper, J. (ed.) Cape Town: African Seabird Group. pp. 451-459.

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Antarctic and sub-Antarctic penguins (Wilson 1983). The northern and southern Gentoo Penguin populations show considerable differences in diet (La Cock et al. 1984, Jablonski 1985, Volkman et al. 1980) and breeding biology (Williams 1980), although throughout this range the species is regarded as an inshore feeder (Croxall & Prince 1980a, Volkman et al. 1980, Williams & Siegfried 1980, Jablonski 1985, Trivelpiece et al. 1986, Wilson et al. 1989). Recent studies of the foraging ecology of pygoscelid penguins have included direct measurements of the foraging range and travelling speed of Gentoo Penguins breeding sympatrically with one or two congeners on or near the Antarctic continent. From these Jablonski (1985) and Trivelpiece et al. (1986) have shown subtle differences in the foraging behaviours of these penguin species and concluded that Gentoo Penguins forage closer to the shore than their congeners. In contrast, Wilson et al. (1989) suggest no significant differences in foraging distances among Adelie (P. adeliae), Chinstrap (P. antarctica) and Gentoo Penguins.

Marion Island ($46^{o}52'S$, $37^{o}51'E$) near the northern limit of the Gentoo Penguin's range holds a small breeding population of this species with other pygoscelids being absent. In spite of this lack of potential competitors, the low breeding success of the Gentoo Penguin at Marion Island (Williams 1980, 1981) suggests they may have difficulty in obtaining sufficent food for successful breeding (La Cock et al. 1984), in contrast to the apparent situation on the Antarctic continent (Volkman et al. 1980). I suggest there may be aspects of the foraging parameters of Gentoo Penguins at Marion Island which reflect a low food availability.

I report here on measurements of foraging parameters and analyses of stomach samples of Gentoo Penguins at Marion Island and, where relevant, compare the results with those obtained at higher latitudes. These results give a more direct assessment of food availability which in turn may suggest explanations for the low provisioning rate of Gentoo Penguins at Marion Island.

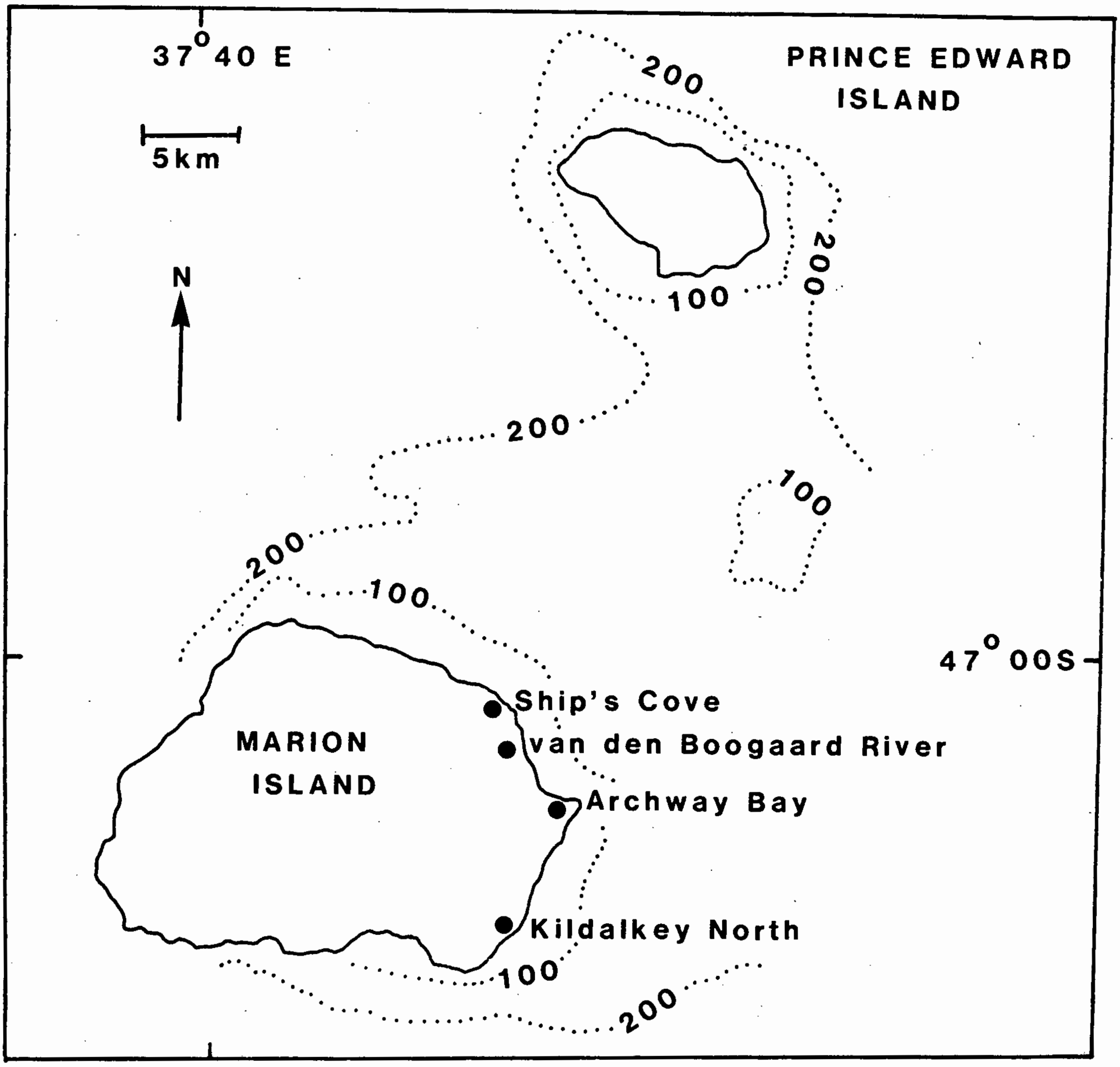
MATERIALS AND METHODS

The study was conducted during September and October 1984 at four breeding colonies along the east coast of Marion Island: Archway Bay, Ship's Cove, Kildalkey North and van den Boogaard River (Fig. 1). Gentoo Penguins breed asynchronously with egg laying commencing in mid-June, peaking in July and relaying by failed breeders continuing through to early November (N.J. Adams pers. obs.). Hence birds at all stages of the breeding cycle were present during this study.

Travelling speed and travelling time were measured using a speedmeter (Wilson & Bain 1984) attached with adjustable hose clamps to feathers along the dorsal midline of the penguin (Lishman & Croxall 1983). The meters consisted of a compression spring with a terminal bung inside a cylindrical tube. A radio-active bead in the bung exposed an X-ray sensitive film sealed inside a light-tight, waterproof, plastic sachet which was taped to the outside of the tube. The speed of travel through the water determined the position of the bung in the tube, which was recorded autoradiographically. The

FIGURE 1

Relative positions of Marion and Prince Edward Islands. The 100 m and 200 m depth contours are indicated.


37°40 E
PRINCE EDWARD ISLAND
5km
N
200
100
200
100
200
100
47°00S
MARION ISLAND
Ship's Cove
van den Boogaard River
Archway Bay
Kildalkey North
100
200

films recorded speed and time spent travelling, allowing one to determine total swimming distance.

The characteristics of each meter differed slightly, however, generally recorded in the range 3.3 km.h^{-1} - 10 km.h^{-1}. The lower limit is not as low as the meters used to record travelling speeds of Jackass Penguins Spheniscus demersus (Wilson & Bain 1984).

Field Procedure:

Archway Bay - Ship's Cove

Between 13h00 - 15h00 on 2 and 3 September, 40 unsexed adult Gentoo Penguins were caught and fitted with speedmeters. The birds, which had 10 to 20-day-old chicks, were released in close proximity to their nests and generally resumed brooding immediately. Subsequently, the nests were visited each afternoon until 7 September to check which penguins had departed to sea and to retrieve speedmeters from birds returning to their nests after foraging. Brooding birds are normally relieved daily by their partners. Most reliefs occur in the afternoon with the relieved partner going to sea immediately and remaining at sea overnight or departing early the next morning and remaining at sea just for the day. (van Zinderen Bakker Jr 1971, Williams 1980). Therefore, the minimum period over which a meter could be recovered from a returning penguin was 48 h. If relief by the partner was delayed until the following day, the meter would be recovered 72 h later. Birds still present on the nest 24 h after attachment of the speedmeter had not been to sea. All meters recovered within 3 d were thus considered to have been on the penguins for a single foraging trip.

Kildalkey North

On 9 and 10 September, I captured 50 adult penguins as they moved down to the sea through a gully from a breeding colony approximately 1 km inland which contained birds at all stages of the breeding cycle. Speedmeters were attached and the penguins individually marked on the chest with waterproof ink. Following release, the time the birds departed to sea was noted, this being generally within 30 min of the meter being attached.

For the duration of the study period (9 - 13 September) a continuous pre-dawn to post-dusk watch (04h00-20h00) was maintained for returning birds from a hide overlooking the landing beach. In addition, on the night of 11 September I checked the beach at two hourly intervals for the prevalence of nocturnal landings. The arrival times of marked birds moving back up the gully to the colony were noted, and individuals captured had their meters removed and a proportion were stomach pumped (Wilson 1984). A small proportion of the metered penguins reached the breeding colony undetected. Consequently, every morning the breeding colony was checked and meters removed from these birds. Continuous observation of marked birds departing and returning at Kildalkey North allowed time at sea to be determined for individual penguins. These time intervals, combined with speedmeter analyses, enabled the proportion of time spent travelling relative to total time at sea to be calculated. Stomach contents were weighed and analysed in the laboratory according to prey type.

van den Boogaard River

On 25 September, 10 speedmeters were attached to Gentoo Penguins of unknown status as they arrived ashore. The birds were individually marked on the chest with picric acid and released. After 16 d, landing beaches in the vicinity of the colony were patrolled regularly and the meters retrieved. Nine of the meters were subsequently recovered at intervals of up to 25 d after attachment.

Speedmeter analysis:

To avoid the problem of latent image fading, all films were developed at Marion Island using Kodak GBX developer. The radio-active bead exposed the film typically in two positions, one representing the zero position (the penguin at rest) and the other representing the normal travelling speed. Since all meters had previously been calibrated for bung displacement against speed through the water, the distance between the two exposed positions was a measure of the travelling speed. The duration of travelling at any particular speed was determined by comparison of the density of exposure with that of control strips. Total distance travelled was calculated as the product of travelling speed and travelling time (see Wilson & Bain 1984 for details).

RESULTS

Ninety-four of the 100 speedmeters attached to penguins were recovered. Thirty-eight could be read for both travelling speed and time spent swimming, and another 15 for travelling speed alone. Other films were unreadable due to accidental exposure to light, leaking film sachets, or absence of a travelling trace due to the bung twisting around its axis so that the bead no longer exposed the film. This does not imply a failure of the device to function, but merely loss of the travelling trace.

Travelling speed:

The travelling speed of Gentoo Penguins was 7.9 ± 1.5 km h^{-1} (range 3.9 - 10.6 km h^{-1}, n = 53) (Fig. 2). Each bird generally had a normal travelling speed represented on the film trace as a single exposure. Two birds had film traces that indicated they had swum at two different speeds during one foraging trip. One bird swam at 4.1 and 8.1 km h^{-1} and the other at 6.2 and 6.6 km h^{-1}.

Travelling time:

Eighty-six per cent of the penguins landing at Kildalkey beach on the 11 September had done so by 18h00 and 97 % had done so by 21h00. Penguins leaving and returning on the same day from Kildalkey North spent 8.1 ± 2.4 h (range 3.7 - 11.7 h, n = 21) away from the island. Of 13 birds which departed for sea after 13h00 only two returned the same day, after 4.8 and 3.7 h at sea respectively. Penguins away overnight returned 23.7 ± 1.9 h (range 20.9 - 26.4 h, n = 11) later. Gentoo Penguins from Kildalkay North spent a median of 16.0 % (range 4.3 - 56.3 %, n = 15) of their time away travelling. There was no significant difference in time spent travelling between birds whose meters were recovered after 48 h or 72 h at Archway Bay and Ship's Cove (median test $X^2_1 = 0.048$, $P > 0.05$). This tends to confirm that meters recovered after 48 or 72 h at Archway Bay and Ship's Cove were from birds that had been away for only one foraging trip. Observed and expected frequencies of travelling times of birds departing from Kildalkey North (median 1.7 h, range 0.2 - 11.2 h, n = 19) and from Archway Bay and Ship's Cove (median 3.7 h, range 0.2 - 12.9 h, n = 19) were compared. The travelling time/frequency distribution (Fig. 3) was dependent on study colony (X^2 =

FIGURE 2

Travelling speed of Gentoo Penguins at Marion Island. Results from different colonies are indicated.

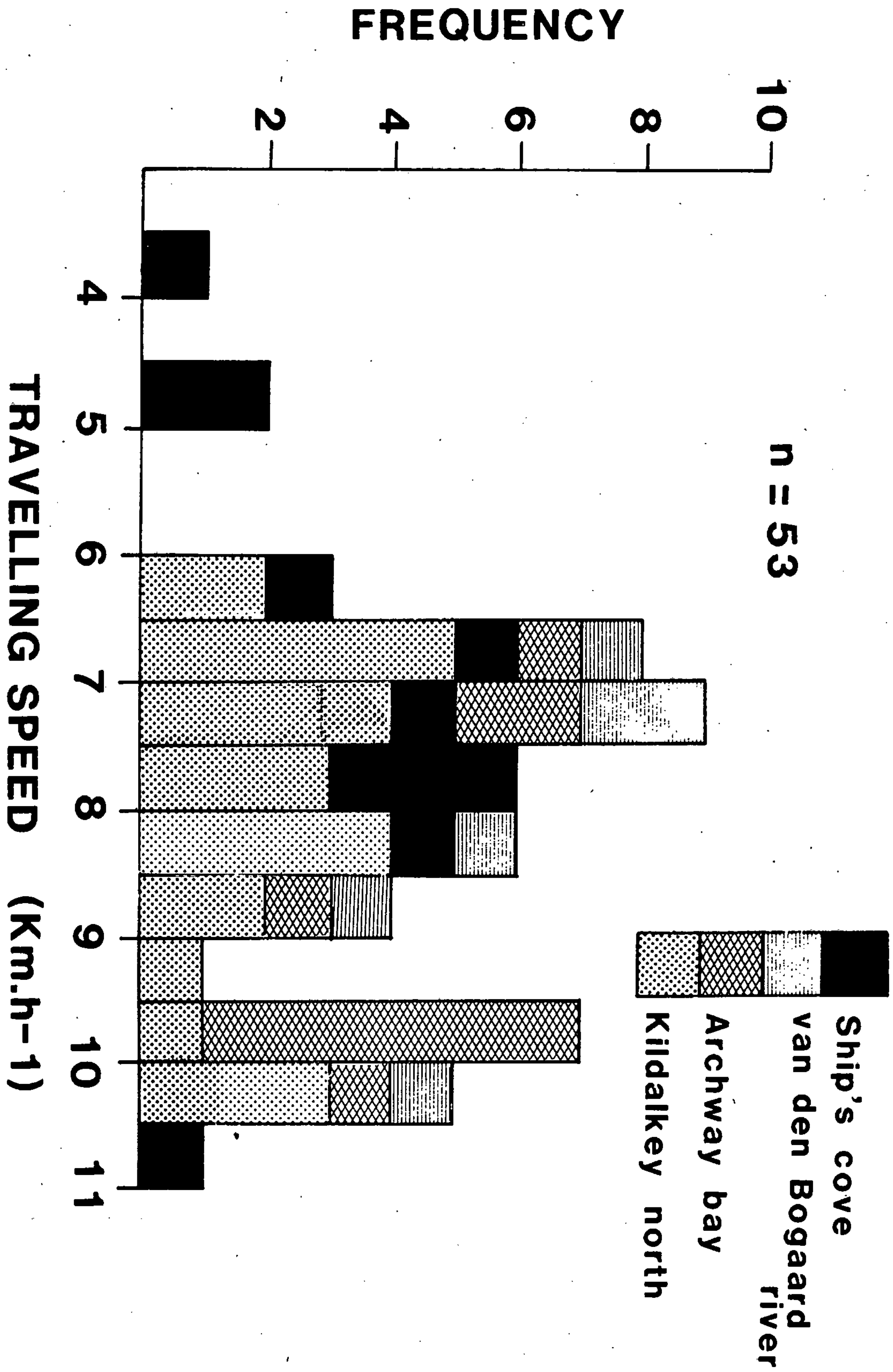
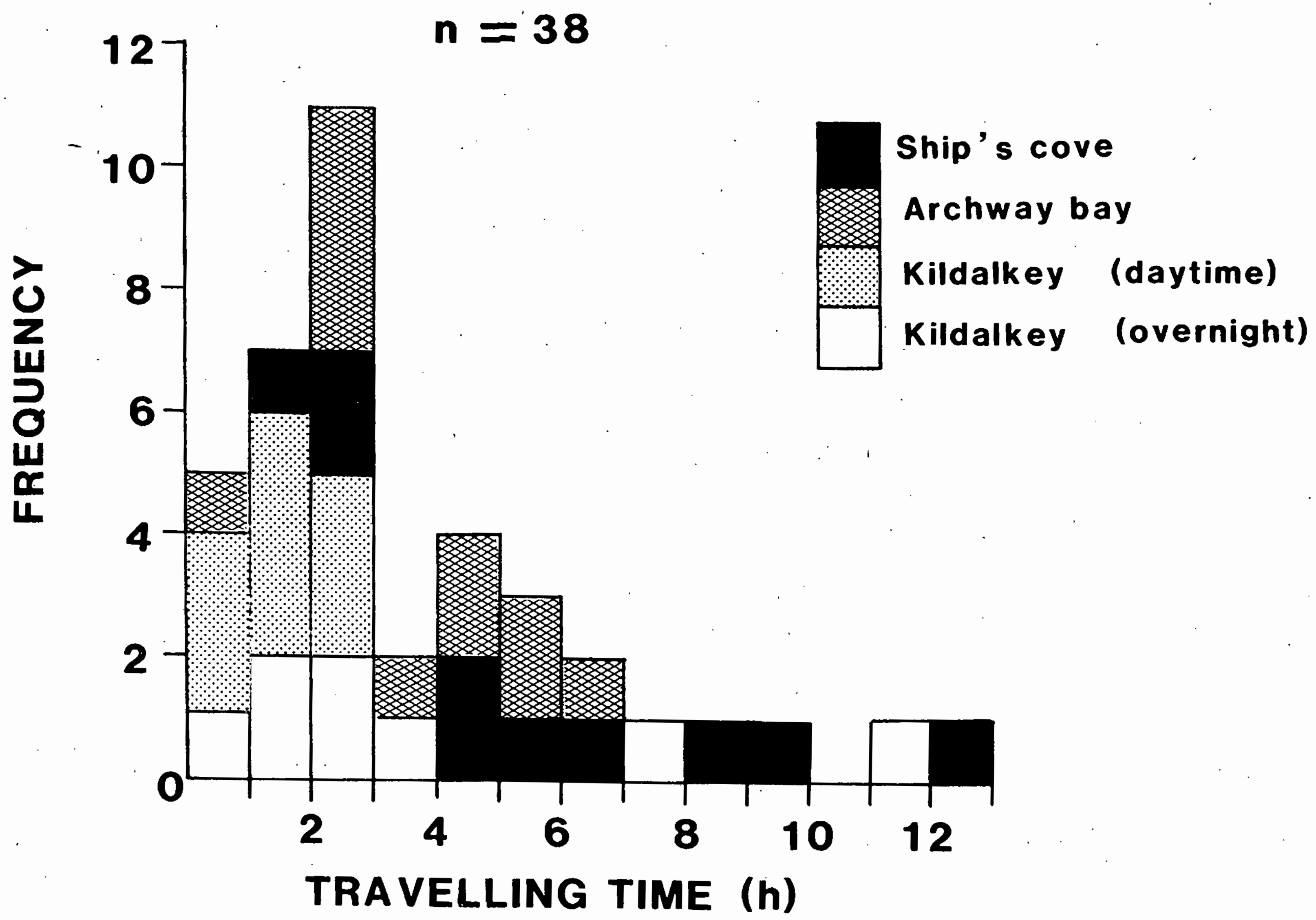

FREQUENCY
2
4
6
8
10
n = 53
4
5
6
7
8
9
10
11
TRAVELLING SPEED (Km.h-1)
Ship's cove
van den Bogaard river
Archway bay
Kildalkey north

FIGURE 3

Travelling time of Gentoo Penguins at Marion Island. Results from different colonies are indicated.


n = 38
FREQUENCY
0
2
4
6
8
10
12
TRAVELLING TIME (h)
2
4
6
8
10
12
Ship's cove
Archway bay
Kildalkey (daytime)
Kildalkey (overnight)

12.41, $P < 0.01$). Birds departing from Kildalkey were observed to travel more frequently in 0-2 h category than expected but less frequently than expected in the 4-6 h category. For birds departing from Archway Bay and Ship's Cove the position was reversed.

Travelling distances:

Penguins away overnight from Kildalkey North did not travel significantly farther than birds only away for the day (median test, $X^2_1 = 1.30$, $P > 0.05$) (Fig. 4). Penguin travelling distances were dependent on study colony ($X^2 = 9.7$, $P < 0.05$). Birds departing from Archway Bay and Ship's Cove travelled distances up to 20 km less frequently than expected and distances above 20 km more frequently than expected (median 30.7 km, range 1.6 - 96.7 km, n = 19). For birds departing from Kildalkey North the position was reversed (median 13.8 km, range 0.64 - 103.0 km, n = 19). Eighty-two percent of all foraging trips were less than 40 km (Fig. 4). Correcting total travel distance for deviation from straight line travel and vertical diving according to the formula:

total distance = 0.38(total distance - vertical distance)

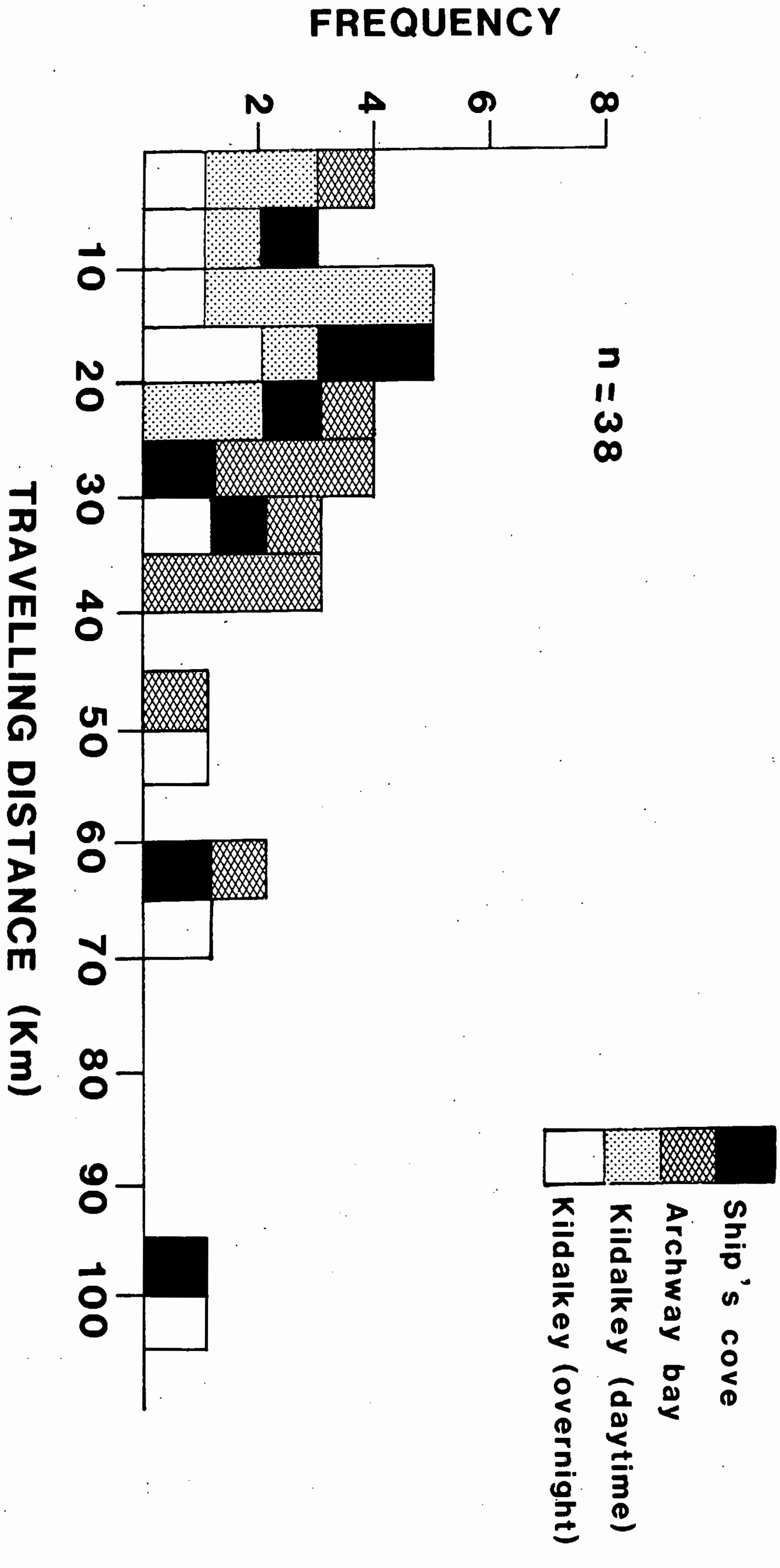
most penguins forage within 11 km of the island (Wilson et al. 1989).

Diet and travelling distance:

Diet samples were generally small (median mass 87 g, range 15 - 402 g, n = 27) and homogeneous. Eleven contained only adult individuals of the shrimp Nauticaris marionis (mean length 31.9 ± 5.3 mm) 10 contained only the fish Notothenia squamifrons (mean length 74.9 ± 11.8 mm) and two contained only the euphausiid Euphausia vallentini (mean length 24.5 ± 1.5 mm).

FIGURE 4

Travelling distance of Gentoo Penguins at Marion Island. Results from different colonies are indicated.



FREQUENCY
2
4
6
8
n = 38
10
20
30
40
50
60
70
80
90
100
TRAVELLING DISTANCE (Km)
Ship's cove
Archway bay
Kildalkey (daytime)
Kildalkey (overnight)

TABLE 1

General composition of the diet of Gentoo Penguins at Kildalkey North, Marion Island

	Fish %	Crustacean %	Cephalopod %
Mass	53.2	46.2	0.6
Frequency of occurence	59.3	63.0	3.7

Other samples were mixed. Stomach sample mass was not correlated with distance travelled (Spearman rank correlation $r_{s(9)} = -0.578$, $P > 0.05$, $n = 11$). The median travelling distance of birds returning with shrimp, however, was 8.75 km (range 6.4 - 13.8 km, $n = 6$), significantly less than the 13.6 km (range 2.2 - 103 km, $n = 5$) recorded for penguins returning with fish (Mann Whitney test, $U_{5,6} = 33$, $P < 0.05$). Two samples containing only euphausiids were from birds that had travelled 7 and 11 km respectively.

DISCUSSION

Foraging parameters:

Trivelpiece et al. (1986) quote a travelling speed for both Gentoo and Chinstrap Penguins of 4.5 ± 0.4 km h^{-1}. However, this value was calculated on the basis of straight-line distances, using radiotelemetry, whereas the penguins probably swam erratically. It also represents an integrated value, including travelling dives and resting between the dives and is not corrected for package size. Wilson et al. (1986) have quantified the effect that attachment of packages of increasing cross-sectional area to penguins has in terms of reduction of travelling speeds. Based on this, speeds quoted here will only be a slight underestimate (< 5%) of the travelling speed, since meters used were small (approximately 2 % of penguin cross-sectional area). Travelling speeds of Gentoo Penguins at Marion Island are similar to those measured at Anvers Island (64°47′, 64°27′W) (Wilson et al. 1989). Lack of detectable intra-individual variation in travelling speed (<0.5 km h^{-1}) of penguins from the van den Boogaard River study colony over a number of foraging trips (16-25, assuming one trip per day) suggests that each penguin consistently travels at what is presumably its own, energetically optimum, travelling speed. Although the speedmeters used in this study only recorded underwater swimming speeds in excess of 3.3 $km.h^{-1}$, evidence from other studies strongly suggests penguins do not swim at these low speeds for sustained periods (Wilson & Bain 1984).

Dorsally mounted speedmeters may underestimate total time travelling (and hence travelling distance) since they fail to record swimming at the surface. However, incidental observations of Gentoo Penguins moving close inshore indicate that they only travel significant distances by underwater swimming and porpoising. Continuous monitoring of radio transmitters attached to foraging penguins at the South Shetland Islands (Trivelpiece et al. 1986) indicates that time on the surface is restricted to bathing, resting between dives and porpoising. Consequently, I assumed time travelled by Gentoo Penguins on the surface was negligible compared to the total time travelled.

Since there was relatively little variation in swimming speeds between individual penguins, the large range in travelling distance reflected a large variation in time spent travelling. Differences in travelling distances between birds departing from different colonies probably reflected differences in the breeding status of metered birds. Metered birds at Kildalkey North included incubating adults and adults attending small chicks, whereas at Ship's Cove and Archway Bay all sampled birds were attending small chicks. Incubating birds presumably travel shorter distances than do adults collecting food to feed chicks, but this could not be tested because I did not record the state of breeding of individual metered penguins at Kildalkey North. The higher median travelling distances of adults attending chicks at Archway Bay and Ship's Cove suggests percent time spent swimming may be higher than the average of 16 % at Kildalkey North. Distances travelled by adults attending chicks at Marion Island are similar to those measured for the same species at Anvers Island (Wilson et al. 1989).

The non-significant difference in travelling distance between penguins away overnight and those away only for the day suggests that Gentoo Penguins may spend most of the night resting on the sea surface, although the possibility of landings at other nearby beaches cannot be excluded. Both possibilities suggest foraging is a largely diurnal activity. Pygoscelid penguins at King George Island (62°09'S, 58°28'W) and Signy Island (60°43'S, 45°38'W) forage throughout the 24 h cycle, although peak foraging is presumed to occur at night (Lishman 1985). Nest relief intervals of Gentoo Penguins feeding small chicks at King George Island are approximately 12 h (Volkman et al. 1980), while actual foraging trips lasted 6.1 h (Trivelpiece et al. 1986). This potentially allows brooded Gentoo chicks to be fed at double the frequency pertaining at Marion Island.

Diet:

The fish Notothenia squamifrons and the shrimp Nauticaris marionis were the two most important items in the diet of Gentoo Penguins at Kildalkey North. The importance of these two items to Gentoo Penguins at Marion Island has previously been documented by La Cock et al. (1984).

The biology of Notothenia squamifrons is poorly known around Marion Island, but evidence from the Crozet Islands indicates that individuals of similar size to those consumed by the Gentoo Penguin are probably demersal (Duhamel & Hureau 1985, Chapter 4). Circumstantial evidence suggests that Nauticaris marionis occurs in the shallow nearshore region around Marion Island (Blankley 1982). The occurrence of demersal and benthic prey in the diet of Gentoo Penguins would suggest that they feed close to the sea bed. Southern Gentoo Penguins feed mainly on the planktonic Antarctic krill Euphausia superba (Volkman et al. 1980, Jablonski 1985).

I was unable to differentiate between commuting distance and distance covered while diving and pursuing prey. However, I suggest that the generally shorter and less variable distances travelled by penguins returning only with shrimp, compared to those returning with fish, indicate that adult N. marionis have a more restricted distribution around Marion Island. Grab samples taken from the sea-bottom at depths from 42 to 210 m, and between 0.3 km and 11 km from Marion Island often contained N. marionis (G.M. Branch pers. comm.). However, trawling around Marion Island conducted at depths between the surface and 300 m up to 25 km from Marion Island failed to recover N. marionis (Miller 1982, Boden & Parker 1985) confirming its benthic nature. Notothenia squamifrons has been recovered at depths from 220 to 315 m at an unspecified distance from Marion Island (Duhamel & Ozouf-Costaz 1985).

Nearshore feeding penguins require predictably distributed prey (Frost et al. 1976). This condition is met by a large, spatially predictable patch of prey or frequently encountered, but randomly distributed, smaller patches of prey (Wilson 1985). In the latter case one should expect a positive correlation between distance travelled and mass of food ingested (Wilson 1985), whereas there was no significant correlation between these two parameters for Gentoo Penguins at Marion Island.

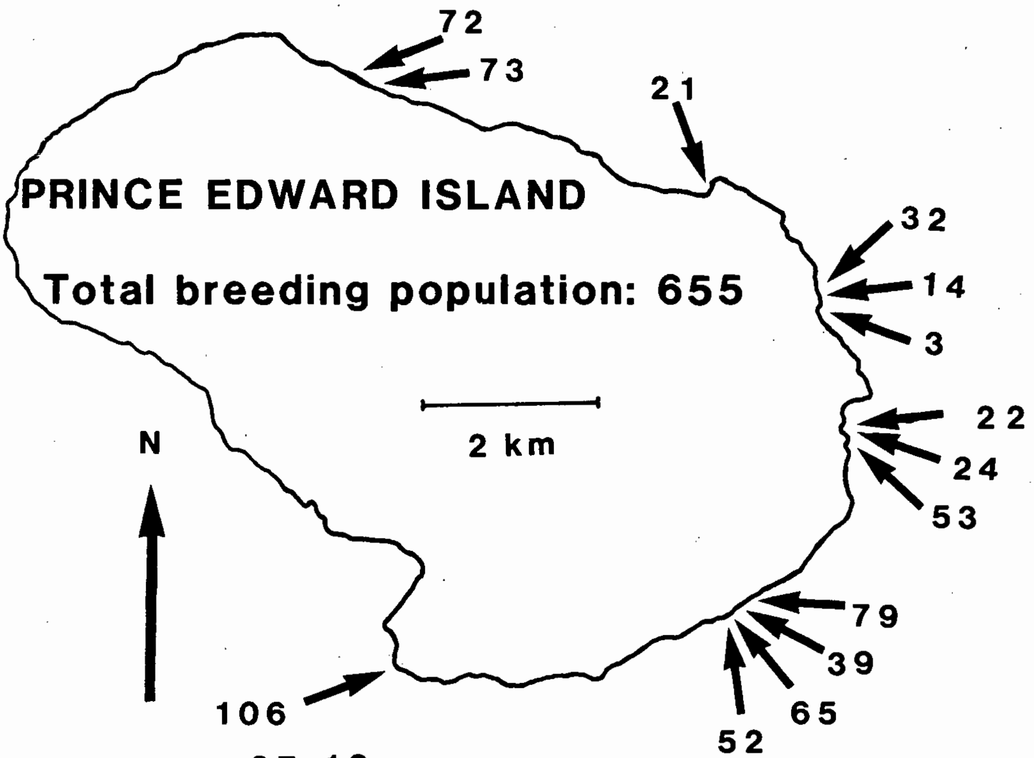
I underestimated average meal sizes of adults feeding chicks since adults at all stages of breeding, including incubating birds were sampled. The small and variable meals recovered during this study were similar in size range to those measured in a previous study (La Cock et al. 1984). However, even maximum meal size of Gentoo Penguins recorded in this study was less than the average meal size at South Georgia (Croxall & Prince 1980b) and at King George Island (Jablonski 1985, Volkman et al. 1980) and consequently consider this to indicate a real difference in the average meal size at Marion Island compared to those at localities further south.

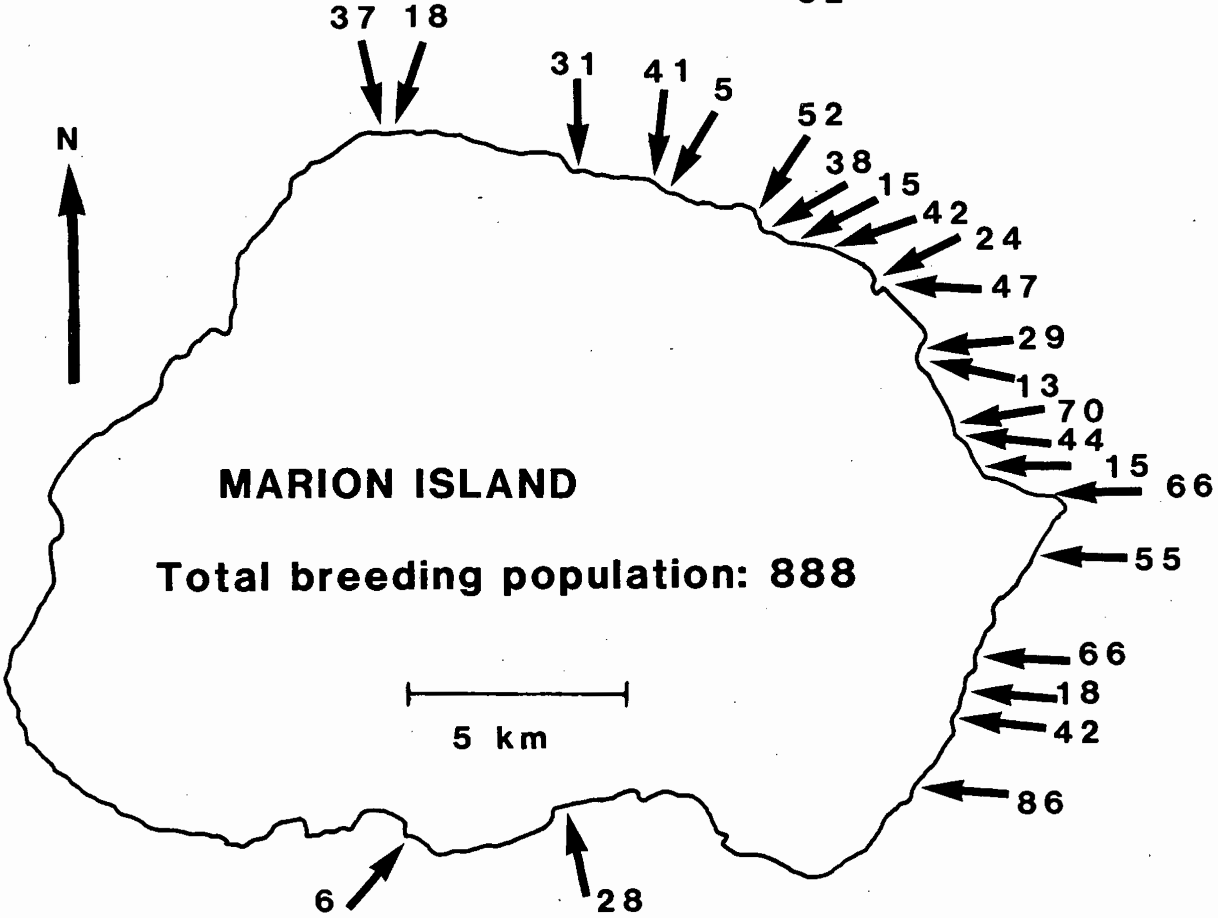
The small, variable meal sizes and the non-significant correlation between meal size and distance travelled are probably related and suggest reduced availability of food for Gentoo Penguins at Marion Island compared with breeding sites at higher latitudes.

Distribution of breeding colonies and potential foraging range: The breeding population of Gentoo Penguins at the Prince Edward Islands is distributed among numerous small colonies (Fig. 5). The spacing of small breeding colonies of nearshore feeding penguins is potentially a mechanism for avoiding intraspecific

FIGURE 5

Distribution and numbers of Gentoo Penguins at Marion Island and Prince Edward Island in August and September 1984 respectively. Arrows indicate the positions of colonies and numbers are breeding pairs.


72
73
21
PRINCE EDWARD ISLAND
Total breeding population: 655
32
14
3
2 km
N
22
24
53
79
39
65
52
106


37
18
31
41
5
52
38
15
42
24
47
N
29
13
70
44
15
66
MARION ISLAND
55
Total breeding population: 888
66
18
42
5 km
86
6
28

competition (Croxall 1984). This mechanism cannot account for the absence of breeding colonies along the western coast of Marion Island or the concentration of penguins on the south-east corner of Prince Edward Island. Williams (1978) suggested a paucity of suitable landing beaches on the western coasts as an explanation. However, selection of breeding sites with respect to favourable foraging areas should also be an important consideration for penguins which feed inshore.

Gentoo Penguins are capable of diving deeply, but most of their dives are less than 40 m (Adams & Brown 1983). The largely demersal and benthic prey of Gentoo Penguins at Marion Island may therefore be more readily available in the area of shallower water off the east coast (Fig. 1). Moreover, there is some evidence of enhanced productivity in this area, although explanations for this differ (Allanson et al. 1985, Grindley & David 1985). The maximum percentage time an individual Gentoo Penguin spent actually swimming while at sea was 56 %. Therefore, travelling at a speed of 7.9 km h^{-1} on a day in mid-summer lasting ca 16 h, a Gentoo Penguin could forage up to 35 km from its colony. In winter, maximum foraging range would be less. Productive foraging areas off the east and south-east coasts would be well beyond the optimal foraging range of a diurnal foraging Gentoo Penguin breeding in winter on the west coast (Fig 1). In addition, the siting of breeding sites in close proximity to feeding areas would minimize the energy costs of commuting between these two areas. The present breeding distribution of Gentoo Penguins at Marion and Prince Edward Islands, therefore, may be partially a consequence of favourable feeding conditions in the shallower water zone between the two islands.

Gentoo Penguins at Marion Island are partly dependent on a localized, demersal and presumably limited food supply in a region of generally deep water. This may partly explain low breeding success and numbers recorded relative to localities at high latitudes.

ACKNOWLEDGEMENTS

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CHAPTER 6

DIETARY DIFFERENTIATION AND TROPHIC RELATIONSHIPS IN THE SUB-ANTARCTIC PENGUIN COMMUNITY AT MARION ISLAND

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I compared the diets of four co-occurring species of penguins at sub-Antartic Marion Island in light of mechanisms thought to result in dietary differentiation. Calculation of overlap indices and correspondence analyses indicated a clear separation in the diets of the three penguin genera, but considerable similarity between the congeneric species pair. The pelagic foraging King Penguin _Aptenodytes_ _patagonicus_ consumed mainly myctophid fish, whereas the near - to offshore foraging Macaroni Penguins _Eudyptes_ _chrysolophus_ and Rockhopper Penguins _E_. _chrysocome_ both consumed predominantly small pelagic crustaceans, although in different proportions. The inshore foraging Gentoo Penguin _Pygoscelis_ _papua_ fed largely on benthic nototheniid fish. Although King Penguins rarely take small prey, differences in diet cannot be accounted for solely on the basis of prey size selection. Different diving capabilities may have some role in dietary differentiation, however, I consider prey availability in the apparently distinct feeding zones to explain most of the differences in the diets of the four species of penguins at Marion Island. The daily population food requirements of the respective penguin species at the Prince Edward Islands increased with increasing species foraging range. The mainly benthic nature of the prey in the inshore area, compared with the more easily replenished pelagic food stocks, probably explains the differences in food availability that sustain the greater food demands for the larger populations of pelagic and offshore foragers.

INTRODUCTION

The Antarctic Peninsula and islands of the sub-Antarctic typically support large populations of up to five sympatrically breeding species of penguins (Wilson 1983). Separation of feeding areas and breeding schedules (Trivelpiece et al. 1987), differing diving capabilities (Trivelpiece et al. 1987) and selection for different prey size (Croxall & Lishman 1987) may be important factors in the ecological segregation of sympatric penguin species.

Recent studies at sub-Antarctic Marion Island (46°52′S, 37°51′E) and Crozet Islands (46°S, 51°E) in the southern Indian Ocean have provided descriptions of the diets of the four different species of breeding penguins which occur at these localities, and some preliminary estimates of various foraging parameters (Adams 1987, Adams & Klages 1987, 1989, Adams & Wilson 1987, Brown 1987, Brown & Klages 1987, Ridoux et al. 1988). In this chapter I compare the diets of the King Penguin <u>Aptenodytes patagonicus</u>, Macaroni Penguin <u>Eudyptes chrysolophus</u>, Rockhopper Penguin <u>E. chrysocome</u> and Gentoo Penguin <u>Pygoscelis papua</u> at Marion Island and evaluate factors that may be important in causing differences in diet.

The breeding schedules of the three genera differ markedly (Fig. 1), King Penguins taking about 14 months to raise a chick, with egg laying occurring from November to April (N.J.A. pers. obs). Gentoo Penguins are resident at Marion Island throughout the year, but have a more restricted breeding season, with egg laying normally starting at the end of June. However, different colonies show considerable asynchrony and failed breeders will relay (Williams 1980a). Most chicks fledge by mid-November. In contrast, breeding activities and moult of Macaroni and Rockhopper Penguins are highly synchronized and restricted to the months October - May with a separation of some three weeks between initiation of breeding between the two species (Williams 1980b). Both species disperse from the island during winter (Williams 1980b). During November - March all four penguin species are present at Marion Island and feed in surrounding waters.

METHODS

All diet samples were collected along a 9 km stretch of the east coast of Marion Island. Because there may be considerable interannual variation in diets of penguins at Marion Island (Brown & Klages 1987, Brown et al. in press), comparisons of diet among the species were based on a comprehensive set of food samples collected throughout one year only (April 1984 - March 1985). The proportions of prey identified to the lowest possible taxon by both actual and reconstituted mass and number from data of Adams & Klages (1987), Brown & Klages (1987) and Adams & Klages (1989) (see Appendix 1), were extracted to perform correspondence analyses (Underhill 1981) and calculate overlap indices. Diet collection procedures and analysis procedures are given in detail in Adams & Klages (1987) and in Brown & Klages (1987). Briefly, samples were obtained from adults arriving ashore after foraging or, on occasions, from large chicks immediately after being fed (King Penguins only). Birds were stomach pumped using the water off-loading technique (Wilson 1984). Samples were sorted within 24 h of collection. Individual samples were separated into fish, cephalopod and crustacean remains and component parts weighed. Comparisons among relative mass of major prey classes were based on proportions of recovered wet mass. Fish species were identified from otoliths, cephalopods from lower beaks, and crustaceans from intact individuals. Proportions by numbers and within class comparisons of well-digested prey, rely on analyses of these hard parts. Unidentified prey was apportioned in the same ratio as identified prey.

Overlap in diet among penguin species was assessed using Morisita's index (Morisita 1959) modified by Horn (1966) (see Diamond 1983). This index, which varies between 1 (complete overlap) and 0 (no overlap), is a relative measure and its value is dependent on the number of prey categories selected. I did not split categories into size classes (cf. Diamond 1983) since major taxonomic classes were generally characterized by a specific range of lengths (squid > fish > crustacean).

Dietary diversity among and within penguin species was compared using the Shannon-Wiener index (Tramer 1969). Indices were calculated both for proportions of prey by mass for lumped samples of the four species (Appendix 1), and as a mean of diversity indices calculated for individual samples. I calculated indices for the whole year and, where appropriate, for samples recovered from December to March only (the period when all species of penguins are present at the island) (Table 2).

Measurements of potential foraging ranges are described in Adams (1987), Adams & Wilson (1987), and Brown (1987) and were obtained during the same year as intensive diet sampling.

RESULTS

There were seasonal changes in the proportions (percent wet mass recovered) of major prey types of penguins at Marion Island (Fig. 1). In absolute terms, King Penguins consumed the largest number of taxa (Appendix 1). However, the diversity index (Table 1) gives little weight to taxa occurring in small proportions and Macaroni Penguins were consequently identified by the Shannon-Wiener index as having the most diverse diet, whether indices were calculated from lumped samples or from the mean of individual samples (Table 1). Lumped sample diversity was, not suprisingly, always greater than the mean of individual diversity. Little overlap is indicated between the diet of King Penguins and Gentoo, Macaroni and Rockhopper Penguins when compared on the basis of numbers (Table 2). In contrast, there is extensive overlap between Gentoo and Rockhopper Penguins. Correspondence analysis illustrates the clear separation of King Penguins from the other three species and identifies myctophid fish and squid as the prey species responsible (Fig.2). Crustaceans common to Gentoo, Macaroni and Rockhopper Penguins account for the high overlap in diet between these species.

Comparison of indices based on percentage mass increases the overlap among King Penguin and other species, but reduces that among Gentoo Penguins and Macaroni and Rockhopper Penguins (Table 3).

These changes can be attributed to the increased importance of fish when diet is analysed on the basis of proportional mass. Increased separation between the diets of Gentoo Penguins and Macaroni and Rockhopper Penguins, is again reflected in

FIGURE 1

Temporal variation in the proportion of the main prey classes in the diet of penguins at Marion Island (redrawn from data presented in Adams & Klages 1987, Adams & Klages 1989 and Brown & Klages 1987).

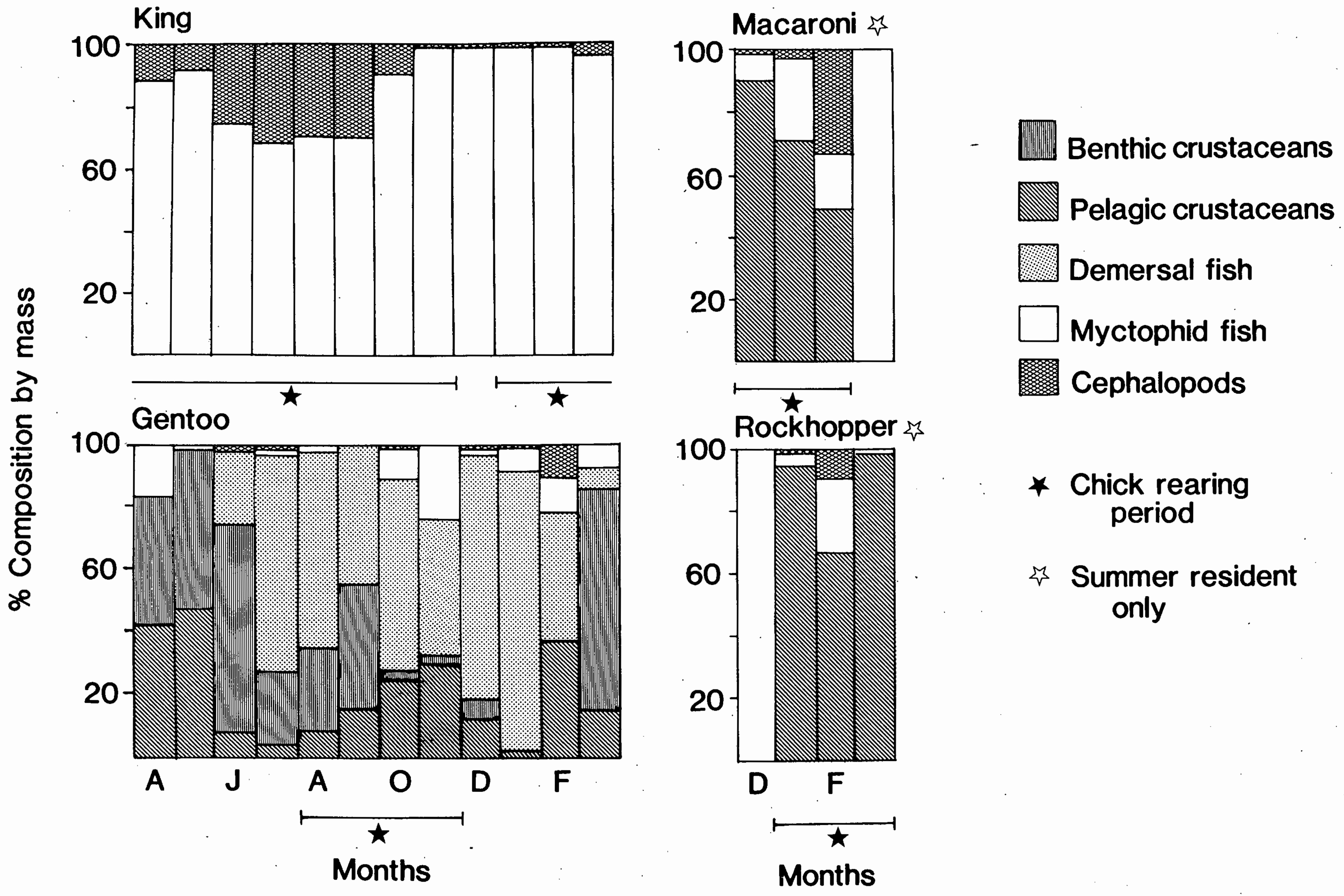
% Composition by mass
King
Gentoo
Macaroni ☆
Rockhopper ☆
100
60
20
A
J
A
O
D
F
D
F
Months
Months
★
▥ Benthic crustaceans
▨ Pelagic crustaceans
░ Demersal fish
☐ Myctophid fish
▦ Cephalopods
★ Chick rearing period
☆ Summer resident only

TABLE 1

Diversity index of diets of penguins at Marion Island. Values are given for lumped samples (H'tot) calculated from Appendix 1 and mean of each individual sample (H'ind) for the whole year and December to March

	Year		December-March	
	H'tot	H'ind	H'tot	H'ind
King Penguin	0.570	0.296	0.537	0.337
Gentoo Penguin	0.753	0.116	0.765	0.198
Macaroni Penguin			0.810	0.345
Rockhopper Penguin			0.518	0.256

TABLE 2

Overlap in the diet of penguins at Marion Island. Categories are as given in Appendix 1 for proportion by numbers

	GP	GP	MP	RP
King Penguin	.001*	.008	.031	.003
Gentoo Penguin			.780	.943
Macaroni Penguin				.920

* comparison based on samples collected over the whole year, remaining comparisons based on samples collected from December to March only.

FIGURE 2

Number of prey species in individual stomach samples as a percentage of total number of samples.

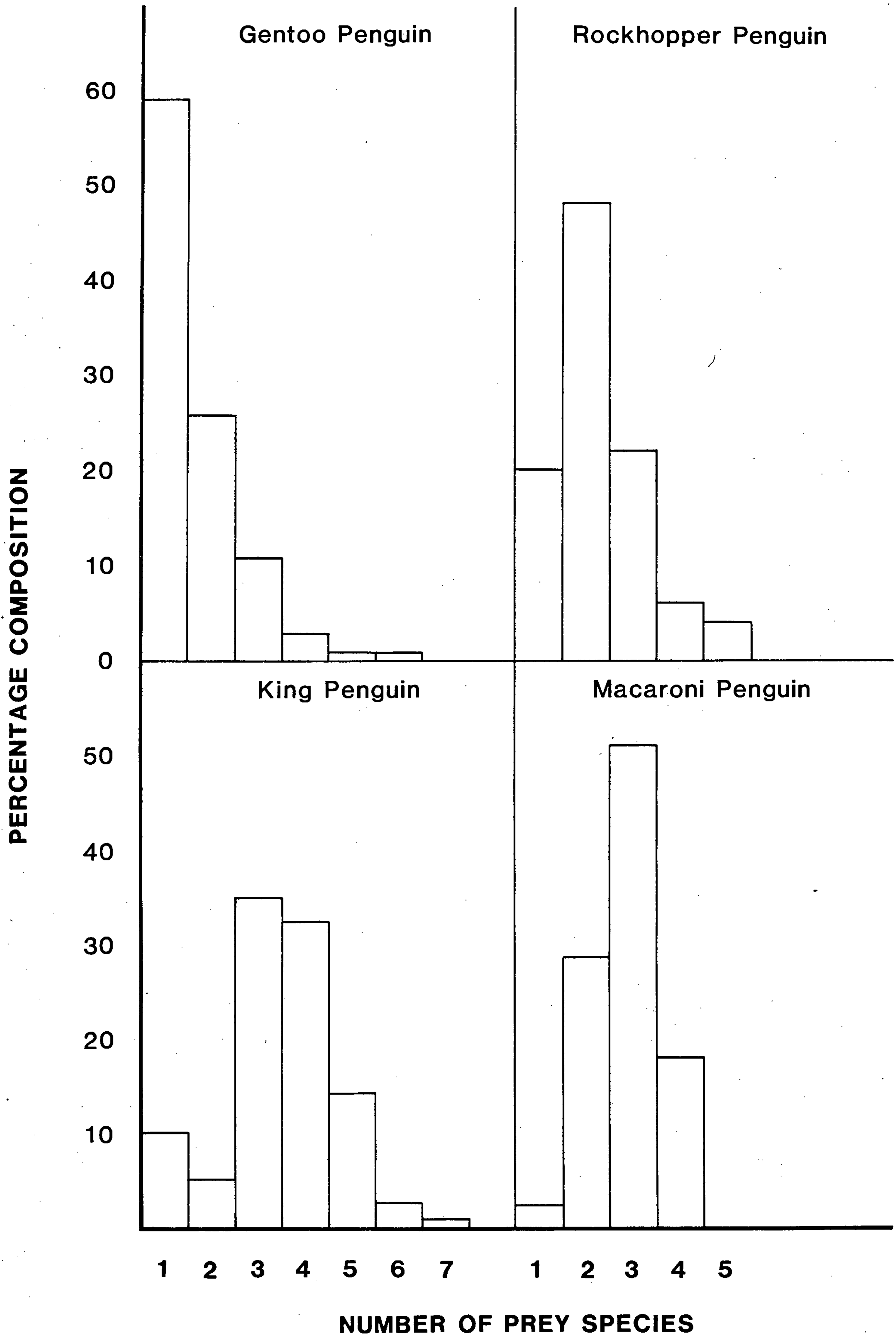
Gentoo Penguin
Rockhopper Penguin
King Penguin
Macaroni Penguin
PERCENTAGE COMPOSITION
60
50
40
30
20
10
0
50
40
30
20
10
1
2
3
4
5
6
7
1
2
3
4
5
NUMBER OF PREY SPECIES

TABLE 3

Overlap in the diet of penguins at Marion Island. Categories as given in Appendix 1 for proportion by mass.

	GP	GP	MP	RP
King Penguin	.014*	.045	.183	.059
Gentoo Penguin			.293	.312
Macaroni Penguin				.833

* comparisons as for Table 2

correspondence analysis (Fig. 3), which identifies nototheniid fish as being the critical factor. Overlap between the congeneric Macaroni and Rockhopper Penguins remains high in both comparisons (Fig. 3, 4).

DISCUSSION

There are inherent biases in diet analyses based on examination of stomach contents, particularly for the well - digested meals of King Penguins, because soft and hard parts of different prey are digested at different rates. Crustaceans, protected by a chitinous exoskeleton, are retained in seabirds stomachs longer than squid flesh, which in turn is retained longer than fish flesh (Wilson et al. 1985, Jackson & Cooper 1988). Gross analyses of soft parts of prey (Fig. 1) will overestimate such prey in the order crustaceans > squid > fish. Relative proportions by numbers and mass of species within the major prey classes of fish and cephalopods (Appendix 1) are based on analyses of otoliths and cephalopod beaks, respectively (Appendix 1). Large cephalopod beaks may remain in the stomachs of predators for many weeks and relative proportions may be overestimated (Furness et al. 1984, Jackson & Ryan 1986). However, large cephalopods, mainly in King Penguin diets, form a very small proportion of the diet, particularly in summer, when all four species are on the island (Appendix 1). Most cephalopod beaks in Macaroni, Rockhopper and Gentoo Penguin diets were small (lower rostral length < 2mm) and recovered from undigested buccal masses. Residence time of otoliths in seabird stomachs ranged upto 30 h (Jackson & Ryan 1986, Jackson & Cooper 1988). Crustacean exoskeletons may remain for longer

FIGURE 3

Correspondence analysis of the diets of penguins at Marion Island. Penguin species with a large proportion of prey species in common, plot close together. Prey consumed largely by one penguin species will plot far from the origin, whereas shared items will lie between the common predators. Data for analysis were percentage numbers from December to March only.✪ 1: King Penguin, 2: Gentoo Penguin, 3: Macaroni Penguin, 4: Rockhopper Penguin. ●, Prey species. A: Krefftichthys anderssoni, B: Electrona carlsbergi, C: myctophid A, D: Protomyctophum normani, E: Protomyctophum bolini, F: Gymoscopelus nicholsi, G:Electrona subaspera, H: Notothenia squamifrons, I: Notothena acuta, J: Paranotothenia magellanica, K: Dissostichus eleginoides, L: Magnisudis prinosa, M: Channichthys rhinoceratus, N: Kondakovia longimana, O: oegopsid A, P: Histioteuthis sp., Q: Brachioteuthis sp., R: octopod A, S: Euphausia vallentini, T: Thyssanoessa vicina, U: Nauticaris marionis, V: Themisto gaudichaudi, W: Primno sp., X: Vibilia sp., Y: Cyllopus sp., Z: Hyperialla sp.

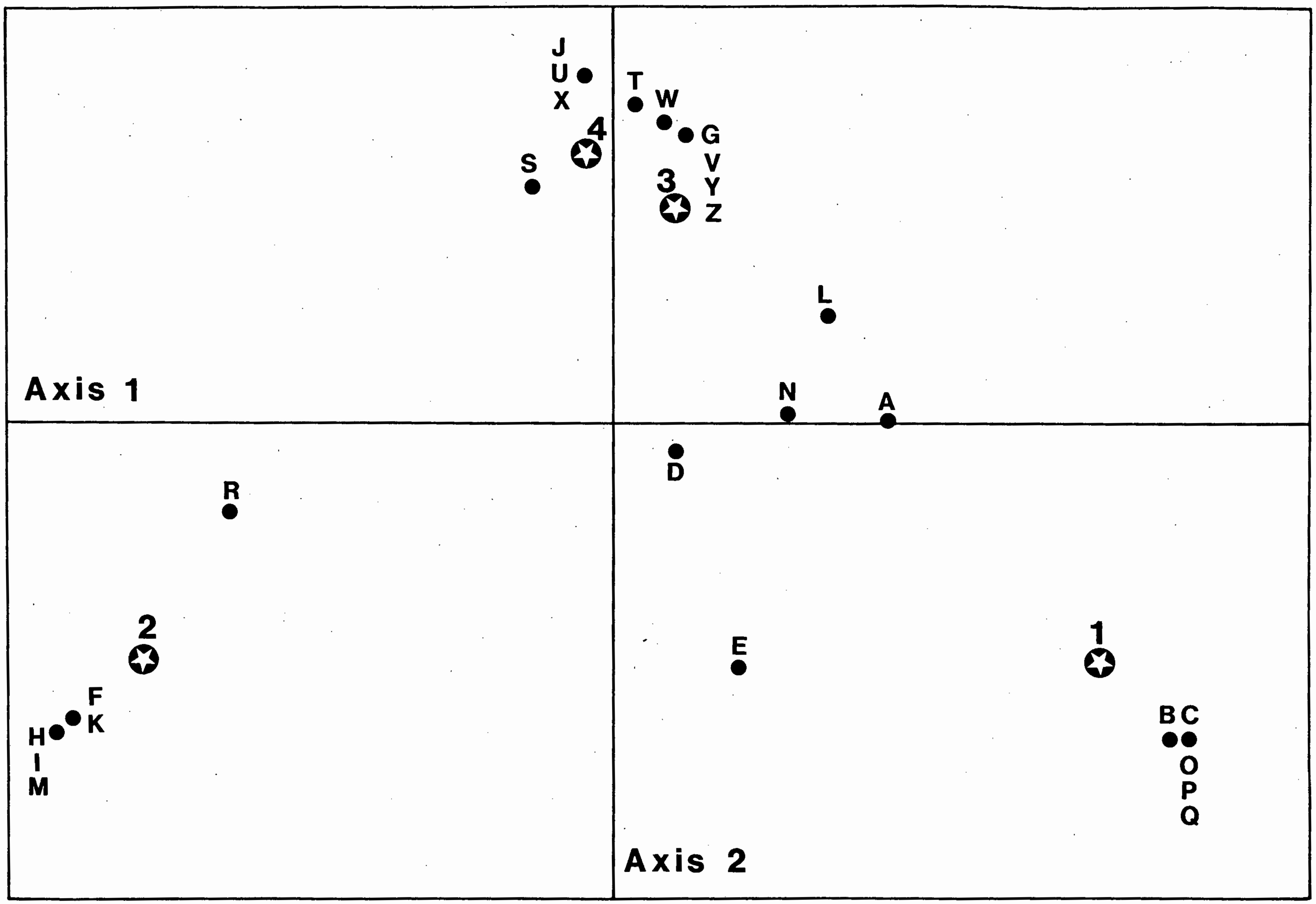
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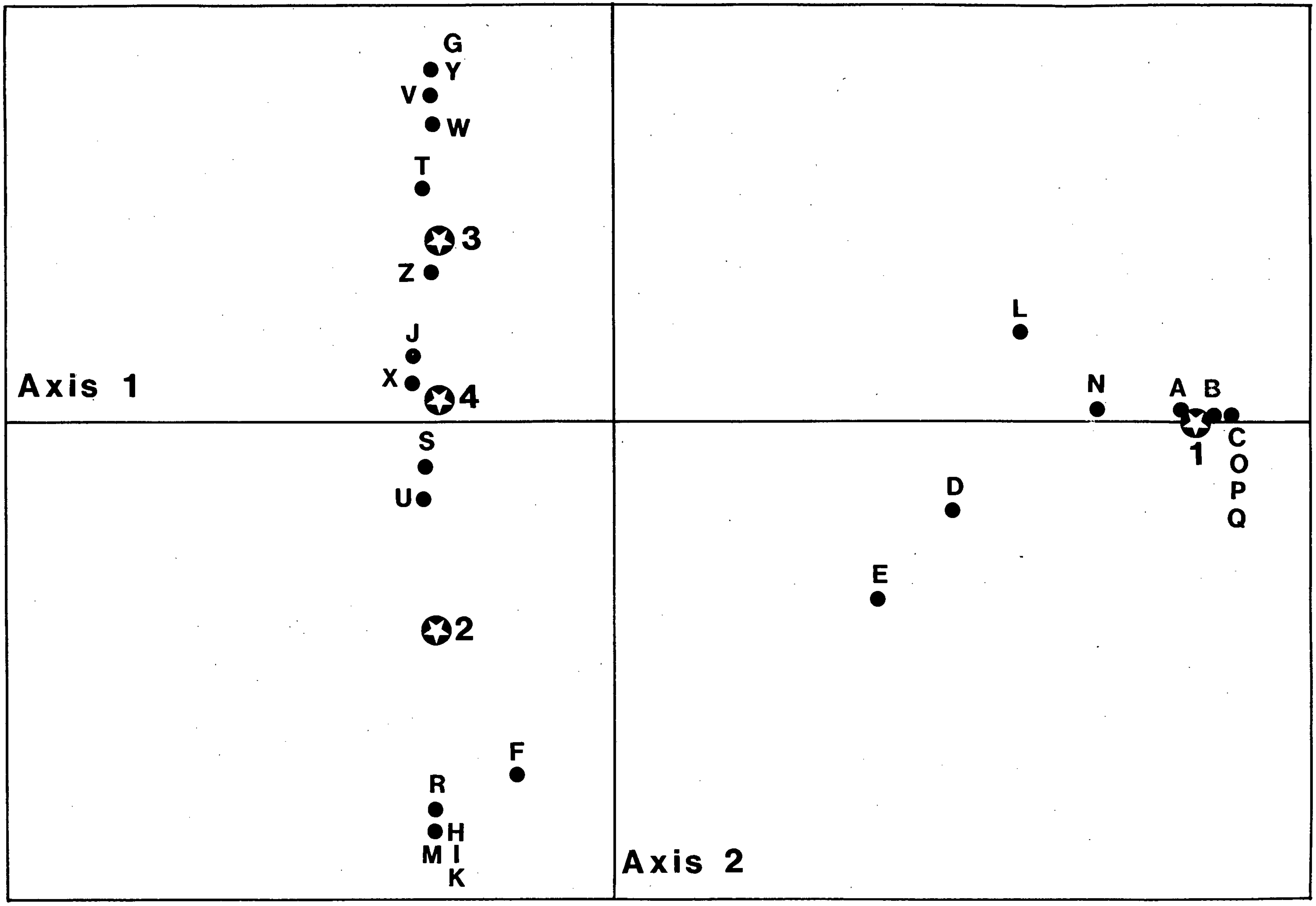
FIGURE 4

Correspondence analysis of the diets of penguins at Marion Island. Data for the analysis was percentage mass for December to March only. Species codes as for Figure 3.



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(Jackson & Cooper 1988). Except for squid beaks, individual stomach samples almost certainly represent prey captured during one foraging trip only. That at least 80 % (by number) of individual diet samples in each penguin species was accounted for by only four out of a possible 35 prey taxa (Fig. 4) further reduces biases that confound interspecific comparisons. Consequently, I considered interspecific comparisons of diet compositions largely justified.

Diets of Antarctic and sub-Antarctic penguins have been perceived as being dominated by a small number of prey species, particularly euphausiids (but see Ainley et al. 1984). Consequently one should expect high dietary overlap, particularly among taxonomically closely related species with similar foraging methods. Although this may be true of penguins and other seabird communities at particular localities (e.g. around the Scotia Sea (Croxall et al. 1985)), it is not the case at Marion Island and some other sites in the Southern Ocean region (Ainley et al. 1984). Average dietary overlap indices of sub-Antarctic and Antarctic seabird communities, on a prey family basis at least, are lower than or equal to some tropical communities (Table 4).

Diversity of prey taken by foraging penguins appears to be a function both of their size and foraging range. The intermediate sized Macaroni and Gentoo Penguins are capable of taking both relatively large and small prey and have a high prey diversity compared to King and Rockhopper Penguins, when the diet of the sample population is considered as a whole (Table 1). The low diversity indices of Gentoo Penguins when diet is considered on an individual sample basis (Table 1),

TABLE 4

Average overlap indices of diets within seabird communities. Analysis categories are prey family by percent numbers and mass as indicated

Overlap index		No.	Locality	Source
No.	Mass	species		
0.84	0.73	5	Aldabra Atoll, tropical	Diamond 1983
0.49	0.44	5	Cousin Island, tropical	"
0.51	-	11	Christmas Island, tropical	"
0.51	0.43	4[a]	Marion Island, sub-Antarctic	this study
0.73	-	9	Farne Island, temperate	Diamond 1983
0.77	-	7	Oceanic, Antarctica	Ainley et al. 1984
0.60	-	6	Continental slope, Antarctica	"
0.41	-	3	Continental shelf, Antarctica	"

[a] penguins only

reflects their short nest relief periods with reduced time to encounter different prey.

Differentiation mechanisms

Prey size:

Prey size may be an important consideration in segregation of diet among co-existing predators of different size. Although penguins at Marion Island are capable of consuming prey ranging over two to four orders of magnitude in mass (Table 5, items are generally small (average length < 100 mm in all cases, Table 6) compared to those consumed by sympatric albatrosses of similar mass to penguins (Berruti & Harcus 1978, Brooke & Klages 1986). Minimum prey size of penguins at Marion Island was similar (Table 6). However, prey of less than 30 mm accounted for only 6 % (by number) of the diet of the large King Penguin, but comprised a substantial proportion of the prey of the three other smaller penguin species. Discrimination of prey based on some minimum size may be more important in causing differentiation of diets of large and small penguins at Marion Island.

Although ANOVA demonstrated significant differences in the mean size of myctophid fish species common to more than one species of penguin (eg. for <u>Protomyctophum</u> <u>normani</u> in the diet of King, Macaroni and Rockhopper Penguins, $F = 164.94$, $F_{0.05,3,983} = 2.61$, $P < 0.005$) (see also Brown & Klages 1987), no consistent relationships between fish size and predator size were evident (Table 6). Similarly, Croxall & Lishman (1987) have cautioned against drawing conclusions about preferential selection for specific prey size classes based on significant differences in length recovered from conspecifics at the same

TABLE 5

Maximum mass of prey items (all squid) recovered from penguin stomach samples at Marion Island. All penguins were capable of taking prey of 0.1g, the minimum size estimated

Species	Max. mass (g)
King Penguin	807
Gentoo Penguin	65
Macaroni Penguin	41
Rockhopper Penguin	15

TABLE 6

Mean length of prey species recovered from stomachs of penguins at Marion Island

	Mean length (mm)			
	KP	GP	MP	RP
FISH				
Myctophidae				
Kreffichthys anderssoni	48.3	49.6	37.3	19.4
Protomyctophum tenisoni		49.2	49.5	45.9
Electrona carlsbergi	82.3	-	76.6	-
Protomyctophum normani	79.7	77.7	68.5	74.8
Nototheniidae				
Notothenia squamifrons	50.7	71.1	-	-
Channichthyidae				
Channichthys rhinoceratus	-	170.3	-	-
CEPHALOPODS				
Kondakovia longimana	73.0	58.5	58.4	60.9
octopoda	-	<10	<10	<10
CRUSTACEANS				
Euphausiacae				
Euphausia vallentini	-	22.5	24.0	24.0
Thysannoessa vicina	-	-	15.0	15.0
Natantia				
Nauticaris marionis	-	35.1	-	-
Amphipoda				
Themisto gaudichaudi	-	-	15.0	-

Average prey item size				
total	49.8	25.8		
December - March	62.0	30.4	21.5	22.3
Culmen length (mm)	133.0	67.0	56.6	46.0

Fish : caudal length, cephalopods: dorsal mantle length, crustaceans: total length.

KP: King Penguin, GP: Gentoo Penguin, MP: Macaroni Penguin, RP: Rockhopper Penguin

TABLE 7

Foraging parameters of penguins at Marion Island. Percent time swimming and estimated foraging range for adults feeding small and large chicks are presented where possible

	Travelling speed (km.h^{-1})	Foraging duration (days)		Foraging range (km)			Source
		small	large	small	large	range	
King Penguin	8.7	12.8	4.0	255	301	75-902	Adams (1987)
Gentoo Penguin	7.9	0.6		14		1-103	Adams & Wilson (1987)
Macaroni Penguin[1]	7.5	1.0 - 2.0	2.5 - 3.5	178		59-303	Brown (1987), Williams (1982)
Rockhopper Penguin[2]	7.4	1.0 - 2.0	2.5 - 3.5	33		2-137	" , "

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[1] Foraging trip durations estimated to nearest 0.5 day. Estimates of foraging range made during late chick-rearing

[2] Foraging trip durations estimated to nearest 0.5 day. Estimates made during early chick-rearing

locality. Maximum size of squid taken was larger than other prey types consumed and increased with penguin size (Table 5) and is probably because of ease of handling of squid compared to fish (Ashmole & Ashmole 1967).

Notwithstanding the absence of smaller prey from the diet of King Penguins, differences in the proportions of major components in the diets of Gentoo, Macaroni and Rockhopper Penguins cannot be explained by selection of prey based on size. Volkman et al. (1980) also rejected the hypothesis that the admittedly similarily sized Pygoscelis penguins partition euphausiids by size.

Diving depths:

If different prey characteristically occur at different depths, segregation of diet by penguins of differing sizes, and hence different diving capability (Stonehouse 1967, Butler & Jones 1982), may occur. Gentoo Penguins at South Georgia (54^{o}S, 38^{o}W) feeding diurnally on benthic fish generally dived deeper (54 - 135m) than krill - feeding Macaroni Penguins (<80 m) (Croxall et al. 1988). Data from Marion Island is restricted to measurements of maximum diving depth alone which indicates dives from less than 20 m to greater than 70 m (Adams & Brown 1983). The foraging range of the Gentoo and Rockhopper Penguins may overlap extensively during early chick rearing. The presence of demersal fish in the diet of Gentoo Penguins, but absent from that of smaller Rockhopper Penguins probably reflect differing diving ability. Although Croxall et al. (1988) noted that half of the dives of King Penguins at South Georgia were shallower than 50 m, the presence of mesopelagic fish and squid in the diet of King Penguins may reflect their ability to dive deep (Kooyman et al. 1982).

Travelling speed:

Travelling speeds of all four species of penguin are similar (Table 7). Maximum speeds attained during prey pursuit will be higher and may show significant differences between species. However, all four penguin species at Marion Island have the ability to catch adult myctophids and juvenile squid. I consider it unlikely that the slight differences in maximum swimming speeds play a significant role in dietary segregation.

Foraging range

There are clear differences in the mean maximum potential ranges of Gentoo, Macaroni, Rockhopper and King Penguins at Marion Island (Table 7). Samples sizes on which estimates of foraging range were made were small and, in addition, data are variable. However, the duration of foraging trips of the four species at Marion Island (Table 7) and elsewhere, support this pattern of zonation (Croxall & Prince 1980, Williams & Siegfried 1980, Williams 1982, Home 1985, Adams 1987). Breeding Gentoo Penguins are restricted largely to inshore waters (Table 7). During the remainder of the year adults do not have to return regularly to the island to feed chicks and foraging ranges may increase. The difference in foraging range between Rockhopper and Macaroni Penguins reflects the difference in chick feeding schedules of adults feeding small and large chicks at the time estimates were made (Table 7). Foraging range of Rockhopper Penguins is probably greater, later in chick rearing, and that of Macaroni Penguins, closer to shore during early chick rearing (Brown 1987). King Penguins are apparently pelagic throughout chick rearing.

I suggest that this zonation accounts for most of the major differences in the diets of the four penguin species. Similarly, Trivelpiece et al. (1987) regarded differences in foraging ranges of Pygoscelis species at King George Island, Antarctica ($62^{o}10'S, 58^{o}30'$) as an important factor affecting trophic interactions. Ainley et al. (1984) have demonstrated that diets of Antarctic seabird species may be different depending on whether birds were sampled from oceanic, continental slope or continental shelf waters, presumably reflecting availability of different prey in these areas. The absence of particular prey species in the diet of one species of penguin at Marion Island, but occurrence in others (Fig. 1, Appendix 1), suggests foraging zones of the different penguins species may, to some extent, be mutually exclusive. Substantial numbers of Macaroni and King Penguins radiating away from large colonies (essentially a point source) will be at relatively high densities in inshore waters and potential local depletion of prey resources (see Birt et al. 1987) may be too great to make foraging profitable. In contrast, the dispersion of relatively small colonies of Rockhopper (pers. obs.) and Gentoo Penguins (Adams & Wilson 1987) along the coastline of Marion Island may reduce intraspecific competition in inshore and nearshore waters (Croxall & Prince 1980, Adams & Wilson 1987).

Changes in the diets of Macaroni and Rockhopper Penguins over chick rearing appear to reflect a change from nearer - shore foraging during early chick rearing to offshore feeding when chicks are larger. The three to four week separation period between the breeding peaks of Macaroni and Rockhopper Penguins at Marion Island is of equivalent length to the guard period of small chicks. Thus the separation in timing of breeding results in differentiation of foraging zone which is, in turn, reflected in the diets of the two species. Timing of breeding at other localities where two congeneric species breed, e.g. Adelie _Pygoscelis_ _adeliae_ and Chinstrap _P._ _antarctica_ Penguins at Signy Island, are also separated by about four weeks, equivalent to the guard period of the latter species (Lishman 1985, Trivelpiece et al. 1987). The staggering of peak food requirements of congeneric species may have an indirect role in causing dietary differences due to separation of foraging zones (see Trivelpiece et al. 1987). I am in agreement with Trivelpiece et al. (1987) and regard specific differences due to separation of foraging ranges, life history patterns and temporal differences in food availability rather than competitive interactions among species.

Foraging range, population size and daily population food requirement

Ashmole (1963) and Diamond (1978) suggested that population sizes of breeding aerial seabirds at oceanic islands are limited by the availability of food. If the amount of food is a function of feeding area for surface feeding seabirds (or volume for penguins) then pelagic feeders should be more numerous than inshore feeders and migrant seabirds more abundant than resident species (Diamond 1978). Migration to alternative feeding areas outside those utilized during breeding increases the effective feeding area and has a more significant effect on population size than pelagic feeding (Diamond 1978). Although, as yet, no food limitation has been demonstrated for penguins at Marion Island, these predictions on the penguin community at the Prince Edward Islands, were tested. Marion Island and Prince

Edward Island (collectively: Prince Edward Islands) are only 22 km apart and I considered the islands to constitute a single breeding site. Because the body mass of King Penguins is some four times greater than Rockhopper Penguins, I considered daily populations food requirement, which takes account of allometric considerations, to be a more appropriate standard for comparison. There was a consistent trend of increasing daily food demand with increased average foraging range of penguins at the Prince Edward Islands (Tables 7 & 8). The relatively small difference in daily food demand between Macaroni and King Penguins (Table 8), may reflect the shorter residence time of the former at the islands.

Particularly during winter, Gentoo Penguins feed on benthic or demersal prey, largely juvenile nototheniid fish and adult shrimp, in the relatively shallow shelf waters around the island itself. Diets of the other penguins species, largely euphausiids and myctophid fish, are mostly pelagic in origin. A pelagic food source, with new stocks moving continously into areas locally depleted by predators, can presumably support larger populations of these predators than can more sedentary demersal organisms utilized by Gentoo Penguins. The major current passing Marion Island is the eastward flowing West Wind Drift. However, components of the Weddell Drift and Agulhas Current System may also penetrate to Marion Island. These currents provide a feasable mechanism for introducing pelagic prey into waters surrounding Marion Island (Boden & Parker 1986). The presence of zooplankton elements, in net hauls and penguin stomachs, more typical of subtropical and Antarctic waters (Brown 1989) suggest this is indeed occurring.

TABLE 8

Estimated breeding population size (pairs) and daily food requirements of penguins at the Prince Edward Islands (Marion and Prince Edward)

	Mean Mass	Feeding rate[a]	Population size		Total biomass	Total daily food
			Marion	Prince Edward		
	kg	$g.d^{-1}$	pairs	pairs	$kg \times 10^3$	requirements $g \times 10^6$
King Penguin	13.1[b]	392	215 230[c]	5 000[c]	5 770	172.7
Gentoo Penguin	6.4[b]	237	888[d]	655[d]	20	0.7
Macaroni Penguin	4.0[e]	190	405 084[f]	17 000[f]	3 968	160.4
Rockhopper Penguin	2.5[e]	139	157 600[g]	3 500[g]	966	44.8

[a] predicted from: feeding rate $(g.d^{-1}) = 0.495$ Body Mass $(g)^{0.704}$ (Equation 37, Nagy 1987); [b] N.J. Adams unpubl. data; [c] Williams et al. (1979); [d] Adams & Wilson (1987); [e] S.R. Henley pers. comm.; [f] Watkins (1987); [g] Fitzpatrick Institute unpubl. data

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APPENDIX 1

Percentage composition of food samples from penguins at Marion Island. Proportions for all samples and samples collected from December to March are given for species resident all year

Prey species	King Penguin				Gentoo Penguin				Macaroni Penguin		Rockhopper Penguin	
	annual		summer		annual		summer					
	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass	No.	Mass
FISH												
Myctophidae												
<u>Krefftichthys</u> <u>anderssoni</u>	54.80	27.13	57.01	21.14	0.01	0.17	0.24	0.32	0.69	3.19	0.07	0.25
<u>Protomyctophum</u> <u>tenisoni</u>					0.01	0.19	0.36	0.44	1.45	12.67	0.21	7.48
<u>Electrona</u> <u>carlsbergi</u>	22.67	51.47	33.43	56.77	0.01	0.13	0.05	0.24	0.02	0.08		
Myctophid A	2.50	3.69	2.02	2.21								
<u>Protomyctophum</u> <u>normani</u>	1.68	2.79	3.85	9.60	0.20	2.78	1.54	6.74	0.35	7.76	0.11	6.15
<u>Protomyctophum</u> <u>bolini</u>	0.40	0.57	0.33	0.41	0.01	0.11	0.25	0.26	0.00	0.09		
<u>Gymnoscopelus</u> <u>nicholsi</u>	0.39	0.55	0.04	0.05	0.01	4.98	0.31	9.51	0.00	0.04		
<u>Electrona</u> <u>subaspera</u>									0.03	0.79		
Nototheniidae												
<u>Notothenia</u> <u>squamifrons</u>	0.02	0.02			2.50	33.40	9.02	36.46	0.00	0.05		
<u>Notothenia</u> <u>acuta</u>					0.01	0.90	0.11	0.72				
<u>Notothenia</u> <u>magellanica</u>	0.02	0.18									0.02	0.12
<u>Dissostichus</u> <u>eleginoides</u>					0.01	0.40	0.08	0.61	0.00	0.01		
<u>Paralepis</u> <u>coreginoides</u>	0.17	0.25	0.03	0.04					0.01	0.10		
Channichthyidae												
<u>Channichthys</u> <u>rhinoceratus</u>					0.20	9.97	1.56	22.57				
Muraenolepidae												
<u>Muraenolepis</u> sp.					0.01	0.37						

CEPHALOPODS												
Kondakovia longimana	16.73	12.93	3.48	9.55	0.01	1.07	0.19	2.92	0.38	13.10	0.04	1.64
Oegopsid A	0.09	0.07	0.04	0.11								
Histioteuthis sp.	0.08	0.12	0.03	0.15								
Alluroteuthis sp.	0.05	0.08										
Moroteuthis sp.	0.05	0.29										
Martialia hyadesi	0.02	0.01										
Gonatus antarcticus	0.02	0.01										
Galiteuthis glacialis	0.01	0.01										
Brachioteuthis sp.	0.01	0.01	0.01	0.04								
Octopoda					1.20	1.03	4.60	3.63	0.02	0.10	0.16	1.64
CRUSTACEANS												
Euphausiacea												
Euphausia vallentini	0.01	0.00			82.60	22.20	80.48	15.57	50.10	32.22	74.55	60.60
Thyssanoessa vicina									34.11	21.86	24.25	19.80
Natantia												
Nauticaris marionis	0.03	0.00			12.90	21.80	0.17	0.00			0.39	0.32
Amphipoda												
Themisto gaudichaudi	0.06	0.00			0.01	0.04	0.27	0.00	9.59	6.15	0.10	0.08
Primno spp.									0.48	0.31	0.10	0.08
Vibilia spp.					0.00	0.00	0.01	0.00			0.20	0.16
Cyllopus spp.									1.55	0.99		
Hyperialla spp.					0.00	0.00	0.07	0.00	0.19	0.12		

CHAPTER 7

BASAL METABOLIC RATES AND METABOLIC RESPONSE TO TEMPERATURE OF KING *APTENODYTES PATAGONICUS* AND GENTOO *PYGOSCELIS PAPUA* PENGUINS

Mean Basal Metabolic Rates (BMRs) of King *Aptenodytes patagonicus* and Gentoo *Pygoscelis papua* Penguins were calculated from the lowest stable measurements of oxygen consumption conducted over at least 24 h. BMRs of King and Gentoo Penguins were 2 237 kJ.d^{-1} and 1 605 kJ.d^{-1}, respectively. Mass-specific metabolism averaged 169 kJ.kg^{-1}.d^{-1} and 255 kJ.kg^{-1}.d^{-1} for King and Gentoo Penguins, respectively. These values were within 20 % of those predicted from allometric equations relating metabolism and body mass and within the range recorded for other species of penguins. Lower Critical Temperature (T_{lc}) of King Penguins was between 0°C and 5°C and the Thermoneutral Zone (TNZ) extended to about 15°C. Metabolic rate of Gentoo Penguins decreased from a maximum at -10°C to a minimum at 20°C and no TMZ could be defined. Measurements of oxygen consumption of King Penguins in water at 5°C were 1.9 times Resting Metabolic Rate (RMR) in air at similar temperatures.

INTRODUCTION

Basal Metabolic Rate (BMR) is an important part of the total energy budget of an animal, being the lowest level of metabolism required for maintenance upon which the energy costs of all other activities, including thermoregulation, are superimposed (Rahn & Whittow 1984). Therefore, BMR provides a baseline measurement against which the energy costs of other activities may be compared.

Previous measurements of metabolic rates of post-absorbative, resting King Penguins *Aptenodytes patagonicus* were 27% higher than predicted from their body mass (Le Maho & Despin 1976) by the equation of Kendeigh et al. (1977) for non-passerines, but

8% lower than predicted for zoo captive individuals in their thermoneutral zone (Gavrilov 1977). Given this variation and that basal metabolic rate of Gentoo Penguins Pygoscelis papua has not previously been measured, I considered it necessary to determine standardized measurements of metabolic rates for comparison with energy costs of other activities presented in subsequent chapters. I attempt also to define the thermoneutral zone of King and Gentoo Penguins. Penguins show many anatomical and physiological adaptations to the aquatic environment in which they spend a considerable amount of time. The cold waters of the sub-Antarctic and Antarctic compound the problem of heat loss to a medium of high specific heat and penguins may be expected to show metabolic adjustments to compensate for additional heat loss. Accordingly, I also examined metabolic responses of King Penguins to immersion in water.

MATERIALS AND METHODS

The study was carried out at sub-Antarctic Marion Island ($46^{o}51'$S, $37^{o}51'$E). Only individuals not undergoing prolonged natural fasts were used. All birds were released after measurements were complete. Oxygen consumption measurements were measured in translucent, airtight cylindrical chambers using an open flow-through system. Two different sized chambers were used, one of 75 l capacity for King Penguins and the other of 45 l capacity for Gentoo Penguins. Birds were not physically restrained but chambers were small enough to prevent excessive activity.

A pump passed air drawn from outside the laboratory through a regulating flow meter before entering the chamber. Air exiting the chamber was passed through a silica gel drying tube, a Rotameter flow meter and a silica gel/Carbosorb/silica gel tube before entering a Taylor Servomex OA570 paramagnetic oxygen analyser. The flow rate was set to produce a drop in oxygen content of between 1 and 2% below that of ambient air, and consequently differed depending on the size of the bird. A thermocouple, inserted into the chamber through a rubber bung, measured chamber temperature. Chamber temperature was not controlled but remained in the range 9.1°C to 17.0°C for King Penguins and 10.8°C to 20.9°C for Gentoo Penguins. Average air temperature at Marion Island is 5.1°C with absolute minimum and maximum temperatures ranging from -6.8°C to 22.3°C respectively (Schulze 1971).

An initial period of between 45 min and 2 h was allowed for birds to settle and for air in the chambers to equilibrate. Thereafter, readings of percent oxygen, flow rate and temperature were taken at 30 min intervals over 24 h at natural photoperiod. The oxygen content of ambient air was checked at regular intervals throughout the run. Oxygen consumption at standard temperature and pressure was calculated using the equation of Hill (1972). Oxygen consumption was converted to an energy equivalent using the relation 1 dm^3 O_2 = 20.08 kJ. The lowest stable levels of at least 2h duration were selected to calculate BMR. Metabolic response to ambient temperature was investigated by measurements of oxygen consumption on four birds for each species at 5°C intervals between -15°C and 20°C. Chamber temperature was controlled by placing in a deep freeze (-15°C to 0°C) or by placing the weighted metabolic chamber in a large, water filled, plastic container. The temperature of the water was controlled by circulating the water through a thermostatically controlled water bath. Measurements of oxygen consumption were recorded every 15 min for at least an hour at each temperature. Equilibration time between each temperature step was at least 1 h. The body temperatures of birds exposed to ambient temperatures between -15°C and 20°C were measured using temperature sensitive transmitters which had been force fed to penguins before the commencement of the oxygen consumption measurements. Pulse frequency was calibrated against temperature. After the end of the experiment penguins were stomach flushed (Wilson 1984) to retrieve the transmitters.

Metabolic response to water immersion were restricted to measurements on King Penguins and at one temperature only, 5°C, the average annual sea surface temperature (SST) at Marion Island (range 2.1° to 8.0°C) (Schulze 1971).

Measurements of oxygen consumption during water immersion were conducted on six unsexed adult King Penguins using an open-mask system coupled to an electro-chemical oxygen analyser (Withers 1977). Birds were placed in a plastic container. A lid clamped to the open end of the container had a small circular hole through which the head and neck of the penguin projected. A plastic mask fitted to the face completely enclosed the gape but left vision unobstructed. A small air pump drew air through the mask and past the bill of the penguin at a rate of 10.5 to 22.5 $l.min^{-1}$. This produced a drop in % O_2, compared to ambient air, of between 0.3 and 1.2%. The sensitivity of the electro - chemical oxygen analyser allowed detection of changes in % O_2 of as little as 0.01%. A flowmeter was placed upstream of the pump and expired air was passed through two tubes of silica gel/carbosorb before entering the oxygen analyser. The small volume of dead air space and relatively high flow rate ensured rapid equilibration and prevented backflow or leakage of air expired by the penguins. Measurements were first conducted on birds in air at ambient temperatures between 6.2°C and 11.2°C, within the thermoneutral zone of King Penguins (see below). Birds were allowed 30 - 45 min to settle after attachment of the mask before readings commenced. Readings of relative oxygen content of expired air were recorded every 15 min for at least 2 h. Oxygen content of ambient air was checked periodically throughout the run and air temperature was measured every 30 min . Fresh water was then added to the chamber until the penguin was immersed in water up to a point between the base of the neck and top of the flippers. Water temperature was maintained at around 5°C by circulating through a cold water bath. Birds were again allowed 30 - 45 mins to settle before readings commenced. Readings of % O_2 were maintained for 2 - 4h. Body temperatures of King Penguins were measured before and immediately after immersion measurements by inserting a thermocouple 10 cm into the oesophagus.

Oxygen consumption of King Penguins was calculated using the equation in Withers (1977) for dry, CO_2 free air. The lowest readings during each run were considered to be the best estimate of resting metabolic rate, in both air or water.

RESULTS

Basal metabolic rates of King and Gentoo Penguins of 2 237 $kJ.d^{-1}$ and 1 604 $kJ.d^{-1}$ respectively were determined from the lowest stable periods of metabolism measured over at least

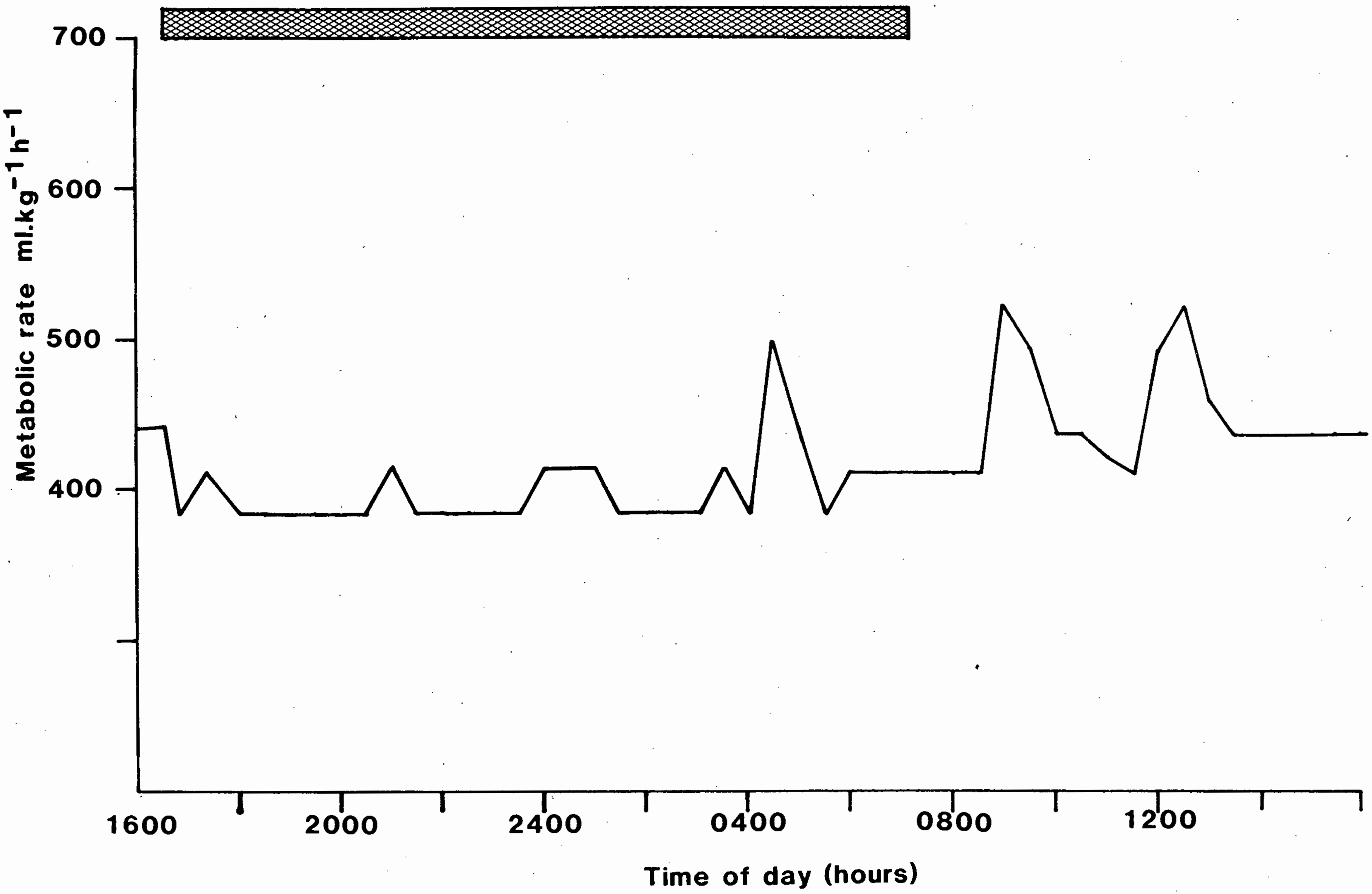
TABLE 1

Basal Metabolic Rate (BMR) and Average Daily Metabolic Rate (ADMR) of King and Gentoo Penguins

Penguin Species	n	Mass kg	BMR $kJ.d^{-1}$	BMR $kJ.kg^{-1}.d^{-1}$	ADMR $kJ.d^{-1}$	ADMR $kJ.kg^{-1}.d^{-1}$
Gentoo	4	6.3	1 604.6	255.1	2 037.6	328.2
S.D.		± 1.1	± 53.9	± 8.6	± 224.8	± 39.9
King	7	13.3	2 237.0	168.6	2 632.3	197.1
S.D.		± 1.8	± 416.0	± 17.5	± 215.9	± 15.8

FIGURE 1

Oxygen consumption of an individual King Penguin over 24h at normal photoperiod. Hatched bars indicate periods of darkness.

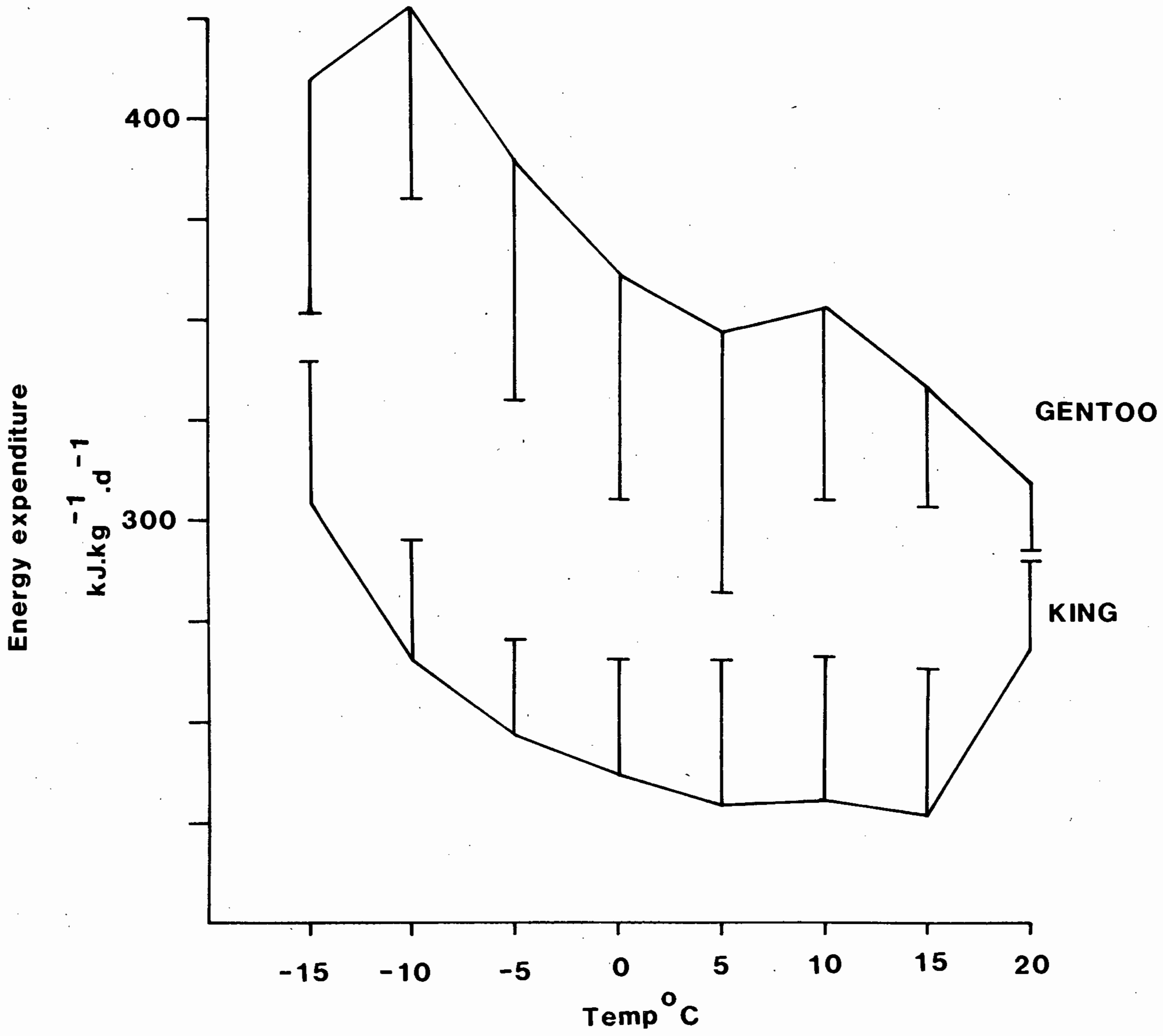

700
600
500
400
Metabolic rate ml.kg^{-1}h^{-1}
1600
2000
2400
0400
0800
1200
Time of day (hours)

24 h (Table 1). Lowest metabolic rates of King Penguins occurred at night. Increases in metabolic rate that occurred soon after day break (Fig. 1) were associated with limited activity in the metabolic chambers. Metabolic rates of Gentoo Penguins showed wider fluctuations than those of King Penguins and no well defined diel cycle in metabolism was evident. The Average Daily Metabolic Rates measured over 24h (ADMR), were 29% and 17% higher than BMR for Gentoo and King Penguins, respectively.

Core body temperatures of both penguin species showed little change over ambient temperatures that ranged from -15°C to 20°C. Body temperatures varied between 37.0 ± 0.7°C at temperatures below 0°C, to 37.4 ± 0.4°C at 15°C for King Penguins (n = 4) and between 37.9 ± 0.3°C and 38.2 ± 0.2°C for Gentoo Penguins (n = 4). Monitored responses of penguins to different experimental temperatures were restricted therefore to adjustments of metabolic rate. Measurements of VO_2 of penguins at the various experimental temperatures were highly variable. King Penguins showed a decrease in mean mass-specific metabolism from -15°C to 5°C (Fig. 2). Mean metabolism was stable in the range 5°C to 15°C but was followed by a marked increase above 15°C. Given the larger variance in the data, the lower critical temperature (T_{lc}, temperature below which metabolism increases above BMR to maintain body temperature) was difficult to define although it was clear that general levels of metabolism at -15°C were higher than those in the range -5 to 15°C and I estimated that T_{lc} was between 0°C and 5°C. The increase in metabolism between 15 and 20°C suggested that penguins were becoming heat stressed. Gentoo Penguins showed a somewhat different pattern (Fig. 2). Metabolism decreased from a maximum at lowest experimental temperatures to a minimum at the highest

FIGURE 2

Mass specific metabolism of King and Gentoo Penguins at temperatures between -15°C and 20°C.


400
300
Energy expenditure
kJ.kg^{-1}.d^{-1}
GENTOO
KING
-15
-10
-5
0
5
10
15
20
Temp ^{o}C

temperature and it was not possible to define a TNZ. Lowest levels of metabolism during runs in which ambient temperature was varied were at all times higher than BMRs measured during the 24 h experiments.

Temperatures of King Penguins before and after water immersion were not significantly different at 36.4 ± 0.7°C and 36.2 ± 0.7°C, respectively. The higher body temperatures measured for penguins monitored at ambient temperatures between -15°C and 20°C probably reflect differences in the site of measurement. Metabolism of King Penguins in water at 5°C averaged 1.91 times RMR in air (Table 2).

DISCUSSION

The Basal Metabolic Rate (BMR) of an organism has been defined as its metabolic rate measured while resting, in a postabsorptive state within its thermoneutral zone (Kendeigh et al. 1977). The conditions under which measurements of BMR of King and Gentoo Penguins were performed fulfil these criteria. Aschoff & Pohl (1970) recognized that BMR differed depending on whether birds were in an active phase of their activity cycle or not. Measurements of the oxygen consumption of nocturnally active procellariiform seabirds show clearly defined diel changes in metabolism with lowest rates occurring during the day (Adams & Brown 1984). However, diurnally active procellariiforms showed a less well defined pattern. Similarly, there was no clear diel pattern of energy metabolism for King and Gentoo Penguins (this study) or for Macaroni and Rockhopper Penguins (Brown 1984). Although the most extended periods of low, stable

TABLE 2

Resting Metabolic Rates (RMR) of King Penguins in air and water

Air		Water		
$kJ.d^{-1}$	$kJ.kg^{-1}.d^{-1}$	$kJ.d^{-1}$	$kJ.kg^{-1}.d^{-1}$	RMR (water)/ RMR (air)
3 350.0	280.7	6 401.2	523.2	1.91
± 426.3	± 38.3	± 856.3	± 104.4	

metabolic rates of King Penguins occurred at night (Fig.1), this was not the case for Gentoo Penguins.

Measurements of the BMR of King Penguins were 4% lower than predicted from their body mass by the equation of Kendeigh et al. (1977), whereas measurements of BMR of Gentoo Penguins were 19 % above predicted levels. Previous measurements of the metabolic rates of resting King Penguins were 1 % lower (Gavrilov 1977) and 27 % higher (Le Maho & Despin 1976), respectively, than values measured in the present study. No comparative measurements are available for Gentoo Penguins. Data on the resting metabolic rates of 10 other species of penguins indicate similar inter-and intraspecific variations around predicted values (Brown 1984).

Penguins generally have body temperatures lower (Le Maho et al. 1976, Stahel & Nicol 1982, Brown 1984) than do other non -passerine birds (McNab 1966), but similar to those measured for procellariiforms (Warham 1971). Warham (1971) has suggested that low body temperatures imply low metabolic rates. However the data indicate that in spite of these low body temperatures and variability in resting metabolic rates, penguins have similar body mass/metabolism relationships to other birds (Croxall 1982, Brown 1984). Such a conclusion does not rule out the existence of other more subtle correlates with metabolism. Ellis (1984) demonstrated a highly significant positive correlation between relative BMR values and breeding latitude for charadriiforms and alcids, similar to that demonstrated for terrestrial birds (Weathers 1979, Hails 1983). Lower latitude seabirds in warm environments, have relatively lower BMRs than do high latitude seabirds in cold environments (Ellis 1984). Penguins have a wide breeding distribution from the tropics to the Antarctic mainland. However, most of the measurements conducted on the lower latitude breeding penguins were performed on birds that had been kept in captivity for extended periods. Such birds appear to have lower metabolic rates than those caught in the wild just prior to measurements (Brown 1984) and invalidated investigation of similar correlations (see Ellis 1984). The importance of obtaining standardized measurements that allow investigation of such potential relationships has been stressed previously (Brown 1984).

The TNZ of adult King Penguins determined here extends below and above the range in mean monthly ambient temperatures at Marion Island (Schulze 1971). Relationships between changes in ambient temperature and metabolic response by King Penguins have been previously examined. The lower critical temperature of King Penguins has been determined at 3°C (Gavrilov 1977) and -5°C (Le Maho 1983). Both values are within the range that is possible for TNZ determined in this study. Barre (1984) has demonstrated winter acclimatization in King Penguin chicks. Lower critical temperature of chicks in winter (T_{lc} = -10°C) was lower than in summer (T_{lc} = 4.8°C). Measurements on adult penguins described here were conducted in April and May during the austral autumn. I did not determine if there was any acclimatization in adults. Such an acclimatization may account for variations in TNZ determined by different studies. The continued decrease in metabolic rate of Gentoo Penguins meant that no TNZ could be defined (see also Brown 1987). It is not clear why this is so, because the T_{lc} of Gentoo Penguins at the Crozet Islands at a similar latitude to Marion Island, was -5°C (Le Maho & Despin 1978). This was close to the -6°C recorded for Gentoo Penguin chicks immediately prior to attaining independence at King George Island, Antarctica ($62^{o}09'S$, $58^{o}28'W$) (Taylor 1985).However, the large variation in metabolic rates among individuals may mask more clearer responses to change in ambient temperature by individual penguins.

The marked increase in metabolic rates of adult King Penguins when immersed in water compared to resting metabolic rates in air is a well described phenomenon. Juvenile King Penguins naturally acclimatized to water at $7^{o}C$ had metabolic rates three times resting metabolic rates in air (Barre & Roussel 1986). Similarly, restrained Adelie Penguins Pygoscelis adelidae increased metabolism 3.4 times when immersed in water at $5^{o}C$ (Kooyman et al. 1976). At water temperatures of $10^{o}C$ mass-specific metabolic rates of King (Barre 1981) and Adelie Penguins (Kooyman et al. 1976) drop 75% and were 54% higher respectively than unrestrained birds. At $5^{o}C$ Little Penguins Eudyptula minor became hypothermic and metabolism peaked at 3.3 times BMR (Stahel & Nicol 1982). All studies point to a considerable rise in metabolism in response to water immersion. Such costs may form a significant proportion of total energy budget of penguins at sea. However, swimming and diving are energetically costly activities (Nagy et al. 1984) and it is probable that while active in the water, King Penguins generate enough heat to maintain thermal balance without additional thermoregulatory response.

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CHAPTER 8

ENERGETICS OF MOULT IN KING APTENODYTES PATAGONICUS AND GENTOO PYGOSCELIS PAPUA PENGUINS

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Penguins have an intense moult, during which time they are confined to land. Energy costs of moult of King Aptenodytes patagonicus and Gentoo Pygoscelis papua Penguins determined from oxygen consumption averaged 3 605 $kJ.d^{-1}$ and 2 180 $kJ.d^{-1}$ or 1.6 and 1.3 x BMR, respectively. Peak values were 4 806 $kJ.d^{-1}$ and 3 174 $kJ.d^{-1}$ for King and Gentoo Penguins, respectively. These had decreased to 2 717 $kJ.d^{-1}$ and 1 506 $kJ.d^{-1}$ by the end of moult as birds lost mass. Mass-specific costs were maintained at high levels throughout most of moult, probably reflecting feather synthesis at a time of reduced insulation. With completion of feather growth energy costs apparently decreased. However, interspecific responses were variable and evidence of direct linking between metabolism and moult processes is unconvincing at present. Measurements of oxygen consumption are precise and allow serial measurements on individual birds but involve removal of the bird from its natural environment. Estimates of moult costs based on mass loss rates require many assumptions and may provide only an average estimate of energy expenditure. Measurements based on isotope dilution rates integrate costs over a number of days and provide the most ecologically meaningful measurements. Calculation of feeding rates of penguins accumulating energy reserves for moult are higher than those sustained by adults feeding chicks. However, energy constraints may be less severe because birds do not have to return regularly to the nest site.

INTRODUCTION

Penguins are the most aquatic adapted of all birds. However, their hydrodynamic efficiency depends, in part, on the condition of their feathers. Feathers wear with age and, to maintain efficiency, must be replaced regularly. New feathers begin forming under the skin when the birds are still at sea and first emerge several days after the birds come ashore to moult, when the feathers are already over half their final length (Groscolas 1978, Brown 1986). In most species of penguins, this process occurs once a year, usually after breeding (Adams & Brown 1990). In contrast to most other avian orders, penguins have a rapid moult associated with fasting periods ranging from 13 - 34 days (Adams & Brown 1990). During this period penguins do not go to sea because of their reduced waterproofing and insulation (Erasmus et al. 1981) and, as a consequence of increased drag, they may, in addition, be simply too slow to catch their prey (Wilson 1985a).

Penguins are generally sedentary during moult (Penney 1967, Cooper 1978) and activity costs will be low. However, moult involves the production of new tissue and must therefore incur some energy cost above that required for normal maintenance (King 1980), apart from any additional costs of thermoregulation due to increased heat loss through heavily vascularized skin. Energy and nutrient reserves to meet these requirements must be accumulated by increasing food intake during a premoult period at sea of 17 - 70 days before commencing their moult fast (Adams & Brown 1990).

The easy accessibility of penguins during moult has made them suitable candidates for studies of the physiology of moult and in particular, the energy requirements associated with it. I present here data on energy cost of moult determined for King <u>Aptenodytes</u> <u>patagonicus</u> and Gentoo <u>Pygoscelis</u> <u>papua</u> Penguins based on measurement of oxygen consumption. Based on rates of mass loss and oxygen consumption measurements, Brown (1985) and Groscolos (1978) identified a number of phases during moult. I examined changes in oxygen consumption by King and Gentoo Penguins during moult in relation to feather growth and synthesis. Overall costs of moult have also been determined from changes in body composition through moult (Williams et al. 1977, Cooper 1978), rates of loss of body mass (Croxall 1982), and rates of dilution of isotopically labelled water (Davis et al. 1989, Gales et al. 1988). The energetics of moult in penguins are reviewed and the four methods of determining such costs are compared and contrasted.

MATERIALS AND METHODS

The study on King and Gentoo Penguins was conducted at sub-Antarctic Marion Island ($46^{o}52'$S, $37^{o}51'$E). Premoult birds, identified by the brownish colour of their plumage and their obesity, were caught prior to commencement of feather loss. Except during measurements of oxygen consumption, birds were housed in separate wooden crates. They were protected from rain, but experienced prevailing ambient conditions.

Rates of oxygen consumption were measured using a positive pressure open flow-system. Two cylindrical, plastic metabolic chambers of approximate volume 75 l and 45 l were used for King and Gentoo Penguins, respectively. Air was pumped through a regulating flowmeter before passing into the chamber. Exhalent air passed through a Silica Gel drying tube, a calibrated flowmeter and a Silica Gel/carbosorb tube before a subsample was fed to a Taylor Servomex OA 570 paramagnetic oxygen analyser. A parallel circuit provided a sample of fresh air for reference and was assumed to have an oxygen content of 20.94 %. Flow rates through the chamber were set between 3.75 $l.min^{-1}$ and 6.25 $l.min^{-1}$ for Gentoo Penguins and between 10.5 $l.min^{-1}$ and 7.1 $l.min^{-1}$ for King Penguins. Chamber temperatures were not controlled and varied between 9.6 and 21.6°C and between 8.2 and 19.6 °C for Gentoo and King Penguins, respectively.

Oxygen consumption was measured at 4d intervals on a maximum of four King and five Gentoo Penguins from prior to first feather loss and until moult was complete. Individual measurements were conducted over a period of 2 - 5 h excluding a period of 1 - 2 h for birds to settle and to allow chamber air to equilibrate. Chamber temperature, air flow and percent oxygen were recorded at 30-min intervals for the duration of the run. Oxygen consumption was calculated from the equation presented in Hill (1972) for dry, carbon dioxide free air and converted to an energy equivalent (1 l O_2 = 20.08 kJ). In addition to oxygen consumption measurements, experimental birds were weighed every two days throughout moult. Collection of feathers over the same interval allowed body mass loss to be corrected for feather loss. Every second day 10 measurements of new feathers protruding through the skin along the mid-dorsal region of the penguin were measured to the nearest mm to monitor feather growth.

RESULTS

Mean moult costs intergrated over the whole period were 3 605 $kJ.d^{-1}$ and 2 180 $kJ.d^{-1}$ for King and Gentoo Penguins respectively, equivalent to 1.6 and 1.3 x BMR (Table 1). Apart from a decrease in energy consumption towards the end of moult, King and Gentoo Penguins failed to show a consistent pattern of metabolism during moult (Fig. 1 & 2). Mean daily energy expenditure of Gentoo Penguins decreased steadily throughout moult from a high of 3 174 kJ.d^{-1} to a minimum of 1 506 kJ.d^{-1} (Fig. 1). However, daily energy expenditure of King Penguins peaked at 4 806 kJ.d^{-1} eight days into moult before decreasing to 2 717 kJ.$^{-1}$ by the end of moult.

Mass specific metabolic rates during moult showed a similarly inconsistent pattern between the two species (Fig. 2). Metabolic rates of King Penguins peaked at 367.1 kJ.kg^{-1}.d^{-1} some 16 d into moult. A slightly lower peak at 8 d coincided with the peak in mass independent metabolic rate. High levels of mass-specific metabolism of Gentoo Penguins between 381 and 411 kJ.kg^{-1}.d^{-1} were sustained throughout moult (Fig. 2) with an apparent decrease at the end of moult although observations were based on a reduced sample size.

Feather growth of King Penguins (Fig. 3) decreased rapidly 18 d after the commencement of feather loss. By 24 d feathers had ceased to grow. No such reduction in growth towards the end of moult was evident in Gentoo Penguins although measurements were terminated at 18 d.

Mass loss corrected for feather loss averaged 273 g.d^{-1} and 191 g.d^{-1} for King and Gentoo Penguins respectively. Energy expenditure calculated from these rates of mass loss ranged between 2 184 kJ.d^{-1} and 4 641 kJ.d^{-1} for King Penguins and 1 552 kJ.d^{-1} and 3 298 kJ.d^{-1} for Gentoo Penguins (Appendix 1).

FIGURE 1

Energy expenditure of King and Gentoo Penguins through moult. Day 0 is the day on which feather loss commenced. Vertical bars indicate standard deviation around the mean.

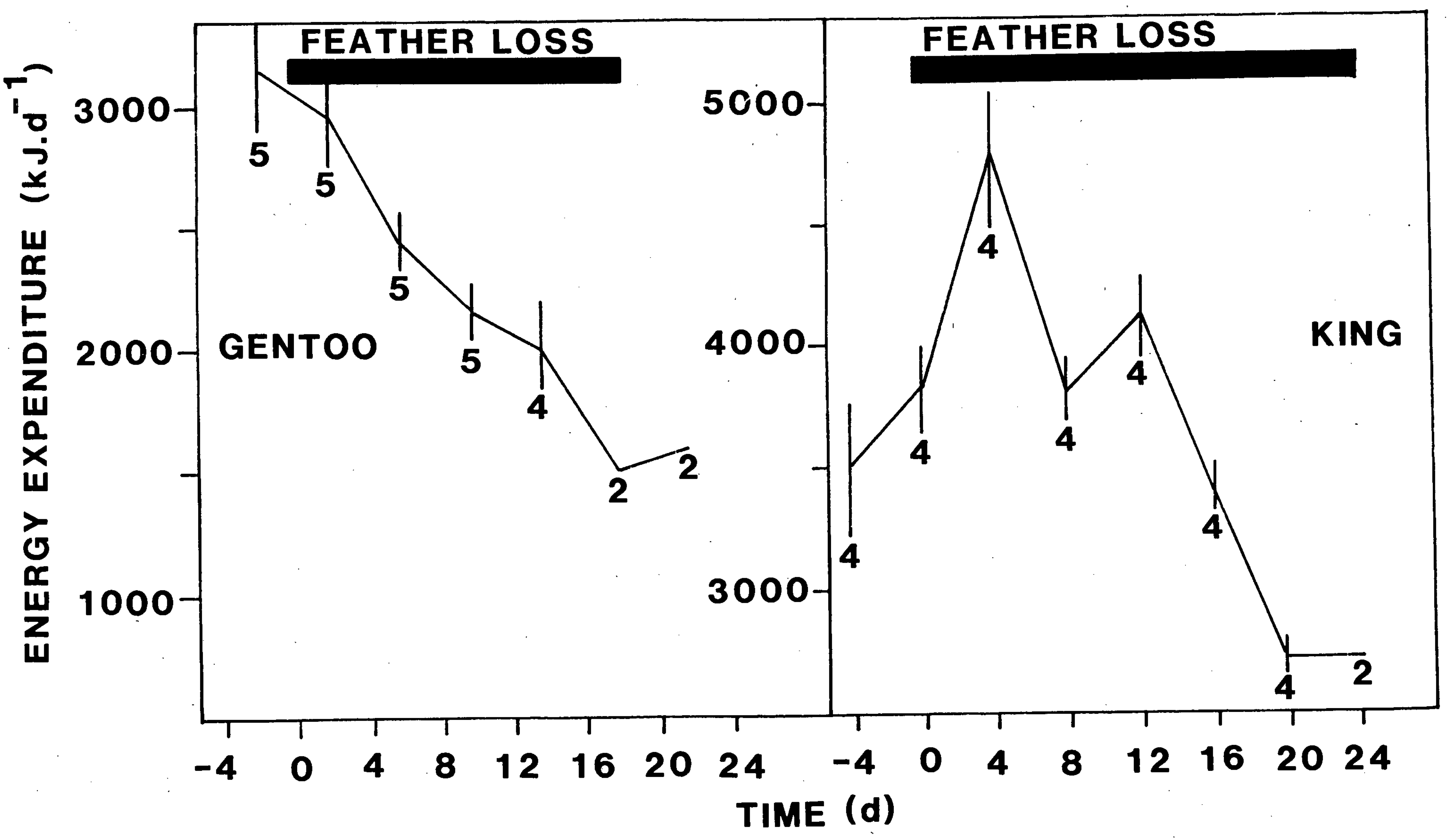

FEATHER LOSS
FEATHER LOSS
ENERGY EXPENDITURE (kJ.d⁻¹)
3000
2000
1000
GENTOO
5
5
5
5
4
2
2
5000
4000
3000
KING
4
4
4
4
4
4
4
2
-4 0 4 8 12 16 20 24
-4 0 4 8 12 16 20 24
TIME (d)

FIGURE 2

Mass specific energy expenditure of King and Gentoo Penguins through moult. Day 0 is the day on which feather loss commenced. Vertical bars indicate standard deviation around the mean.

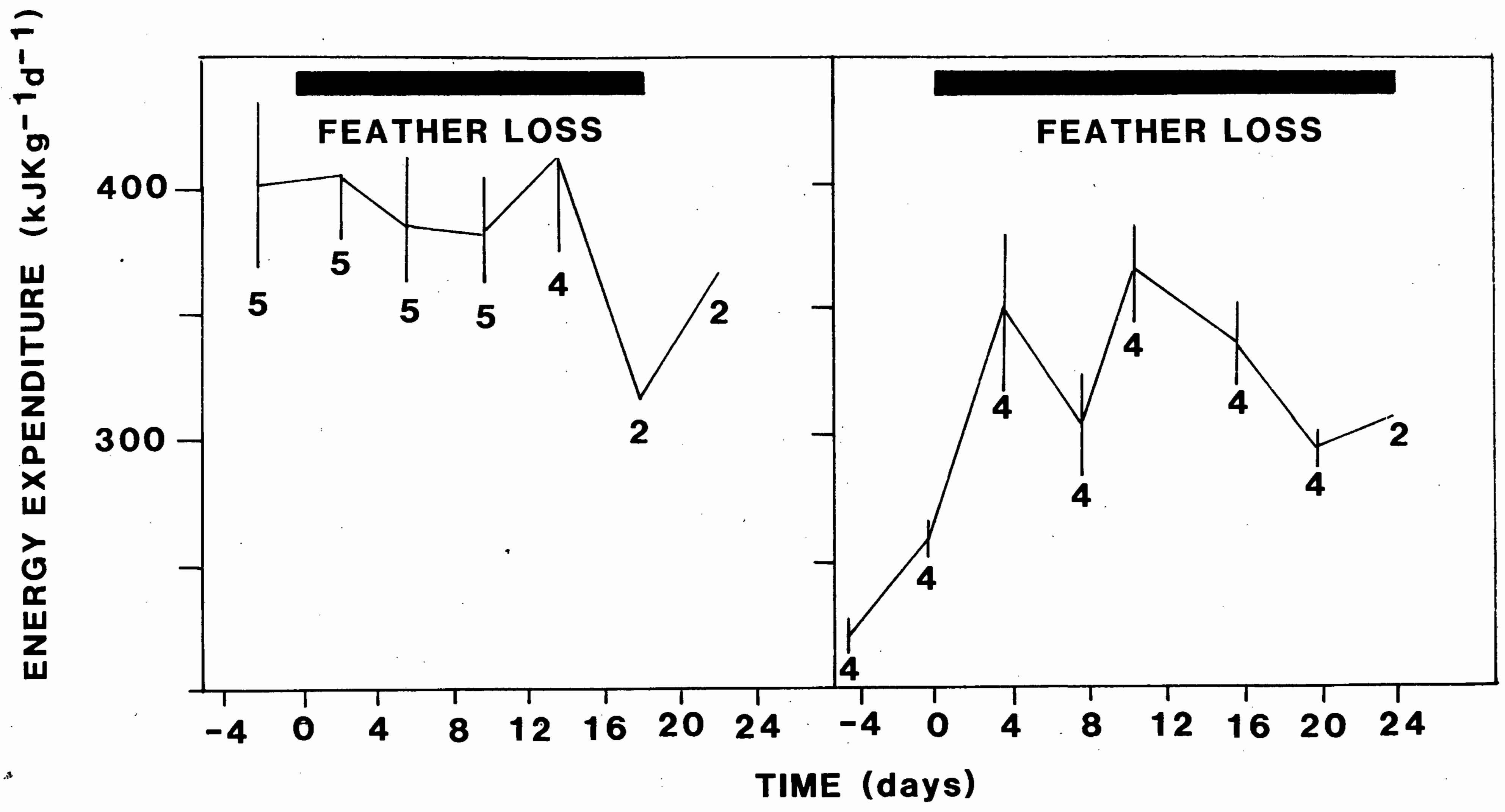
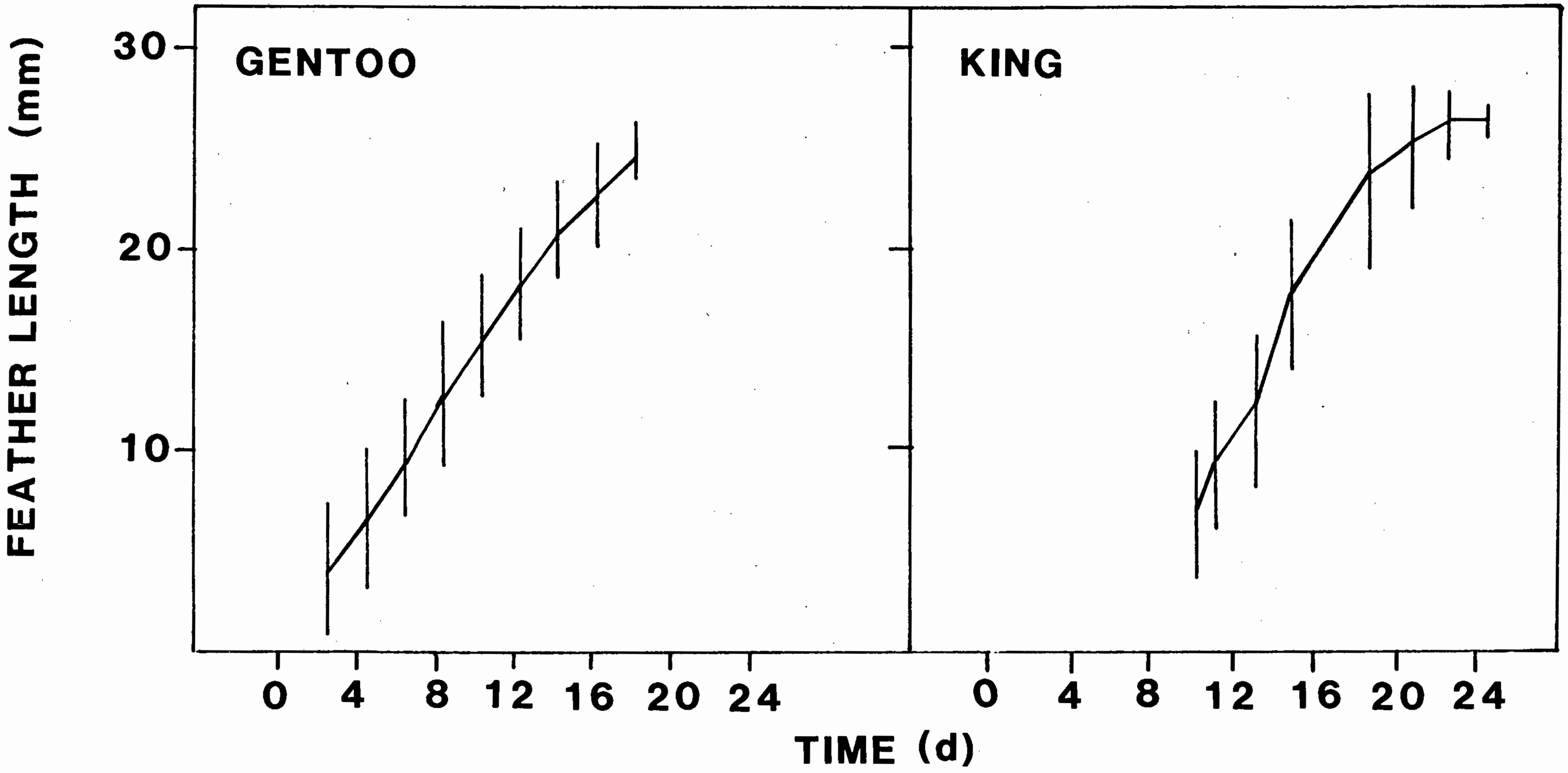

ENERGY EXPENDITURE (kJKg^{-1}d^{-1})
400
300
FEATHER LOSS
5
5
5
5
4
2
2
FEATHER LOSS
4
4
4
4
4
4
4
2
-4
0
4
8
12
16
20
24
-4
0
4
8
12
16
20
24
TIME (days)

FIGURE 3

Feather growth of KIng and Gentoo Penguins through moult.


GENTOO
KING
FEATHER LENGTH (mm)
30
20
10
0
4
8
12
16
20
24
0
4
8
12
16
20
24
TIME (d)

DISCUSSION

Most estimates of the energy expenditure of penguins during moult are integrated over the whole of the moult period or simply quote a single figure (eg. Davis et al. 1989, Baudinette et al. 1986, Croxall 1982). However, based on rates of body mass loss and on the pattern of feather replacement of individual moulting Emperor Penguins _Aptenodytes forsteri_, Groscolas (1978) recognized three different stages of moult. During the first stage, body mass loss was steady and relatively low. Stage two was characterized by an increase in the rate of loss of body mass which coincided with the loss of old feathers and a concomitant decrease in thermal insulation. Feather growth proceeded at a steady rate during these two stages. A progressive decrease in the rate of body mass loss in stage three was attributed to the cessation of feather synthesis and an increase in thermal insulation. However, mass loss in King and Gentoo Penguins (this study) and in other penguins, including Macaroni and Rockhopper (Williams et al. 1977), Jackass _Spheniscus demersus_ (Cooper 1978) and Little _Eudyptes minor_ (Gales et al. in 1988) decreased linearly with time and showed no relation to the patterns of mass loss identified by Groscolos (1978). Such changes in rates of daily body mass and feather synthesis may be reflected in rates of energy expenditure. However, energy expenditure (kJ.d^{-1}) of Gentoo (this study), Macaroni and Rockhopper (Brown 1985) Penguins was merely correlated with decrease in mass during moult. The peak in energy expenditure (kJ.d^{-1}) of King Penguins during the first few days of moult is in marked contrast to measures of other penguins through moult.

Mass - specific metabolism may be more indicative of the processes of moult than absolute metabolism. Patterns of mass - specific metabolism of King and Gentoo Penguins during moult did not coincide (Fig 2). Nevertheless, both these two species and Macaroni and Rockhopper Penguins (Brown 1985) demonstrated maximum mass-specific rates of energy expenditure during the first part of moult. This was presumably during the overlap period between new feather synthesis and old feather loss, when insulation was at its least efficient and thermoregulatory costs were high. Baudinette et al. (1986) noted that the increase in heat production during moult in Little Penguins correlated with increased thermal conductance as new feathers were synthesized. Consistent with this, moulting Emperor Penguins were hyperthermic during feather synthesis, body temperature increasing by ~ $1^{o}C$ after initiation of feather synthesis (Groscolas 1978). Maximum mass-specific energy expenditure during moult peaked from 34 % greater than mean resting levels in non - moulting Rockhopper Penguins (Brown 1985) to 96 % greater than the figure for non - moulting King Penguins (this study). Mass specific metabolism declined towards the end of moult, concomitant with completion of feather synthesis and a general increase in insulation as new feathers completed their emergence through the skin. Feather synthesis is completed before the end of visible moult and during the last stages of moult, when energy costs were lowest, new feathers are merely emerging through the skin (Groscolas 1978).

Invoking of thermoregulatory costs to explain high metabolic requirements of moulting penguins measured in chamber experiments (eg. Brown 1985) may be inappropriate because such measurements were conducted at ambient temperatures between 8 and 22°C, within the thermoneutral zone of most non-moulting penguins (Chapter 7, Stahel & Nicol 1982, Le Maho et al. 1976). Additional work is needed to separate and quantify costs of thermoregulation and costs due to feather growth and synthesis.

Measurements of oxygen consumption of moulting penguins, as described above, are potentially the most precise and require no knowledge of the proportions of metabolites oxidized during the fast. The maximum error that can be incurred by assuming only one type of metabolite is oxidized is 6 % (Schmidt-Nielsen 1979) and this will be reduced if a mixture of metabolites is oxidized or simultaneous measurements of carbon-dioxide production are made. The technique is also conducive to serial measurements on individual birds, potentially allowing detection of patterns in metabolism that may correlate with other moult processes. However, the use of metabolic chambers, while allowing the physical environment of the bird to be controlled, necessitates the removal of the penguin from its natural environment. This may result in stress to the birds with consequent elevated rates of oxygen consumption (VO_2), particularly during initial measurements.

Measurements of rates of loss of body mass of moulting penguins may be conducted on free - living birds. These may be converted to energy expenditure if the proportions of the different metabolites oxidized are known (Croxall 1982). In practice, these data are available for a few species only (Table 2). Implict in calculations of energy expenditure from rates of mass loss is the assumption that mass loss comprises a constant

TABLE 2

Changes in lipid and protein composition in three species of moulting penguins

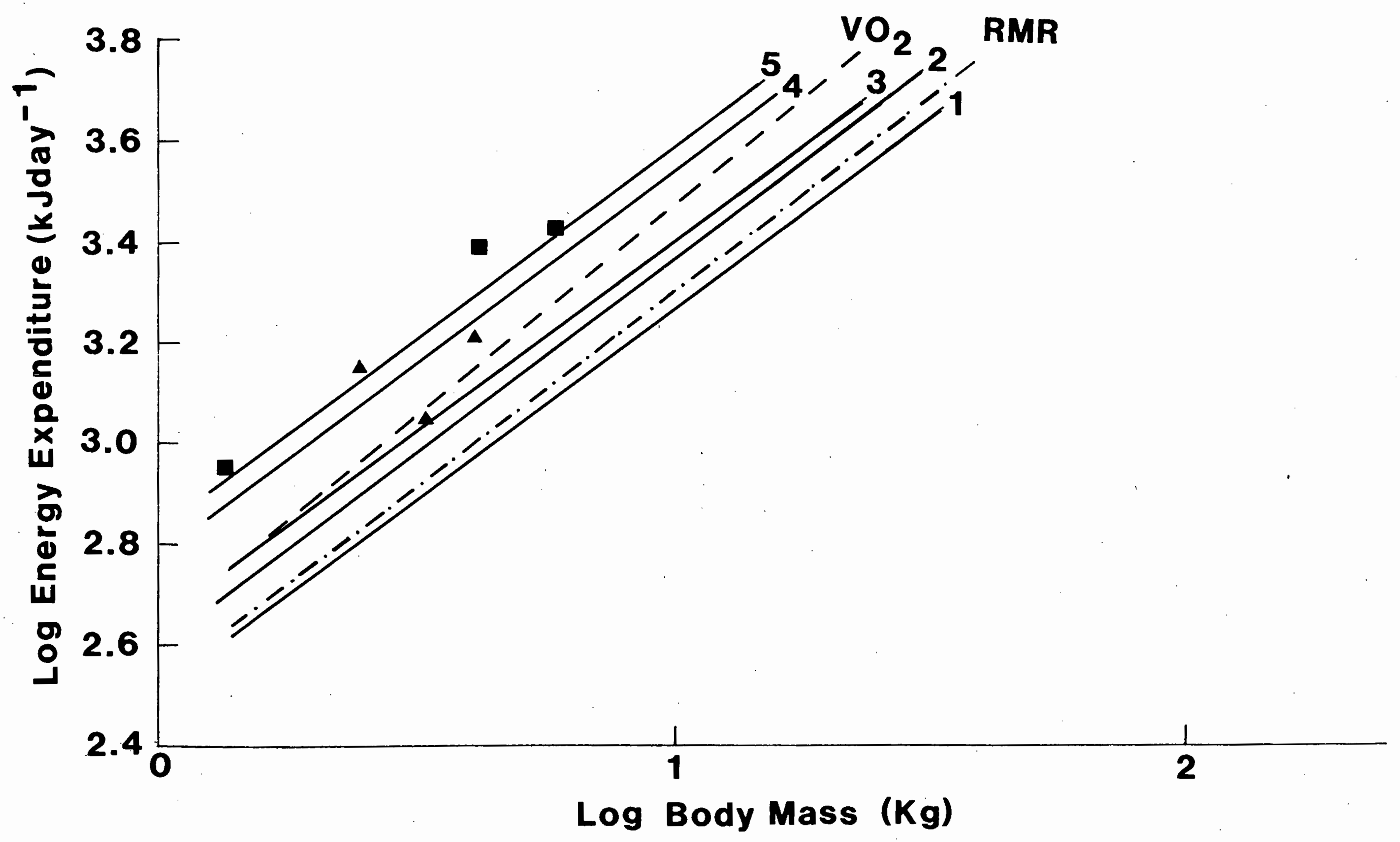
Species	Mass of lipid				Mass of non-feather protein				Energy expenditure	References
	Initial	Final	Diff.	$g.d^{-1}$	Initial	Final	Diff.	$g.d^{-1}$	$kJ.d^{-1}$	
Jackass Penguin	848	373	475	27	855	642	213	12	1 233	Cooper 1978
Rockhopper Penguin	937	125[a]	812	33	739	400[a]	339	6	1 410	Williams et al. 1977
Macaroni Penguin	1 296	100[a]	1 196	38	1 187	800[a]	387	7	1 626	Williams et al. 1977

[a] Estimated from figures

FIGURE 4

Relationship between log daily energy expenditure and body mass in moulting penguins, calculated from data presented in Appendix 1. Regressions based on mass loss data converted to energy expenditure based on body composition analyses of Emperor (1), Adelie (2), Jackass (3), Macaroni (4) and Rockhopper (5) Penguins, oxygen consumption measurements of moulting penguins (VO2) and Resting Metabolic Rates (RMR) of non-fasting birds (Appendix 2). Values obtained directly from body composition analyses ● and from isotope dilution rates ■ are indicated. Regression equations are as follows:

$y = 2.50W^{0.77}$, $r^2=0.93$ (Emperor)
$y = 2.59W^{0.77}$, $r^2=0.93$ (Adelie)
$y = 2.63W^{0.77}$, $r^2=0.93$ (Jackass)
$y = 2.77W^{0.77}$, $r^2=0.93$ (Macaroni)
$y = 2.82W^{0.77}$, $r^2=0.93$ (Rockhopper)
$y = 2.64W^{0.83}$, $r^2=0.93$ (VO2)
$y = 2.52W^{0.78}$, $r^2=0.93$ (RMR)


Log Energy Expenditure (kJday^{-1})
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
0
1
2
Log Body Mass (Kg)
VO$_2$
RMR
5
4
3
2
1

loss largely reflect the differences in the proportions of fat oxidized by penguins during moult. Estimates of energy expenditure of moult of small penguins based on oxygen consumption are closest to mass loss estimates based on changes in body composition of moulting Jackass Penguins (23% fat), but for large penguins are closer to those based on Macaroni Penguins (36% fat) (Fig. 4).

Differences in the magnitude of moult costs obtained using different techniques and data are more obvious when ratios of estimated energy costs of moult are compared to resting metabolic rates of penguins (Appendix 2). Mean energy expenditures during moult range from slightly less to more than twice resting levels (Table 4). The higher energy cost of moult determined from isotope dilution rates may reflect the greater activity of free ranging birds and higher costs of thermoregulation, at least compared to birds upon which measurements of oxygen consumption were made.

Total cost of moult ranged from 6 252 kJ to 159 755 kJ for Little and Emperor Penguins, respectively, based on lowest estimates of daily energy expenditure. The range extended from 13 286 to 33 9479 kJ for the same species using highest rates (Table 5). General patterns relating total energy expenditure during moult to body mass were similar to those of daily energy expenditure to body mass. Mean exponent of the regressions relating total energy expenditure to body mass was 1.02, steeper than that of daily energy cost to mass and reflecting the longer moult periods of the larger penguins. Percentage body mass loss showed no significant correlation with penguin body mass. There was little difference between Little Penguins,

TABLE 4

Ratio of energy cost of moult of penguins (Table 2 and 4, Appendix 1) to resting metabolic rate predicted from regression of mass against metabolic rate derived from data presented in Appendix 2

Source	No. Species	Mean ratio ± 1 S.D.	Range
Mass loss			
1) Emperor	13	0.95 ± 0.11	0.81-1.16
2) Adelie	13	1.19 ± 0.15	1.02-1.46
3) Jackass	13	1.31 ± 0.16	1.12-1.60
4) Macaroni	13	1.79 ± 0.22	1.53-2.18
5) Rockhopper	13	2.03 ± 0.26	1.73-2.47
Body composition	3	1.73 ± 0.34	1.46-2.11
VO_2	5	1.41 ± 0.10	1.38-1.47
isotope dilution	3	2.19 ± 0.19	2.04-2.40

TABLE 5

Total energy expenditure during moult. Values based on mean daily energy expenditures for each species presented in Tables 2, 4, Appendix 1 and mean moult length Table 1. values for body mass loss are based on changes in body composition of Emperor (1), Adelie (2), Jackass (3), Macaroni (4) and Rockhopper (5) Penguins

Penguin Species	Energy expenditure kJ							
	Body mass loss					Body comp.	VO_2	isotope
	1	2	3	4	5			
Little	6 252	7 816	8 597	11 723	13 286		9 194	13 748
Galapagos	7 933	9 917	10 908	14 875	16 858			
Jackass	12 714	15 893	17 482	23 839	27 017	24 044		
Rockhopper	16 452	20 566	22 622	30 848	34 519	34 686	25 978	
Snares Crested	20 736	25 920	28 512	38 880	44 064			
Fiordland	20 072	25 090	27 599	37 635	42 653			
Macaroni	24 490	30 612	33 673	45 918	52 041	43 739	40 861	65 402
Erect Crested	26 656	33 320	36 652	49 980	56 644			
Adelie	29 118	36 398	40 037	54 596	61 876			
Gentoo	31 408	39 260	43 186	58 890	68 952		42 510	52 683
Yellow-eyed	26 944	33 680	37 048	50 520	57 256			
King	63 350	79 187	87 106	118 781	134 618		97 335	
Emperor	159 755	199 693	219 663	299 540	339 479			

which lost 39% of their initial mass over an estimated 15 day moult, and Emperor Penguins which lost 45% over 34 days. Similarly, there was no significant correlation between percentage body mass loss and latitude when all 13 species were considered. The hypothesis of Cooper (1978), based on more limited data, that penguins at higher and colder latitudes have higher proportional mass loss than species at lower latitudes is therefore not substantiated.

The synchronized moults of most high-latitude penguins (Croxall 1984) and variable premoult period of, particularly, temperate inshore feeding penguins (e.g. Richdale 1957) suggest there are constraints on the timing of moult related to local food availability. This may reflect the considerable energy cost of the premoult foraging period (Gales et al. 1988). Estimated feeding rates that must be sustained by premoult foraging penguins to accumulate energy reserves for moulting can be calculated by combining information on total energy cost of moult, energy costs of foraging, energy content of prey and length of the premoult foraging period. Sufficient data for such calculations are available for only four species of penguins (Table 6). The calculations of premoult food accumulation rates are sensitive to estimates of energy cost of foraging at sea. Calculations are not comprehensive and are intended also to show the variation in food accumulation rates arising from use of different input values. Foraging costs estimated from water-turnover rates for Macaroni and Gentoo Penguins (Davis et al. 1983) are low and result in relatively low food accumulation rates. Recent estimates for these species based on CO_2-production rates determined from doubly labelled

TABLE 6

Estimated food accumulation rates during premoult foraging periods of penguins

Species	Mean[1] premoult period days	Metabolizable energy content of prey $kJ.g^{-1}$ wet	Penguin mass kg.	At sea[2] energy exp. $kJ.kg^{-1}.day^{-1}$	Total energy[3] cost of moult kJ	Total energy[4] expend. $kJ.day^{-1}$	Food[5] accum. $g.day^{-1}$
Little Penguin	40	3.58[a]	1.304	1 170[a]	13 748	1 983	488
				1 124[b]		1 923	473
Jackass Penguin	35	5.13[c]	3.279	1 565[c]	24 044	6 045	1 178
Macaroni Penguin	32	3.50[d]	4.692	786[e]	40 861	5 386	1 539
	21	2.73[f]	3.900[f]	1 780[f]	51 100[f]	10 178	3 728
Gentoo Penguin	50	3.73[g]	6.801	1 662[g]	42 510	12 434	3 334
				613[e]		5 300	1 420
	10	2.63[f]	6.100	1 400[f]	56 700[f]	15 716	5 975

[1] Premoult lengths from Table 1. [2] Estimates of at sea energy expenditure are determined from at sea foraging costs of adults attending chicks. [3] Total energy cost of moult calculated from direct methods : VO2 measurements, body composition analyses or isotope dilution rates (Table 6). [4] Total energy accumulated per day includes cost of foraging at sea and energy accumulated for conversion to energy reserves corrected for biosynthesis of these reserves (1.33 X estimated energy cost (Ricklefs et al. 1988).

[a] Green unpubl. in Gales et al. 1988. [b] Costa et al. (1986). [c] Nagy et al. (1984). [d] Brown 1987. [e] Davis et al. 1983. [f] Davis et al. 1989. [g] Robertson et al. 1988

water of adults attending chicks, are considerably higher (Davis et al. 1989). The minimum feeding rate of Little Penguins, accumulating reserves over a 40 d premoult period, was 473 $g.d^{-1}$. Recalculating food accumulation rates for a 7 d premoult period (the minimum recorded) indicates the species is capable of accumulating food at the rate of 1 127 $g.d^{-1}$. Minimum and maximum feeding rates calculated for Gentoo Penguins were 1 420 and 5 975 $g.d^{-1}$, respectively. These very high maximum rates are a consequence of the short premoult period and relatively high at-sea energy costs. It is impossible that a penguin could assimilate and process a daily food intake almost equal to its own body mass. In addition, I may have overestimated food accumulated as energy reserves because masses of penguins at the end of moult are generally lower than at the start of the premoult foraging period. Nevertheless, these calculations suggest birds may potentially accumulate energy reserves for moult extremely quickly when food is available. Differences in the duration of the premoult foraging period may reflect local variation in food availability. For example, Macaroni Penguins at South Georgia, south of the Antarctic Polar Front, have a premoult foraging trip of approximately half that of the species at Marion and Macquarie islands (Croxall 1984).

Daily feeding rates of penguins attending chicks over one complete foraging attendence cycle were generally lower than those of premoult foraging penguins (Croxall & Lishman 1987, Croxall et al. 1988). This indicates that the premoult period may be at least as energy demanding as chick rearing. However, the fact that penguins accumulating nutrients and energy reserves for moult are not constrained by the necessity to return to the colony to feed chicks, may reduce their vulnerability to variations in food supply close to their breeding colonies.

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APPENDIX 1

Energy expenditure of moulting penguins determined from rates of loss of body mass and energy equivalent of mass loss from Table 3 (1: Emperor Penguin, 2: Adelie Penguin, 3: Jackass Penguin, 4: Macaroni Penguin, 5: Rockhopper Penguin)

Species	Mass mid point g	Mass loss $g.d^{-1}$	Energy expenditure $kJ.d^{-1}$					References
			1	2	3	4	5	
Little Penguin	1 312	53	424	530	583	795	901	Kinsky 1960
	1 134	58	464	580	638	870	986	Kinsky 1960
	1 319	49	392	490	539	735	833	Richdale 1940
	1 350	43	344	430	473	645	731	Reilly & Balmford 1975
Galapagos Penguin	2 150	84	672	840	924	1 260	1 428	Boersma 1976
	1 980	61	488	610	671	915	1 037	Boersma 1976
	2 188	93	744	930	1 023	1 395	1 581	Boersma 1976
Jackass Penguin	2 413	71	568	710	781	1 065	1 207	Cooper 1978
	3 243	92	736	920	1 012	1 380	1 564	Cooper 1978
Rockhopper Penguin	2 900	71	568	710	781	1 065	1 207	Warham 1963
	2 571	82	656	820	902	1 230	1 394	Williams et al. 1977
	2 725	92	736	920	1 012	1 380	1 564	Duroselle & Tollu 1977
	2 947	78	624	780	858	1 170	1 236	Brown 1985
	3 005	95	760	950	1 045	1 425	1 615	Brown 1986
Snares Crested Penguin	3 105	96	768	960	1 056	1 440	1 632	Warham 1974b
Fiordland Penguin	3 970	88	704	880	968	1 320	1 496	Warham 1974a
	3 671	105	840	1 050	1 155	1 575	1 785	Warham 1974a

Macaroni Penguin	5 300	87	696	870	957	1 305	1 479	Warham 1971
	4 120	105	840	1 050	1 155	1 575	1 785	Williams et al. 1977
	5 200	125	1 000	1 250	1 375	1 875	2 125	Croxall 1982
	4 600	132	1 056	1 320	1 452	1 980	2 244	Brown 1985
	4 813	120	960	1 200	1 320	1 800	2 040	Brown 1986
Erect Crested Penguin	5 292	128	1 024	1 280	1 408	1 920	2 176	Warham 1972
	4 395	110	880	1 100	1 210	1 650	1 870	Warham 1972
Adelie Penguin	4 812	184	1 472	1 840	2 024	2 760	3 128	Cendron 1953
	4 994	162	1 296	1 620	1 782	2 430	2 754	Penney 1967
	5 175	151	1 208	1 510	1 661	2 265	2 567	Penney 1967
	5 610	193	1 544	1 930	2 123	2 895	3 281	Bougaeff 1975
Gentoo Penguin	6 300	200	1 600	2 000	2 200	3 000	3 740	Mougin 1972
	7 600	210	1 680	2 100	2 310	3 150	3 570	Croxall 1982
	6 504	194	1 552	1 940	2 134	2 910	3 298	this study
Yelloweyed Penguin	6 169	151	1 208	1 510	1 661	2 265	2 567	Richdale 1957
	5 852	140	1 120	1 400	1 540	2 100	2 380	Richdale 1957
	5 284	130	1 040	1 300	1 430	1 950	2 210	Richdale 1957
King Penguin	15 563	275	2 200	2 750	3 025	4 125	4 675	Stonehouse 1960
	16 000	317	2 536	3 170	3 487	4 755	5 389	Stonehouse 1960
	14 042	287	2 296	2 870	3 157	4 305	4 879	Stonehouse 1960
	14 070	370	2 960	3 700	4 070	5 550	6 290	Mougin 1974
	12 800	267	2 136	2 670	2 937	4 005	4 539	Barre 1975
	14 975	264	2 112	2 640	2 904	3 960	4 488	Barret 1976
	13 125	273	2 184	2 730	3 003	4 095	4 641	this study
Emperor Penguin	27 410	691	5 528	6 910	7 601	10 365	11 747	Le Maho & Delclitte 1974
	27 000	583	4 664	5 830	6 413	8 745	9 911	Le Maho et al. 1976
	27 650	488	3 904	4 880	5 368	7 320	8 296	Groscolas 1978

APPENDIX 2

Oxygen consumption measurements of resting, nonmoulting penguins.

Species	Mean mass g	Metabolic Rate $kJ.day^{-1}$	Reference
Little Penguin	1 259	340	Baudinette et al. 1986
	1 055	286	Baudinette et al. 1986
	1 150	571	Pinshow et al. 1977
	900	383	Stahel & Nicol 1982
Jackass Penguin	2 880	533	Erasmus & Wessels 1985
Humboldt Penguin	3 870	820	Drent & Stonehouse 1971
Rockhopper Penguin	2 506	863	Brown 1984
	2 330	504	Gavrilov 1977
Fiordland Penguin	2 600	598	Drent & Stonehouse 1971
Macaroni Penguin	3 870	747	Gavrilov 1977
	3 780	1 161	Brown 1984
Adelie Penguin	4 500	1 562	Le Resche & Boyd 1969
	3 970	1 057	Kooyman et al. 1976
Gentoo Penguin	6 290	1 605	Chapter 7
Yelloweyed Penguin	4 800	996	Drent & Stonehouse 1971
King Penguin	13 270	2 237	Chapter 7
	12 662	2 877	Le Maho & Despin 1976
	11 080	1 888	Gavrilov 1977
Emperor Penguin	31 750	5 791	Dewasmes et al. 1980
	24 800	4 239	Le Maho et al. 1976
	23 370	3 704	Pinshow et al. 1976
	20 790	3 307	Pinshow et al. 1977

CHAPTER 9

ENERGY EXPENDITURE DURING INCUBATION IN KING PENGUINS *APTENODYTES PATAGONICUS*

Direct measurements of energy expenditure of incubating King Penguins *Aptenodytes patagonicus* based on rates of oxygen consumption, amounted to 3 128 kJ.d^{-1} (1.45 x BMR) and were not significantly different from energy expenditure of non-incubating, resting birds. This indicates that maintenance of egg temperatures during incubation is an insignificant proportion of maintenance costs. Male birds undertook 57 % of incubation duties, a significantly greater proportion than females (43 %). Based on this difference alone, total energy expended by males to incubate its single egg was 97 x 10^3 kJ, 23 % higher than in females.

INTRODUCTION

Energetics of avian incubation may be analysed at a number of different levels from examination of heat transfer between the egg and incubating bird at the lowest level (Kendeigh et al. 1977, Turner 1990) to adult energy budgets during the incubation period at the highest level (Pettit et al. 1988). I examine here the occurrence of any change in adult metabolism of King Penguins associated with incubating the egg. At this level, energy costs of incubation of several Southern Ocean seabirds have been determined from rates of mass loss converted to energy equivalents (Croxall 1982) and from direct measurements of oxygen consumption (Brown 1984, Brown & Adams 1984).

Mass loss data indicate that on average energy costs of fasting penguins incubating eggs in the colony average 39 % higher than basal metabolism (Croxall 1982). Although such estimates are based on unvalidated assumptions of the composition of metabolites oxidized, measurements provide estimates of average metabolic rate on undisturbed birds over several days. The values obtained are close to those of female Macaroni Penguins determined during initial stages of incubation by the doubly labelled water method (Davis et al. 1989). Direct measurements of oxygen consumption during incubation are few because many birds are intolerant of the required experimental manipulation without desertion of eggs. Some seabird species, breeding on islands free of endemic terrestrial predators, are however, tolerant of human disturbance and direct measurements of oxygen consumption in the field are possible (Grant & Whittow 1983, Brown & Adams 1984). At present, direct measurements of the oxygen consumption of incubating penguins are restricted to laboratory measurements on Macaroni _Eudyptes chrysolophus_ and Rockhopper _E. chrysocome_ Penguins (Brown 1984) and metabolic rates are lower than measurements of Resting Metabolic Rate (RMR).

King Penguins lay one large egg which they incubate on their feet for about eight weeks (Stonehouse 1960, Barrat 1976). In common with other species of offshore feeding seabirds, male and female penguins share incubation, fasting for a number of days. I present direct measurements of energy expenditure of incubating King Penguins _Aptenodytes patagonicus_ in the field. Results are compared to energy costs derived from other methods and I attempt to resolve the differences highlighted above.

MATERIALS AND METHODS

To determine if there were any differences in division of incubation shifts between sexes and hence, differences in energy budgets, I monitored the length of incubation shifts of King

Penguins from daily checks of sexed, flipper banded adults at a colony of approximately 1 000 pairs at Archway Bay, Marion Island (46°53'S, 37°54'E). Prospecting pairs were captured, measured and banded prior to egglaying. Males are generally larger than females (Barre 1976, Stonehouse 1960). On subsequent daily checks I noted date of egg laying and length of individual incubation shifts. The initial sequence of incubation shifts confirmed sexing, based on measurements, in all but two cases.

Due to the high rate of egg desertion, only eight of 35 banded pairs successfully completed incubation. I elected not to measure metabolic rates of sexed pairs monitored for incubation shift length to reduce disturbance and chance of desertion. Measurements of oxygen consumption were conducted on nine unsexed incubating King Penguins in the colony using an open-mask system (Withers 1977). Birds incubating within about 3 m of the edge of the colony were selected. A mask, constructed from a soft plastic reagent bottle and contoured to fit the face, was fitted. The mask completely enclosed the gape but left vision unobstructed. I restricted measurements to calm days since wind pressure on the side of the mask agitated the penguins.

A small air pump, powered by a portable generator, was used to draw air through the mask and past the bill of the penguin. Air flow was maintained between 8.7 and 11.2 $l.min.^{-1}$. This resulted in a drop in % O_2, compared to ambient air, of between 0.6 and 1.4 %. A flowmeter was placed upstream of the pump and expired air was passed through tube of silica gel/carbosorb before entering a paramagnetic oxygen analyser. The small volume of dead air space and relatively high flow rate ensured rapid equilibration and prevented backflow or leakage of air expired by the penguin. Birds were allowed 30-45 min to settle before readings commenced. Readings were subsequently recorded every 10 min for between 1.5 and 3.5 h. Oxygen content of ambient air was checked periodically throughout the run and air temperature was measured every 30 min using a portable Bailey-BAT 12 telethermometer. After the completion of oxygen consumption measurements birds were weighed by carefully being lifted in a rope harness.

A similar mask system was used to determine the energy consumption of non-incubating birds. Six adult King Penguins were captured and transported to the laboratory for measurement. Birds were confined overnight in wooden holding pens at ambient temperature before measurements commenced.

Oxygen consumption of King Penguins was calculated using the equation in Withers (1977) for dry, CO_2 free air. The lowest stable periods during each run were considered to be the best estimate of the energy cost of incubation.

RESULTS

Mean incubation period of eight pairs of King Penguins that hatched chicks was 54 d (Table 1). The total incubation period normally comprised four shifts (excluding the initial short shift of less than 24 h by the female immediately after laying) (Table 1). Completed shifts in which the partner deserted in the subsequent shift were similar in length to those recorded for successful incubations (Table 1). Males undertook 57 % of incubation duties a significantly greater proportion than

TABLE 1

Incubation shift length of King Penguins at Marion Island

Shift number	1	2	3	4	5	Total		Total
Sex	♀	♂	♀	♂	♀	♀	♂	♀+♂
Average shift length (days)	16.3	17.6	13.8	8.6	2.5	30.6	23.5	54.1
S.D.	2.2	2.7	1.7	2.1		1.8	1.4	1.0
Range	(21-12)	(23-12)	(17-12)	(11-5)	(3-2)	(28-34)	(21-26)	(52-55)

females (43 %) (Wilcoxon paired sample test, $T_+=36$, $P<0,01$).

Stable periods of VO_2 during incubation lasted between 25 and 50 min. All measurements of oxygen consumption were performed at ambient temperatures in the range 7.9 - 12.2 ^oC within the birds' thermoneutral zone (see Chapter 7, Le Maho 1983), and metabolic rates were presumably unaffected by the small changes in ambient temperature. Energy expenditure of incubating birds was not significantly different from resting whether compared on a mass-specific ($t = 1.353$, $P > 0,05$) or per bird basis ($t = 0,296$, $P > 0,05$), but was 37% and 45% higher than predicted for birds of equivalent body mass (Table 2) and measured BMR, respectively. Assuming no sex-specific differences in metabolic rate, total cost of incubation, not including at - sea costs between incubation shifts, was 95 717 kJ for male King Penguins and that of females was 23% lower at 73 508 kJ.

DISCUSSION

Measured metabolic rates of incubating King Penguins were lower, although not significantly so, than those measured for resting birds suggesting that maintenance of incubation temperatures of the egg by parent birds is an insignificant proportion of maintenance costs. Oxygen consumption measurements of incubating Rockhopper and Macaroni Penguins (Brown 1984), and tropical Procellariiformes (Grant & Whittow 1983) conducted on birds incubating in metabolic chambers, were similarly lower than those of resting birds. The particularly low values for Eudyptes penguins which were conducted over 24 h (Brown 1984) may be a consequence of incubating birds spending a considerable proportion of their time asleep (Groscolas 1988). Although close to resting metabolic rates of non-incubating birds measured in a similar way, incubation metabolic rates of King Penguins measured in the colony were 45% higher than measured BMR (Chapter 7). Possible interaction with other colony members may give rise to generally elevated metabolic rates of King Penguins. Such a difference is probably also partly attributable to the experimental technique used. Measurements of BMR were conducted on unrestrained birds in plastic chambers (Chapter 7). The use of a mask on incubating birds allows measurements to be conducted within colonies but may stress birds and consequently elevate metabolism (Brown & Adams 1984). Alternatively, Grant (1984) suggested that the technique may increase the rate of Evaporative Water Loss (EWL) and the associated cooling may result in increased metabolism to compensate for additional heat loss. However, measurements of rates of water loss of fasting but non-incubating King Penguins using an open flow through mask system were 53 % lower (N.J. Adams unpublished data) than those predicted from body mass from the equation of Skadhauge (1981).

Incubation costs for King Penguins calculated from mass loss data were 51 % higher than predicted BMR (Croxall 1982), close to the value from direct measurements of oxygen consumption (Table 2) and towards the upper range of that calculated for six penguins (range 2 - 57 %). These calculations assumed that loss of body mass comprised 55.5 % fat, 9.2 % protein and 35.3 % water and was determined from fasting non - moulting Emperor Penguins Aptenodytes forsteri (Groscolas & Clement 1976). These calculations assumed that loss of body mass comprised 55.5 % fat, 9.2 % protein and 35.3 % water and was determined from fasting non - moulting Emperor Penguins Aptenodytes forsteri

TABLE 2

Energy costs of incubation of King Penguins

n	Mean Mass	Incubation costs		RMR[a]	BMR[a]	BMR[b]
		$kJ.d^{-1}$	$kJ.kg^{-1}.d^{-1}$	$kJ.d^{-1}$	$kJ.d^{-1}$	$kJ.d^{-1}$
9	12.8 ± 1.3	3128 ± 638	244 ± 41	280.7	168.2	177.7

[a] Chapter 7, [b] Kendeigh et al. 1977.

(Groscolas & Clement 1976). Assumptions underlying such estimates of energy expenditure based on mass loss require validation. It is now clear that composition of body mass changes through fasts and in addition may vary from species to species (Groscolas 1988). Furthermore, rates of body mass loss at the beginning and end of long term fasts are higher than during the mid fast period and use of these figures may lead to considerable overestimates of incubating metabolic rates (Groscolas 1988). Many measurements of mass loss of incubating birds may have been determined at inappropriate times.

The general conclusion of the studies is that costs of maintenance of egg temperatures during incubation are an insignificant proportion of maintenance costs. However, because direct measurements of energy costs of incubation of seabirds determined from oxygen consumption have been conducted over small portions of the day (Grant & Whittow 1983, this study) or lowest metabolism values selected to calculate incubation costs (Brown 1984), we should expect these values to be lower than those estimated by mass loss alone and direct isotope based measurements of free living birds. In particular, costs of nest site defence may be appreciable for colonially nesting seabirds. Such differences are probably not related to considerations of heat transfer between egg and adult (See Kendeigh 1973, King 1973).

Incubation duties of King Penguins are not equally apportioned between sexes (Stonehouse 1960, Barre 1976, this study) and on average males undertake longer shifts, particularly, during the second half of the incubation period (Table 1). Although, total energy cost of incubation fasts is 23 % higher for males than females, total energy costs over the whole incubation period will be higher for female penguins due to their longer at - sea period. However, any energy constraints during incubation are likely to arise from the need to accumulate energy reserves at sea to maintain energy balance during incubation which includes shifts that may last as long as 23 d and thus are likely to be more severe on males. A similar division of time and energy contribution between male and female birds has been described for Wandering *Diomedia exulans* (Croxall & Ricketts 1983) and Laysan Albatrosses *Diomedea immutabilis* (Pettit et al. 1988).

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CHAPTER 10

EMBRYONIC METABOLISM, ENERGY BUDGETS AND COST OF PRODUCTION OF KING *APTENODYTES PATAGONICUS* AND GENTOO *PYGOSCELIS PAPUA* PENGUIN EGGS

Embryonic energy expenditure and allocation of stored energy in fresh eggs to growth and maintenance of King Aptenodytes patagonicus and Gentoo Pygoscelis papua Penguin embryos were examined by measuring oxygen consumption and by gross tissue analyses of fresh eggs and hatchlings. Embryonic oxygen consumption (MO_2) was similar to that of precocial or semi-precocial hatchlings, although behavioural traits suggest altricial hatchlings. In spite of the relatively longer incubation period and contrary to expectations, relative yolk contents of fresh King and Gentoo Penguin eggs were similar although energy density of King Penguin eggs was slightly higher. However, hatchling mass of King Penguins was considerably smaller as a percentage of initial egg mass than that of Gentoo Penguins and most other bird species. The pelagic feeding King Penguin retained greater yolk reserves at hatching than did the inshore feeding Gentoo Penguin. The generally low energetic efficiency of embryonic growth of King Penguins compared to Gentoo Penguins can be ascribed to their relatively small hatchling size but relatively long incubation period. Based on estimates of yolk composition and length of yolk formation, daily cost of egg production of King Penguins was estimated at 9.0% of Basal Metabolic Rate and 5.4% of BMR for the two-egg clutch of Gentoo Penguins. The relatively high cost for King Penguins largely reflects the short formation time of their eggs.

INTRODUCTION

Relationships between rates of embryonic gas exchange, egg composition and energetics of embryonic development in relation to incubation period and maturity at hatching of seabirds, especially Procellariiformes and tropical seabirds, have received considerable attention (Brown & Adams 1988, Pettit et al. 1982a, 1982b, Vleck et al. 1979, Whittow 1980, Whittow 1983, Williams & Ricklefs 1984) and the results extensively reviewed (Pettit et al. 1984, Ar et al. 1987, Vleck & Vleck 1987). The prolonged incubation periods of these two groups , which appear to be associated with their pelagic feeding habits (Whittow 1980), have a number of consequences. Total oxygen consumption of the embryo is large (Pettit & Whittow 1983, Whittow 1983, Brown & Adams 1988) due to high maintenance costs. Since the embryo has to depend on energy incorporated into the egg prior to laying, these species generally lay only one large egg of high energy content (Sotherland & Rahn 1987).

Penguins (Sphenisciformes) display a more diverse array of reproductive traits than Procellariiformes (Croxall 1984). The King Penguin <u>Aptenodytes</u> <u>patagonicus</u> is a pelagic forager (Adams 1987), with many features in common with the Procellariiformes, including laying a single large egg and having a relatively long incubation period (Stonehouse 1960, Chapter 9). In contrast, the Gentoo Penguin <u>Pygoscelis</u> <u>papua</u> is an inshore feeder (Adams & Wilson 1987), has a relatively short incubation period and a normal clutch size of two (Williams 1980, Croxall 1984). In this chapter, I present measurements of embryonic metabolism of King and Gentoo Penguins and determine egg energy budgets in order to allocate energy reserves of fresh eggs to embryonic tissue, maintenance and storage reserves of hatchlings. Results are considered in the light of potential consequences of differences in relative incubation length of King and Gentoo

Penguins. Finally based on analyses of egg compositions and determinations of the length of yolk formation I estimate the energy cost of egg production by female penguins.

METHODS

Nests of Gentoo Penguins and banded pairs of King Penguins at two small colonies at Marion Island ($46^o53'S$, $37^o54'E$) were checked daily and the dates of egg laying and hatching noted.

Egg temperatures

Egg temperatures of 4 pairs of King Penguins were measured at intervals of 5d from 10d into incubation through to 45d using blown, water filled eggs containing temperature sensitive transmitters (Minimitter Co. Indianapolis) (see Brown & Adams 1988). Eggs containing transmitters were substituted for fertile eggs which were then brought back to the laboratory for oxygen consumption measurements. Measurements of incubation temperatures were made before replacing the fertile egg, 24h later.

Embryonic oxygen consumption:

Measurements of embryonic oxygen consumption (MO_2) were first conducted 6 d and 10 d after laying for Gentoo Penguins and King Penguins, respectively, and continued at intervals of 5 d until hatching. Eggs were placed in a closed respiratory system in a hot room set between 34 - 35^{o}C, close to the mean incubation temperature measured for King (see below) and reported for Gentoo Penguins (Burger & Williams 1979). Respiratory chambers consisted of plexiglass syringes (Brown & Adams 1988). I used large syringes (maximum volume 2 800 ml) for King Penguin eggs and smaller syringes (maximum volume 1 400 ml) for Gentoo

Penguin eggs. Syringe volume could be varied by moving the plunger and was adjusted according to the age of the embryo. Chamber volume was corrected for air displaced by eggs and hatchlings. Volume of eggs was determined by water displacement. Water content of hatchlings was high (approximately 80%) and volume of hatchlings (ml) was assumed to be equivalent to mass (g). The error in conversion is likely be to be less than 3% when the volume of the syringe is considered. I allowed embryos to reduce O_2 content of the chamber by 0.5 - 2% before measuring MO_2. Young embryos depleted O_2 at a very slow rate and chambers were sealed for 24h, whereas substantial drops in O_2 concentration occurred in as little as 10 min for pipped eggs. Final oxygen content in the chamber was determined by injecting chamber air, from which H_2O and CO_2 were removed, into a Taylor Servomex paramagnetic oxygen analyser at a constant rate. MO_2 was calculated from the equation in Vleck et al. (1979) and corrected to STPD. I returned eggs to the nest site after measurement. Means are given as $\pm$ 1 standard deviation.

Egg and hatchling composition:

After thawing, whole eggs collected under permit were separated into egg shell, albumen and yolk. Component parts were then dried to constant mass at 55°C. Water content was determined from differences in wet and dry mass. Energy determinations of egg contents of King and Gentoo Penguins collected at Marion Island have been published previously (Sotherland & Rahn 1987 after Williams et al. 1982). Percent ash was determined by burning dried samples in a muffle furnace at 450°C for 6 h.

Newly hatched chicks (<1 d) were collected under permit and dissected to remove the yolk sac from the body of the chick. These two components were weighed and dried at 55°C to constant mass. Lipid content of dried carcasses was determined by hexane-acetone extraction for 45 min at 70°C. I assumed the rest of the ash-free dry mass comprised protein.

Egg formation:

Newly laid eggs from both species collected under permit were weighed, wrapped in aluminium foil and frozen at -18°C until processed. Shells and albumen were separated from the yolks which were then fixed in 4 % formalin at room temperature for approximately 48 h. Fixed yolks were cut in half through the blastoderm. One of the halves was then stained in a 6% potassium dichromate solution at 55°C for 12 h. Stained eggs were sectioned to a thickness of between 3-5 mm and the number of pairs of light and dark yolk rings counted (see Grau 1976).

RESULTS

King Penguins had incubation periods 28 % longer than predicted from fresh egg mass (Rahn & Ar 1974), whereas those of Gentoo Penguins were similar to predicted values (Table 1). Although there was some suggestion that egg temperatures measured during the initial stages of incubation were lower than during the latter stages, there was insufficent data to test for systematic trends in dummy egg temperatures. Mean temperature of artifical eggs incubated by King Penguins was 34.2 ± 1.5°C.

Embryonic oxygen consumption:

In spite of the differences in mass, there were no significant

TABLE 1

Measured and predicted incubation periods from estimated egg mass of King and Gentoo Penguins.

	n	estimated fresh egg mass (g)	incubation length (d)	
			measured	predicted
Gentoo Penguin	7	122.6	35.7	34.1[a]
		± 13.7		37.6[b]
King Penguin	8	324.6	54.1	42.2[a]
		± 22.5		49.9[b]

Incubation period predicted from:

a: $I\ (d) = 12.03W^{0.217}$ (Rahn & Ar 1974)

b: $\mathrm{Log}\ I\ (d) = 0.97 + 0.29\,\mathrm{Log}W$ (Vleck & Vleck 1987) differences between MO_2 of Gentoo Penguin A and B eggs and only combined measurements are presented (Table 2). MO_2 of both King and Gentoo Penguin eggs increased throughout incubation (Fig. 1). Logistic curves were fitted to pre-pipping data of embryonic MO_2 of King and Gentoo Penguins using the method of Ricklefs (1967) as were exponential curves from semilog transformations of the data (Table 2). Logistic relationships best described the relationship between MO_2 and length of incubation for King Penguins but exponential relationships best described the relationship for Gentoo Penguin embryos. All fits were good (correlation coefficients > 0.90). MO_2 increased sharply after initial pipping, peaking in King Penguin hatchlings at 3251 $ml.O_2d^{-1}$, approximately 2.5 times prepipping levels and at 1839 $ml.O_2.d^{-1}$ in Gentoo Penguins, approximately twice prepipping levels. Although prepipping MO_2 of King and Gentoo Penguins were below values predicted by equations based mainly on data from precocial birds, they were 77 % and 56 % higher than predicted for altrical birds (Table 3). Total oxygen consumption by embryos over the whole incubation period was determined by graphical integration of areas under plots of oxygen consumption vs time (Fig. 1) and amounted to approximately 311 for King Penguins and 101 for Gentoo Penguins, close to values predicted for precocial birds (Table 4). Fifty-three percent of the total oxygen consumption of both King and Gentoo Penguins occurred in the pip to hatch interval. Total energy expenditure of embryos calculated from oxygen consumption was 614 and 207 kJ for King and Gentoo Penguins, respectively.

Egg and hatchling composition:

Percent yolk content (28%) and water content (78%) of King and Gentoo Penguin eggs were similar (Table 5). Total energy

TABLE 2

Logistic and exponential curve fits: prepipping MO_2 vs day of incubation for King and Gentoo Penguin embryos

	Exponential equation[a]		Logistic equation[b]	
King Penguin	$MO_2 = 6.22e^{0.11t}$	r=0.94	$MO_2 = 1525.0/1 + e^{-0.038(t-50)}$	r=0.97
Gentoo Penguin	$MO_2 = 1.76e^{0.20t}$	r=0.99	$MO_2 = 859.6/1 + e^{-0.076(t-31)}$	r=0.92

[a] MO_2 in $ml.d^{-1}$, e base of natural logarithms, t day of incubation

[b] MO_2, e and t as above, numerator is asymptote of the embryo oxygen consumption vs day of incubation curve.

TABLE 3

Pre-pipping oxygen consumption (MO_2) of King and Gentoo Penguin embryos

	n	day of incubation	prepipping MO_2	(MO_2/day)		
			measured $ml.O_2.d^{-1}$	predicted[a] $ml.O_2.d^{-1}$	predicted[b] $ml.O_2.d^{-1}$	predicted[c] $ml.O_2.d^{-1}$
Gentoo Penguin	7	31	761.0 ± 127.1	894.0	809.3	488.1
King Penguin	3	50	1334.3 ± 164.4	1795.9	1417.2	752.3

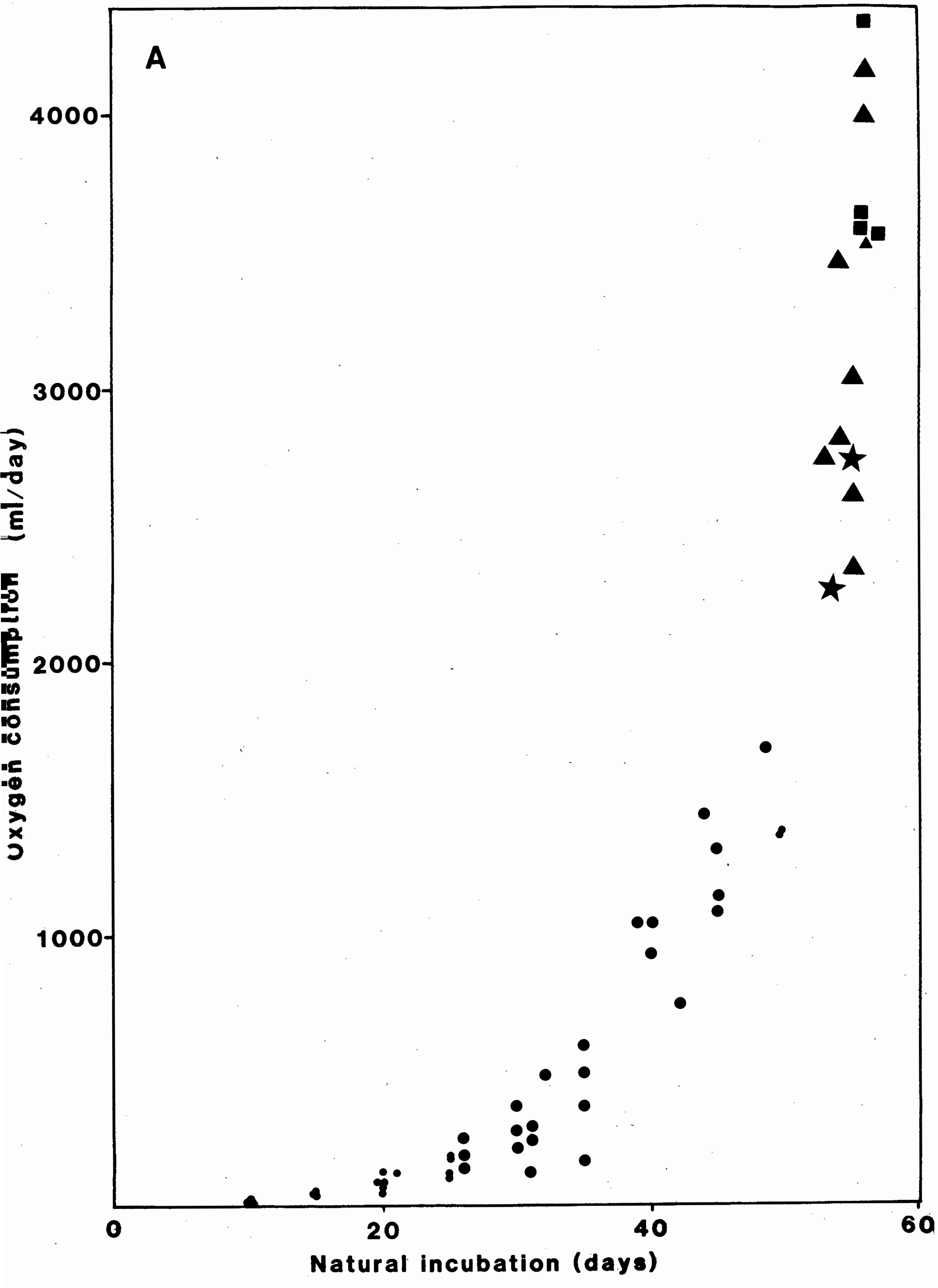
[a] : $MO_2 = 28.9W^{0.714}$, where W is fresh egg mass in g (Hoyt & Rahn 1980, data based primarily on precocial birds)

[b] : $MO_2 = 139W^{0.85}/I^{0.65}$, where W is as above and I is incubation period in days (Hoyt & Rahn 1980, data based primarily on precocial birds)

[c] : $MO_2 = 186.4W^{0.767}/I^{0.762}$, where W and I are as above (Bucher 1983, for altricial birds)

FIGURE 1

Oxygen consumption of King (V) and Gentoo (B) Penguin embryos as a function of age. ● unpipped eggd, ★ fractured eggs, ▲ pipped eggs, ■ hatchlings.


A
4000
3000
2000
1000
Oxygen consumption (ml/day)
0
20
40
60
Natural incubation (days)

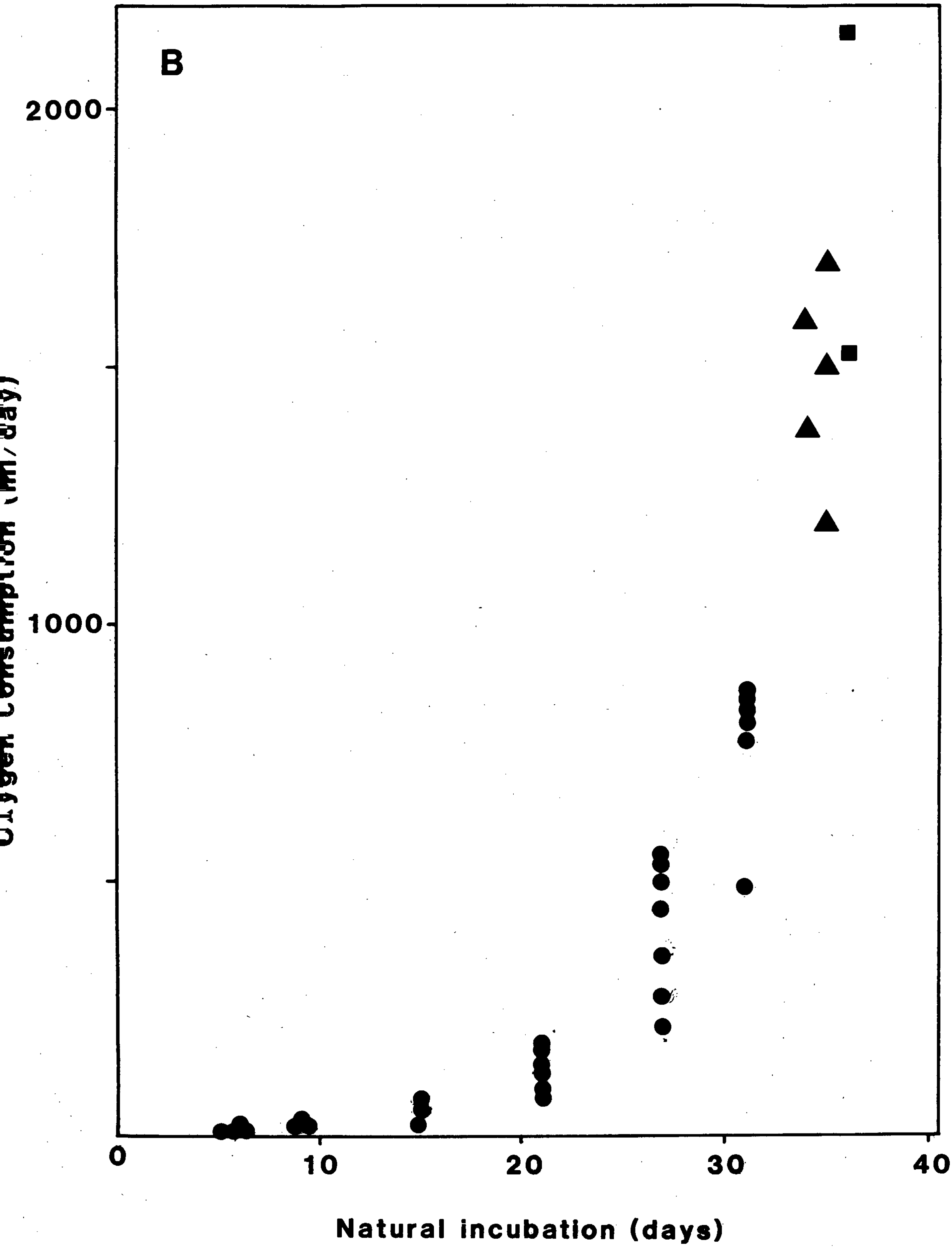

B
2000
1000
0
10
20
30
40
Natural incubation (days)

TABLE 4

Total oxygen consumption (MO_2) of King and Gentoo Penguin embryos through natural incubation

		total MO_2		prepipping MO_2		pip to hatch MO_2		predicted total	ratio measured/
	n	ml	$ml.g^{-1}$ egg	ml	% of total	ml	% of total	precocial[a] MO_2 ml	predicted
King Penguin	3	30 588	94.2	14 194	46.4	16 394	53.6	31 278	0.978
Gentoo Penguin	7	10 293	84.2	4 820	46.8	5 473	53.2	10 846	0.949

[a] Log MO_2 = 1.407 + 0.85logW + 0.55logI, where W is fresh egg mass in g and I is incubation period in (Ackerman et al. 1980).

TABLE 5

Composition of King and Gentoo Penguin eggs

species	n	fresh egg mass (g)	egg content (g)	yolk content (% egg content)	water content (% wet mass)	energy content $kJ.g^{-1}$ (wet)[a]	total energy content (kJ)
King Penguin	6	330	286	28.1	77.7	6.1	1751
		± 34	± 28	± 2.7	± 1.0		
Gentoo Penguin	5	130	116	28.1	78.9	5.6	646
		± 11	± 9	± 3.5	± 1.2		

[a] Calculated by Sotherland & Rahn (1987) from data in Williams et al. (1982)

contents of King and Gentoo Penguins excluding shells were 1751 kJ and 644 kJ, respectively. Hatchling composition of King and Gentoo Penguins is given in Table 6. Although the energy density of Gentoo Penguins hatchlings (4.9 $kJ.g^{-1}$) was greater than that of King Penguins (4.2 $kJ.g^{-1}$) yolk reserves of Gentoo Penguins were only 3.1 % of total hatchling mass considerably less than the 8.6 % of King Penguins. Consequently, based on the resting metabolic rate of hatchling, time required by Gentoo Penguin hatchlings to deplete energy available in the yolk sac was about half that of King Penguins (1.2 vs 2.2 d) (Table 6).

Efficiency of development and energy budget

Estimates of the energy efficiency of embryonic development of King and Gentoo Penguins can be calculated from data presented in Table 5 and 6 (Table 7). Production efficiency and storage efficiency (see Table 7 for definitions) of Gentoo Penguin hatchlings, 77 % and 68 % respectively, were considerably higher than those of King Penguins, 50 % and 53 %. However, the total energy expenditure of embryos expressed a percentage of energy in fresh eggs was similar at around 34 %. A simplified energy budget for King and Gentoo Penguin eggs on hatching was calculated (Table 8). Energy costs were allocated to hatchling content, yolk reserve, maintenance and tissue synthesis. Fourty one percent of the energy available to King Penguin embryos was allocated to maintenance and tissue synthesis, 11 % higher than that allocated by Gentoo Penguins. In contrast, the amount of energy invested in King Penguin hatchlings (47 %), was considerably less than the 65 % allocated to Gentoo Penguin hatchlings.

TABLE 6

Composition of hatchlings of King and Gentoo Penguins

species	n	total mass (g)	yolk free mass (g)	water content % yolk free mass	yolk reserve g	energy content $kJ.g^{-1}$	yolk mass % total	yolk energy content $kJ.g^{-1}$	days wet yolk reserve
King Penguin	3	183	167	82	15.8	4.2	8.6	10.7	2.2
		± 12	± 11	± 0.4	± 4.0				
Gentoo Penguin	4	96	93	80	3.0	4.9	3.1	12.8	1.2
		± 25	± 25	± 1.5	± 1.0				

TABLE 7

Energetic efficiency of embryonic development in King and Gentoo Penguins

	production[a] efficiency %	total consumed[b] energy %	Storage efficiency[c] of hatchling %
King Penguin	49.6	35.6	52.7
Gentoo Penguin	77.2	33.9	67.7
Adelie penguin[d]			54.0

[a] (yolk-free hatchling energy content + yolk reserve energy content) : (energy content of fresh egg) x 100

[b] total volume of O2 consumed by embryo (Table 4) converted to kJ as a % of energy in fresh egg

[c] [yolk free hatchling energy content : (hatchling energy content + consumed energy)] x 100

[d] from Bucher et al. (1986)

TABLE 8

Energy budget of King and Gentoo Penguin eggs on hatching

	King Penguin energy cost		Gentoo Penguin energy cost	
	kJ	%	kJ	%
Hatchling	701	47	456	65
Yolk reserve	169	11	38	5
Maintenance	614	41	207	30
Total	1484		607	

Cost of yolk production:

The mean number of yolk rings counted in Gentoo Penguin eggs was 14.3, significantly different from the mean of 8.3 for King Penguins (Table 9). This data combined with that on energy content of eggs allowed calculation of energy cost of yolk production (Table 10). Daily energy cost of yolk production was 201 $kJ.d^{-1}$ and 87 $kJ.d^{-1}$ for King and Gentoo Penguins, respectively.

DISCUSSION

Oxygen consumption and total energy expenditure:

The pattern of embryonic oxygen consumption of King and Gentoo Penguins (Fig. 1), and the close fit of both logistic and exponential curves (Table 2) to this pattern is similar to that described for Rockhopper and Macaroni Penguins embryos (Brown 1988). On the basis of behavioural and morphological traits penguin hatchlings have been classified as semialtrical (Nice 1962). Vleck & Vleck (1987) have indicated that metabolic rates of altrical embryos increased continuously throughout incubation whereas metabolic rates of precocial embryos increased until they approached hatchling mass at about 80% of their way through incubation at which stage metabolic rates declined. Such a decline was noted for Adelie Penguins (Bucher et al. 1986) but not for King and Gentoo Penguins (Fig. 1) or for Macaroni and Rockhopper Penguins (Brown 1988). However, the lack of any detectable decline in MO_2 towards the end of incubation may have reflected the limited number of measurements prior to pipping because other metabolic indices of maturity indicate semi-prococial hatchlings. Oxygen consumption of prepipping King and Gentoo Penguin embryos was closer to that predicted for

TABLE 9

Yolk deposition time of penguins

	Gentoo Penguin	King Penguin	Adelie Penguin	Fiordland Penguin	White flippered Penguin
Deposition time (d)	14.3 ± 2.1	8.3 ± 1.0	15	16A, 17B[a]	14
n	5	6			

Additional data from Grau (1984)

[a] First (A) and second (B) laid eggs

TABLE 10

Estimated cost of yolk production of Gentoo and King Penguins

	deposition time (d)	mass of yolk (g)	energy density $kJ.g^{-1}$ (wet)	total energy kJ	rate of energy deposition $kJ.d^{-1}$	total energy $kJ.d^{-1}$ [a]
King Penguin	8.3	80	16.7	1 336	161	214
Gentoo Penguin	14.3	33	15.4	508	35.5	47

[a] assuming a 75 % conversion efficiency (Brody 1945)

precocial or semi-precocial chicks than for altrical chicks. Predicted energy costs calculated from the equation for altricial birds (Bucher et al. 1986) underestimated measured costs for penguins by 30 - 56.4 % (Table 2). Indices of metabolic maturity, based on the ratio of mass independent metabolism of hatchlings to mass independent metabolism (MIM) (Bucher 1987), were 0.50 and 0.33 for King and Gentoo Penguins respectively. Adelie Penguins had an MIM index of 0.52 (Bucher et al. 1986). These values range from the upper limit of that recorded for birds regarded as altrical (Nice 1962) to values equal or above that for birds regarded as precocial or semi-precocial.

Measurements of MO_2 of embryos over the whole incubation period are now available for six species of penguin (Bucher et al. 1986, Brown 1988, this study). Variation within total mass-specific oxygen consumption of the six species of penguin embryos throughout incubation was unrelated to both incubation length or egg size. and averaged 96.5 ± 13.0 $mlO_2.g^{-1}$ fresh egg mass (range 83.7 - 126.7 $mlO_2.g^{-1}$) close to that reported for many other species (Rahn & Whittow 1988). Brown & Adams (1988) noted that total oxygen consumption of embryos of high latitude Procellariiformes was considerably higher than in tropical species. These differences arise primarily from the high pre-pipping to hatchling metabolic rates of the high latitude birds and may be related to the higher thermoregulatory demands of chicks of Procellariiformes reared at high latitudes (Brown & Adams 1988). Pipping to hatchling metabolism of King and Gentoo Penguins averaged 53% of total metabolic costs, 10 % higher than that of high latitude Procellariiformes. However, there is as yet no data from temperate and tropical penguin species to test if a similar difference in embryonic metabolism exists between high and low latitude penguins.

Embryo composition, energy efficiency of growth and embryonic energy budget:

Comparisons of the egg composition of inshore and offshore feeding terns indicated that the increased maintenance requirements of embryos of offshore feeding terns with prolonged incubation are met by relatively higher yolk content (Sotherland & Rahn 1987). Given the prolonged incubation period of King Penguins and hence relatively high maintenance costs we should expect relative yolk contents to be higher than that of Gentoo Penguins. In fact values were identical (Table 5) and close to those determined for eight other species of penguins (Williams et al. 1982). However, an explanation may be found in the hatching mass of King Penguins which averaged only 51% of initial egg mass considerably less than the 72% of Gentoo Penguins and the average hatching mass of 30 bird species of 67% (Rahn et al. 1984). Such small hatchlings would serve to reduce maintenance costs and the need for relatively high yolk contents.

More recent reviews (Pettit et al. 1984, Rahn & Whittow 1988, Sotherland & Rahn 1988) have reaffirmed that relative egg content of the egg is related to both developmental status of the hatchling and relative length of incubation period. Based on the high proportion of yolk in semialtrical penguin and petrel eggs, Williams et al. (1982) had previously suggested that there was no simple relationship between egg composition and hatchling precocity. However the classification used by Williams was based on Nice (1962). A physiologically based classification (Bucher 1987) may provide a sounder basis to investigate relationships between egg composition and hatchling maturity. Egg compositions of penguins are consistent with metabolic indicies of maturity (see above) which suggest more precocial than altrical hatchlings (see also Montevecchi et al. 1983).

During incubation yolk mass decreases as the embryo utilizes energy and nutrient reserves. On hatching some yolk reserves still remain. Although the high water content, and hence low energy density of King Penguin yolk reduced the effective difference in energy reserves between the two penguin species (Table 6), the relative proportion of yolk in King Penguins hatchlings was nearly three times that of Gentoo Penguin hatchlings. Williams et al. (1982) suggested that the time before regular post-hatching feeding is established was correlated with the size of the energy reserves of the hatchling. Pettit et al. (1984) suggested a similar correlation between the time required for depletion of such energy reserves and the length of the incubation shift near hatching and feeding intervals of inshore and offshore tropical terns. King Penguins have long incubation shifts (Chapter 9) and feeding intervals (Adams 1987) compared to Gentoo Penguins (Adams & Wilson 1987). suggesting a similar relationship between amount yolk reserves and feeding interval.

Discussion of data on the composition of eggs and hatchlings leads onto a consideration of efficiency of embryonic development. Estimates of the energetic efficiency of embryonic development in avian eggs may be made by comparing energy values of hatchlings and yolk reserves and that consumed by the embryo with energy values of fresh eggs (Table 7). Such comparisons may reveal differences that reflect species adaptations to variations in incubation period. I ignored energy content and metabolism of extra-embryonic membranes in calculation of estimates (see Pettit et al. 1984, Vleck & Vleck 1987).

A number of terms have been defined to describe the efficiency of embryo development. Gross production efficiency is the total energy content of the hatchling including its reserves relative to the energy content of the fresh egg (Pettit et al. 1984). Recent reviews indicate that this value is independent of maturity at hatching (Ar et al. 1987, Sotherland & Rahn 1987, Vleck & Vleck 1987). Production efficiences should be low for embryos with long development periods in which maintenance costs account for a significant proportion of the energy budget, particularly if hatchlings are small. The low percentage production efficiency of King Penguin hatchlings of 49 % were consistent with this. This value is at the lower limit of that determined for tropical seabirds which have more mature and hence more energy dense hatchlings but relatively longer incubation periods (Pettit et al. 1984). The comparatively shorter incubation period and large hatchlings of Gentoo Penguins resulted in a production efficiency of 77 %, 10 % higher than that of tropical Procellariiformes (Pettit et. al. 1984). No comparable data exists for comparison with other high-latitude seabirds.

Energetic storage efficiency (Pettit et al. 1984), also referred to as gross production efficiency (Bucher et al. 1986), is defined as the energy content of the hatchling as a percentage of this energy plus consumed energy. Total energy consumed by developing embryos, calculated from total MO_2 (Table 4) of King and Gentoo Penguin eggs, as a percentage of energy in the fresh egg was similar at 35 % (Table 7) and within the range of that calculated for similar sized eggs of tropical procellariiforms (Pettit et al. 1984). Consumed energy includes that needed for maintenance, synthesis of tissue and any cost of embryonic activity. Presumably the relatively large total maintenance costs associated with prolonged incubation of King Penguin embryos were matched by the relatively higher growth costs of the proportionately larger Gentoo Penguin hatchlings. Measurements of consumed energy will overestimate metabolic costs of producing embryonic tissue alone, because they include work of maintaining and synthesising respiratory and excretory extra-embryonic tissues. However, such costs are likely to be small. The relatively high energy content (large embryo) of the Gentoo Penguin in relation to consumed energy (short incubation period) resulted in a high energetic storage efficiency compared to King Penguins (Table 7). Values for King and Gentoo Penguins at 53 % and 68 % respectively showed considerable overlap with those of tropical Procellariiformes which varied from 58 % for small petrels to 72 % for larger albatrosses.

The relative allocation of energy to the various defined budgeting units (Table 8) can be understood also in terms of the prolonged incubation but relatively small hatching size of King Penguins compared to Gentoo Penguins. A relatively low percentage of total energy was allocated to hatchlings. The high maintenance costs are consistent with the prolonged incubation.

Energy costs of yolk production

Duration of yolk formation in Gentoo Penguins was similar to that determined for other penguin species (Grau 1984) but considerably different to that of King Penguins (Table 9), which in turn was similar to that determined for small Charadriiformes (Grau 1984). The reasons for this marked difference are not clear. The technique requires the counting of daily yolk rings. Astheimer & Grau (1985) noted less distinctly layered, more homogeneous material towards the edge of the yolks which they related to the cessation of feeding of Adelie Penguins during late egg formation. The eggs of the pelagic King Penguin showed a similar trend. I may not have identified all outer layers and consequently would underestimate duration of yolk formation.

Assuming penguins laid down yolk at a constant rate throughout the deposition period and the energy value of dry yolk was 33.0 $kJ.g^{-1}$ (Sotherland & Rahn 1987) , I estimated King Penguins take 8.3 days to complete yolk formation and laid down yolk at an energy equivalent of 161 $kJ.d^{-1}$. Gentoo Penguins took 14.3 d to lay down the yolk at a rate of 36 $kJ.d^{-1}$. If I underestimated the time taken for King Penguins to lay down yolk and it took a similar length to Gentoo and other penguins the rate becomes 93 $kJ.d^{-1}$. Synthesis of egg material is less than 100% efficient. Assuming a conversion coefficient of 75% (Brody 1945), energy cost of yolk production was 201.0 $kJ.d^{-1}$ for King Penguins and 43.8 $kJ.d^{-1}$ for Gentoo Penguins representing 9.0 and 2.7 % of Basal Metabolic Rate (BMR) (Chapter 7) respectively . Gentoo Penguins normally have a two-egg clutch with a laying interval of approximately 2 d. Formation of eggs is therefore largely simultaneous and daily costs would be 5.4 % d^{-1}. Although peak energy costs during egg formation may be associated with the formation and secretion of albumin rather than yolk production, when compared to the cost of other activities, energy cost of egg production is low and energy limitions are unlikely to affect egg production. Asterheimer & Grau (1985) have suggested that female protein reserves, or the physiological ability to mobilize them, may play a far more critical role in timing of egg formation in penguins than energy constraints.

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CHAPTER 11

ENERGETICS OF CHICK GROWTH OF KING *APTENODYTES PATAGONICUS* AND GENTOO *PYGOSCELIS PAPUA* PENGUINS

Changes in the composition of body components of King and Gentoo Penguin chicks through growth are described and energy budgets determined. Development of King Penguin chicks was interrupted by a winter - fasting period during which growth ceased. The onset of this period in April was abrupt and independent of chick age. Absolute energy expenditure of chicks was correlated with their mass. Mass-specific metabolism of King Penguins peaked at approximately 14 d before decreasing and then stabilizing at levels close to that at hatchling. Changes in mass-specific metabolism of Gentoo Penguins were less marked but showed a similar pattern. Concomitant with a decrease in body water content of penguin chicks from hatching was an increase in body energy content. Protein levels of King Penguin chicks were maintained throughout the winter starvation period. Mass loss through winter was largely of lipid reserves. The total energy requirements for growth and maintenance of King Penguin chicks were 756 840 kJ. Large changes in the proportional allocation of energy requirements to growth and maintenance occurred. During winter, energy requirements were allocated solely to maintenance. The relatively high allocation of the total energy budget by chicks of offshore feeding King Penguin to lipid accumulation especially during the first 90 d of growth, reflects their long feeding intervals and winter fast. Chicks of inshore feeding Gentoo Penguins accumulated lipid and protein throughout the growth period. Total energy requirements for growth and maintenance of the smaller Gentoo Penguin chicks were considerably less than King Penguin chicks at 137 575 kJ. Because Gentoo Penguin chicks are fed frequently, they have little need to accumulate large lipid reserves and although percent relative allocation of the total energy budget to growth was high, that specifically allocated to lipid accumulation was low.

INTRODUCTION

Energy, delivered by adult seabirds to their chicks, is allocated between growth (including biosynthesis), maintenance (including heat increment of digestion and thermoregulation) and activity. The nature of this allocation may be influenced by the distribution and availability of food. Chicks of pelagic seabirds, which are fed at intermittant and irregular intervals (Ricklefs 1983a, Ricklefs et al. 1985), may allocate more of their energy intake to fat accumulation and growth from an earlier age than do chicks of inshore foraging species (Ricklefs & White 1981). Although recent work has questioned that such accumulations in chicks of pelagic seabirds are a consequence of energy constriants (Taylor & Kanazewski 1989, Schaffner 1990), large lipid reserves may be adaptive in the event of extended periods of poor feeding conditions.

The King Penguin Aptenodytes patagonicus is a pelagic forager (Adams 1987) and has many of the breeding adaptations characteristic of such birds and which are presumed to reflected energy limitation (Lack 1968). In particular, the single chick has an exceptionally long fledging period of some 310 d (Stonehouse 1960, Barrat 1976, Croxall 1984). Seasonal changes in diet (Adams & Klages 1987) and frequency of chick feeding (Cherel et al. 1987) suggest a decrease in food availability over the austral winter. In contrast, Gentoo Penguins Pygoscelis papua are inshore feeders (Adams & Wilson 1987, Trivelpiece et al. 1986) and feed their chicks regularly. The chick-rearing period is some 105 d (Williams 1980). Although at Marion Island only one chick per brood is ever raised to independence, two chicks normally hatch (Williams 1980).

In this study I estimated energy expenditure of chick growth of King and Gentoo Penguin chicks at sub-Antarctic Marion Island. This information was combined with data in changes in body composition to construct energy budgets of chicks from hatching to independence. Differences in energy budgets of penguin chicks, in terms of energy delivery allocated to maintenance and tissue growth, are evaluated in relation to rates of food provisioning by pelagic and inshore feeding species. Estimates of the energy cost of chick growth of King Penguins are of additional interest because this species is the most important avian consumer of marine resources in the waters around the Prince Edward Islands (Marion and Prince Edward) (Chapter 12) and energy costs of chick rearing may increase the impact on food resources substantially.

METHODS & MATERIALS

Penguin growth:

At Marion Island the majority of King Penguin chicks hatch from mid-January to mid-February and depart to sea from mid-October to mid-November (pers. obs). Late chicks hatch until April. I determined hatching dates of late chicks in 1984 by daily checks of individually marked adult pairs at a colony of King Penguins at Archway Bay. After the brood and guard phase, both adults are engaged in foraging for the chick simultaneously and chicks form large creches. Therefore, to identify study chicks , I fitted temporary plastic flipper bands. Weekly measurements of mass, culmen and foot length of known aged chicks were made for a maximum of 170 d, by which time all chicks had died. The low masses at death suggested that starvation was the primary cause. These data were supplemented by measurements of chicks hatched from January - February 1985 and followed until the beginning of May 1985. The growth of additional groups of chicks was monitored at two-weekly intervals from May 1984 and June 1986 until fledging. The age of most of this group could be estimated from measurements of known - aged chicks. Measurements of chicks estimated to be within two weeks of age, were lumped. During June and September - November, I weighed a sample of 10 chicks daily to determine mass loss rates. These rates were determined over a minimum of 4 d. Initial measurements were made at least 2 d after a feed. I assumed that any food in the gut would have been processed by this stage.

I determined the hatching dates of Gentoo Penguin chicks at Trypot Beach, Marion Island from regular checks of marked nests at 2d intervals during the austral winter of 1984. Measurements of mass, culmen and foot length of these chicks were made at 5d intervals until chicks were 20d old. Thereafter, measurements were made weekly. Flipper tags attached to chicks before the end of the guard phase allowed study chicks to be identified in small creches.

Energy metabolism:

Oxygen consumption of between four and nine King Penguin chicks was measured in the laboratory at weekly intervals on known aged chicks from 0 - 90d old. Thereafter, measurements were conducted at intervals of two weeks until fledging. Age of these chicks was estimated from measurements of culmen and foot length. King Penguins do not construct a nest but incubate their egg and brood the chick on their feet (Stonehouse 1960). Chicks up to the age of about five weeks are closely brooded and guarded (pers. obs). Once such chicks have been removed, adults generally abandon the breeding site. Accordingly these chicks were sacrificed under permit for body composition analyses (see below). Older chicks were returned to the colony within 24h. Measurements of oxygen consumption on Gentoo Penguin chicks were conducted on five known - aged chicks at 5 to 7d intervals. Because adult birds construct a nest I was able to return chicks after measurements.

I measured oxygen consumption in an open flow-through system consisting of, in series, a pump, a regulating flowmeter, a chamber for the bird, a Rotameter flowmeter, tubes containing Silia Gel/Carbosorb to remove water vapour and carbon dioxide, and finally a Taylor Servomex OA 570 paramagnetic oxygen analyser. I used four different sized chambers of 10, 25, 75 and 100 l depending on chick size. Air flow through the system was regulated to produce a drop of between 1 - 2% in oxygen concentration between ambient inlet air and outlet air and ranged from 84 to 9 150 ml.min^{-1} depending on chick size. The oxygen analyser was calibrated assuming the oxygen content of ambient air to be 20.94%. Chamber temperature was monitored by a thermocouple inserted into the chamber through a rubber bung. For King Penguin chicks 28d and younger and Gentoo Penguin chicks 20d or younger, experimental temperature was controlled by placing the metabolic chamber into a thermostatically controlled water bath. Chamber temperature was regulated between 10 and 25°C. I determined oxygen consumption of these chicks at intervals of 5°C to establish the lowest stable metabolic rate consistent with maintenance of body temperature at or near adult level. Body temperatures of chicks were measured by thermocouples inserted into the oesophagus and taped to the lower bill. King Penguin chicks older than 28d and Gentoo Penguins older than 20d were generally too large to be brooded by adults and thereafter measurements were made at ambient temperatures. Before measurements of oxygen consumption commenced, I allowed 45 min for the chamber air to equilibrate and for the chick to settle. Thereafter, chamber temperature, body temperature of young chicks, flow rate and percentage O_2 in effluent air were recorded at 15-min intervals over a period of 2 - 6 h. In the case of young chicks, monitoring periods were restricted to 1 h at each temperature with a 45-min equilibration period between each temperature change. Oxygen consumption was calculated from Hill (1972) using the equation for dry, CO_2-free air and corrected to the energy equivalent (1 dm^3 O_2 = 20.1 kJ).

King Penguin chicks being brooded and approaching fledging are fed regularly (Adams 1987, Cherel et al. 1987) and measurements of oxygen consumption may include a component required for digestion of food (specific dynamic action, SDA) (see Kendeigh et al. 1977). In contrast, from May to September chicks are fed irregularly and fast for long periods (Cherel et al. 1987, N.J. Adams unpublished data). Gentoo Penguin chicks are fed on most days (pers. obs.) and measurements of oxygen consumption will probably include an SDA component. Measurements on adult Little Penguins <u>Eudyptula</u> <u>minor</u> suggest that after feeding, oxygen consumption may increase to 1.87 times that of resting post absorptive levels (Baudinette et al. 1986).

Body composition:

I sacrificed, under permit, 28 King Penguin chicks and 13 Gentoo Penguin chicks at intervals throughout the growth period. Chicks were weighed , sealed in plastic bags and then frozen before analyses. Later, chicks were thawed and their stomach contents removed. Carcasses were then dissected into: integument (skin, subcutaneous fat and feathers), internal organs, and body musculature and skeleton. Components were minced and dried to constant mass at 55°C to estimate water content. Aliquots of dry samples were analysed for lipid content by hexane extraction for 45 min at 70°C. Further aliquots were ashed in a muffle furnance for 6 h at 500°C. Energy content of individual chicks was calculated from energy equivalents of 38 $kJ.g^{-1}$ lipid and 20 $kJ.g^{-1}$ non-lipid dry mass (Schmidt-Nielsen 1979).

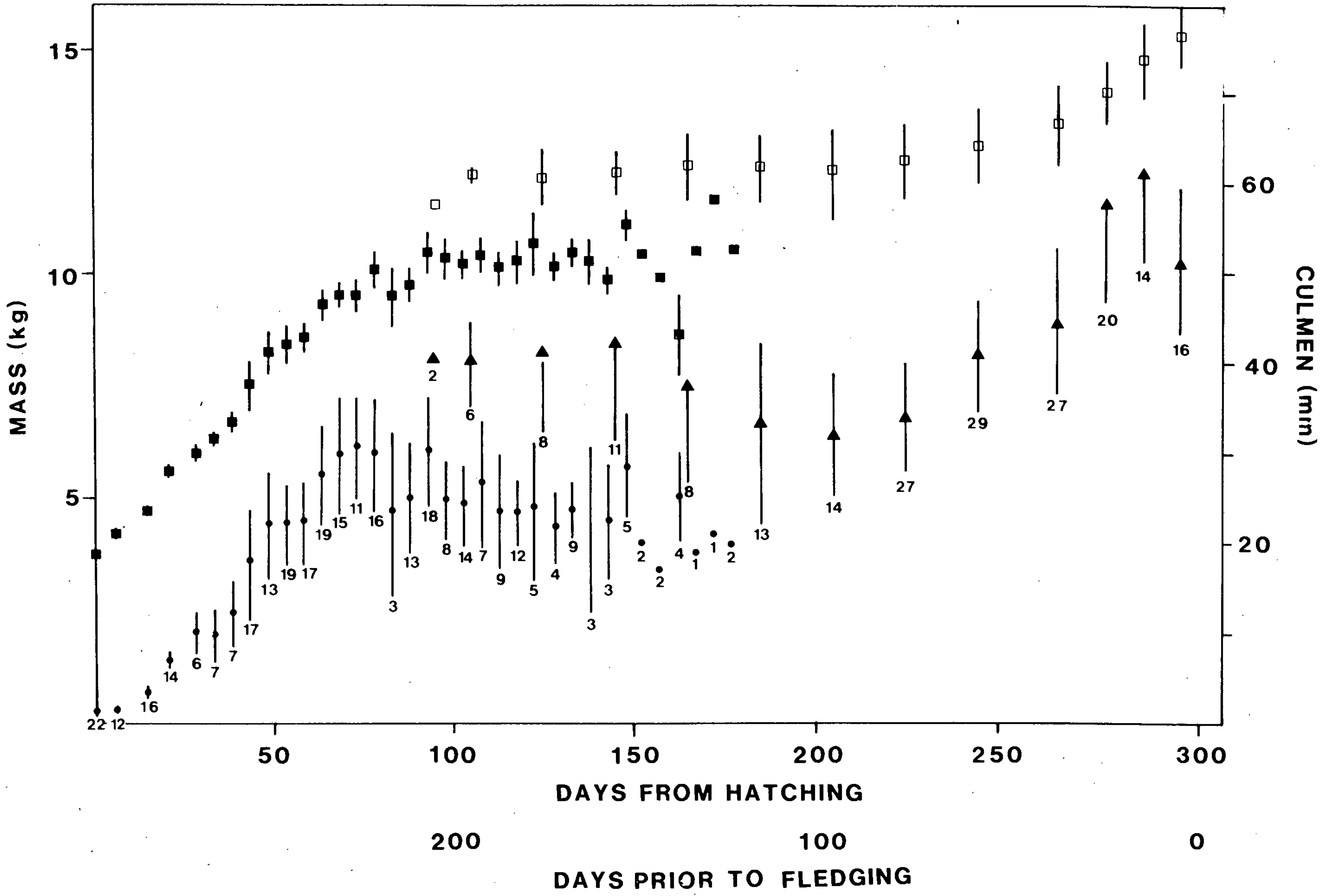
RESULTS

Growth:

Growth of King Penguin chicks from hatching to 170 d and from 200 d prior to fledging to independence is summarized in Fig. 1. Chicks weighing only 6 kg or less 70 d after hatching, did not survive the winter fast, generally starving to death at a

FIGURE 1

Masses and culmen lengths of King Penguin chicks as a function of age. ● masses of known age chicks, ▲ masses of chicks prior to fledging, ■ culmen lengths of known aged chicks, ☐ culmen lengths of chicks prior to fledging. Bars indicate one SD above and below the mean.


MASS (kg)
5
10
15
CULMEN (mm)
20
40
60
DAYS FROM HATCHING
50
100
150
200
250
300
DAYS PRIOR TO FLEDGING
200
100
0
22
12
16
14
6
7
7
17
13
19
17
19
15
11
16
3
13
18
8
14
7
9
12
5
4
9
3
3
5
2
2
4
1
1
2
2
6
8
11
8
13
14
27
29
27
20
14
16

mass of about 3 kg. Peak mass of successful chicks immediately prior to this fast period was at least 8 kg. Chicks lost mass and showed no increase in culmen length over the winter fast period. Approximately 70 d before independence, mass increased rapidly to a peak of 12 kg, 92 % of adult mass. Chicks attained independence at a mass of about 10 kg. Similarly culmen measurements increased with mass during the first 70 d of growth. Thereafter, growth ceased until 50 d prior to hatching. Growth rates of King Penguin chicks expressed as a daily increment were calculated over two - week periods throughout the year (Fig. 2 a-c). The rapid growth of small chicks in February and early March was followed by a sudden decrease in late March and April when chicks began to lose mass, and in addition, showed no incremental length increase in culmen length. Initiation of growth (mass and culmen) in August and September after the winter fast occurred at a similar time in 1984 and 1986. Growth of feet was complete by the end of the initial growth phase.

Mass and culmens of Gentoo Penguin chicks from hatching to independence at about 100 d are illustrated in Fig. 3. In contrast to King Penguins, no period of mass recession occurred during mid - growth. Chicks attained independence at about 4 600 g or 73 % of adult mass. The second of the two chicks normally hatched by Gentoo Penguins never survived beyond 20 d.

Energy expenditure:

King Penguin chicks are brooded and guarded by adults for about 28-35 d. Measurements of oxygen consumption and body temperature at a range of ambient temperatures (Fig. 4) indicate that at 28 d chicks are still unable to maintain body

FIGURE 2A

Daily change in mass of King Penguin chicks averaged over two or three week periods, February to December.

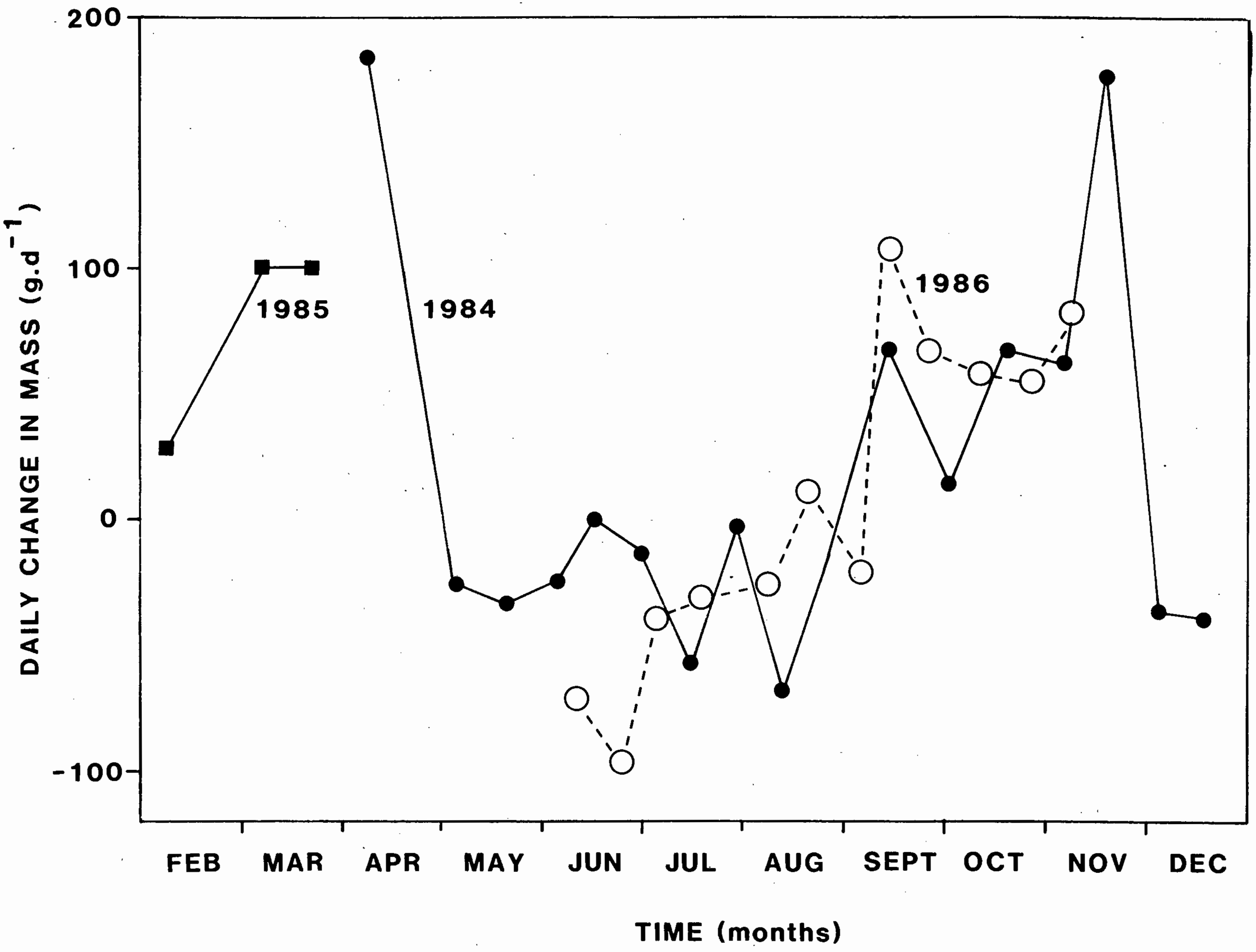

200
100
0
-100
DAILY CHANGE IN MASS (g.d^{-1})
1985
1984
1986
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
TIME (months)

FIGURE 2B

Daily change in culmen length of King Penguin chicks averaged over two or three week periods, February - December.

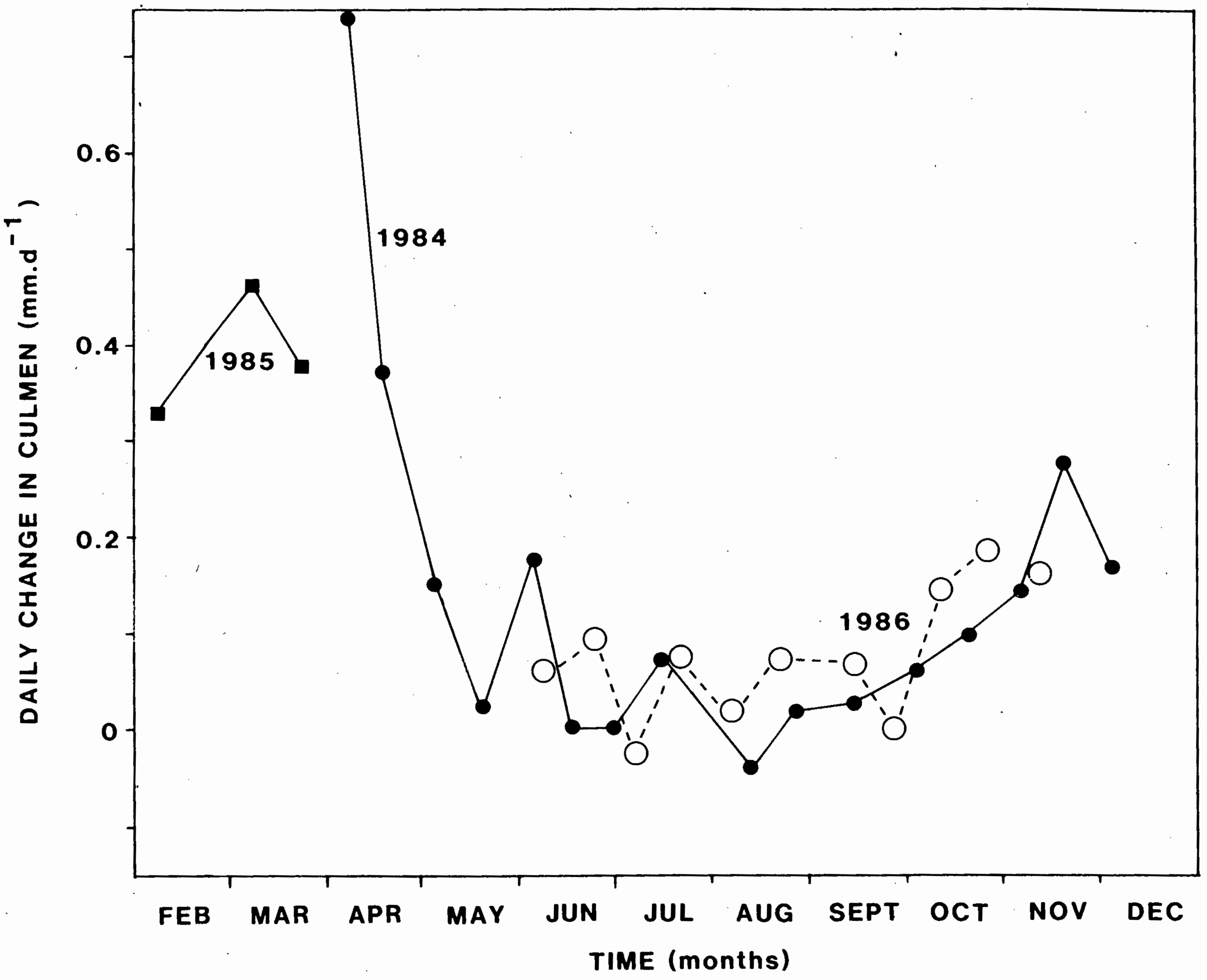

DAILY CHANGE IN CULMEN (mm.d^{-1})
0.6
0.4
0.2
0
1985
1984
1986
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
TIME (months)

FIGURE 2C

Daily change in foot length of King Penguin chicks averaged over two or three week periods, February to December.

FIGURE 3A

Masses of A and B chicks of Gentoo Penguins as a function of age.

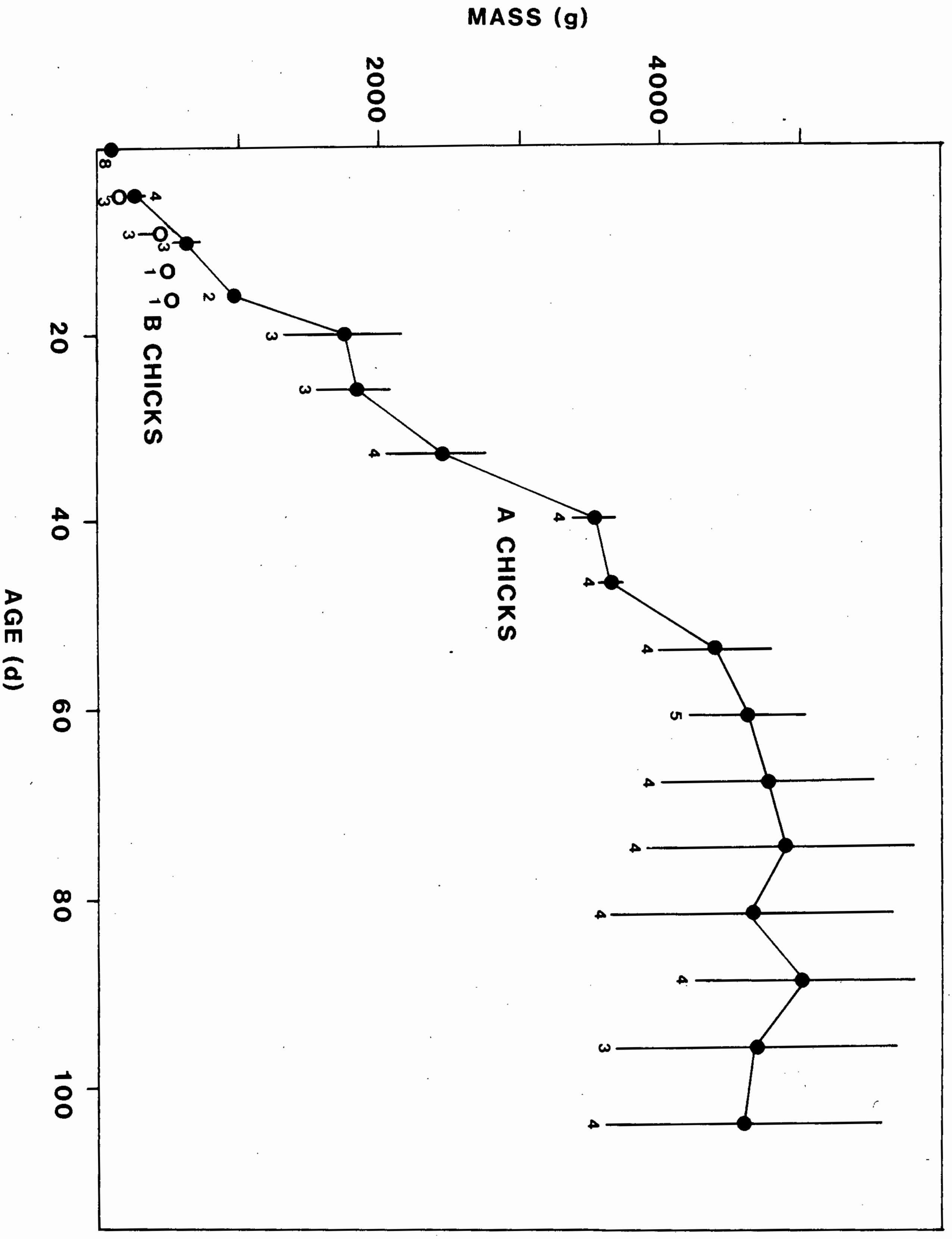

MASS (g)
2000
4000
AGE (d)
20
40
60
80
100
A CHICKS
B CHICKS
8
4
3
3
3
1
1
2
3
3
4
4
4
4
5
4
4
4
4
3
4

FIGURE 3B

Culmen lengths of A and B chicks of Gentoo Penguins as a function of age.

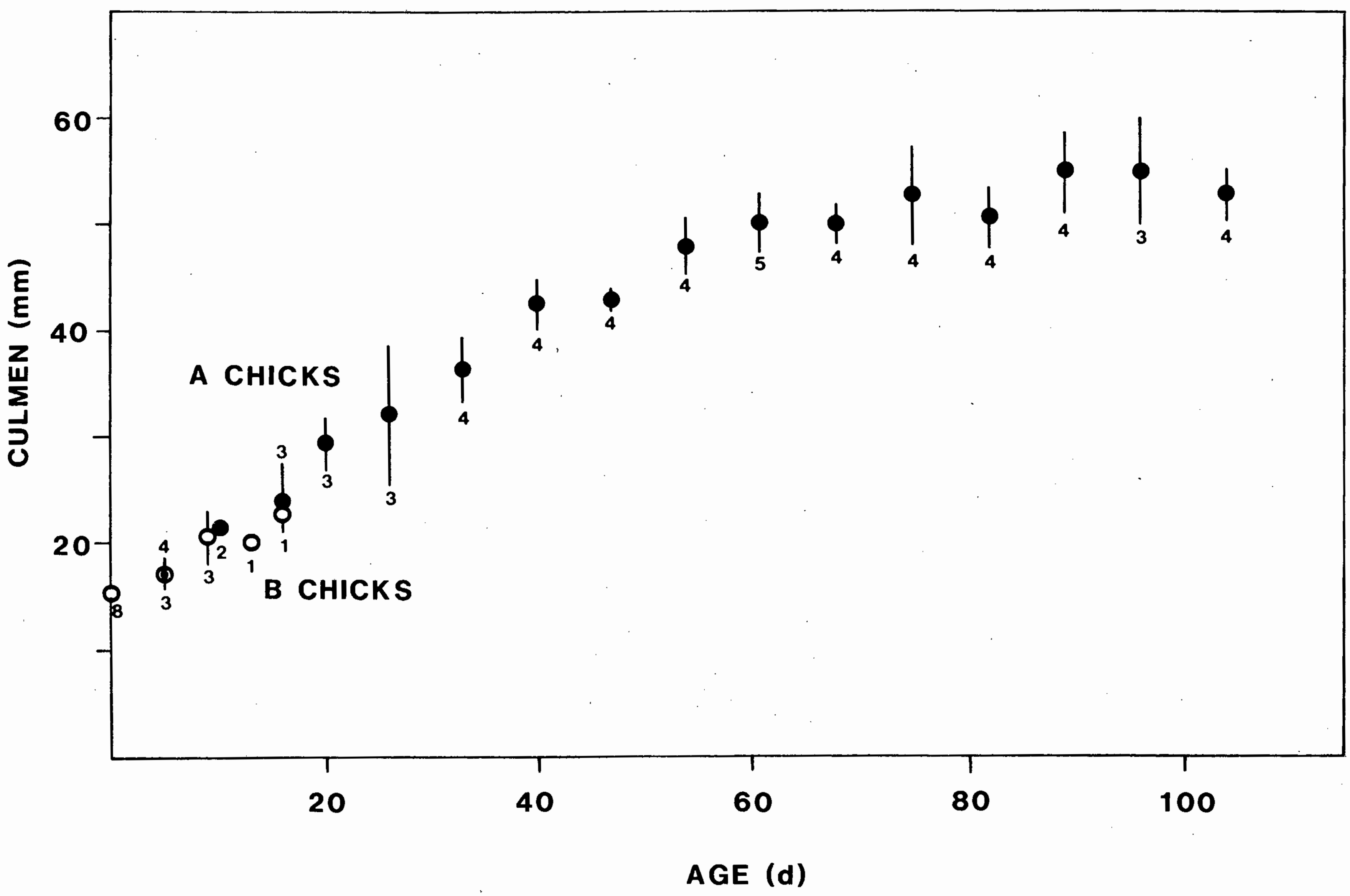
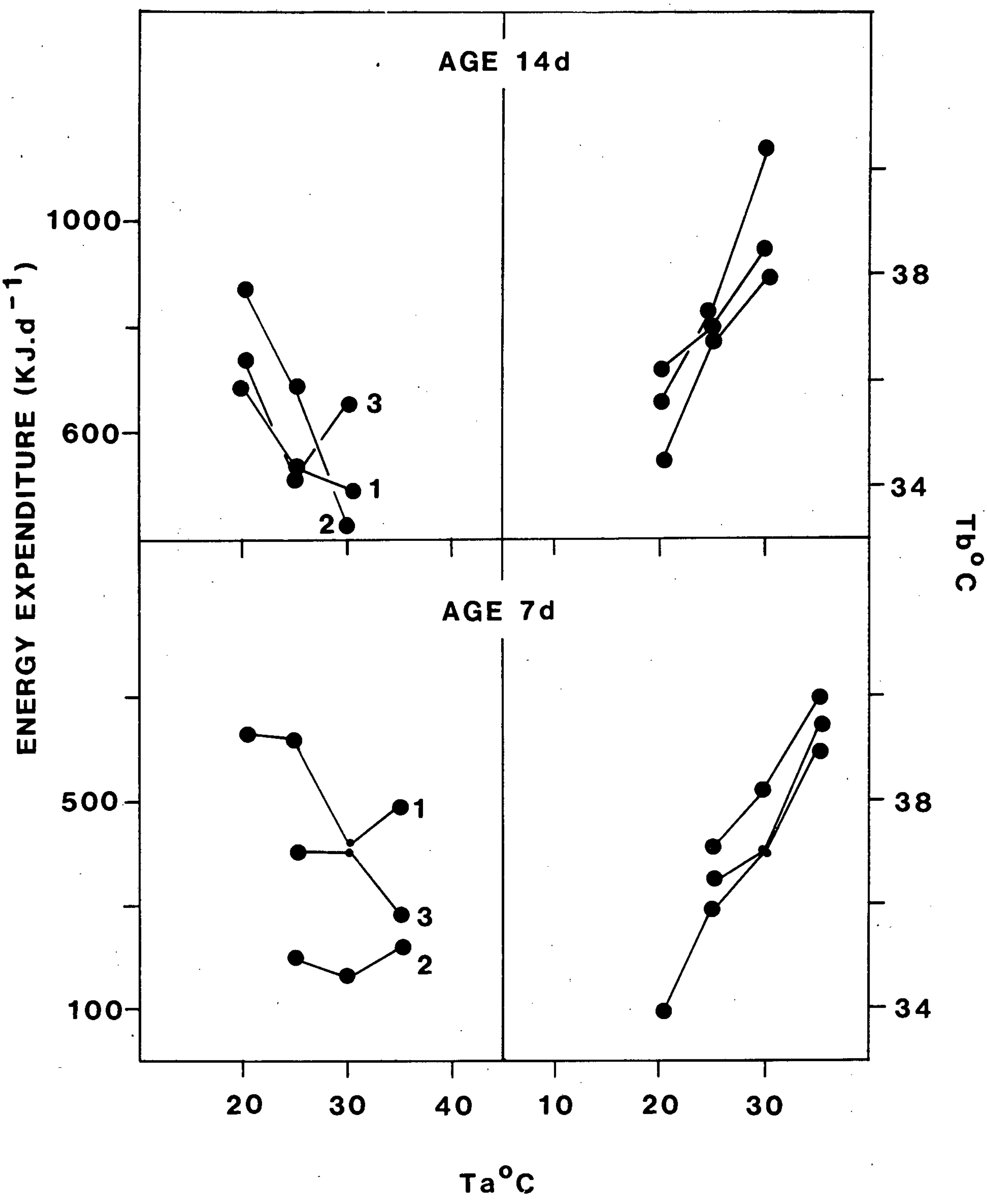
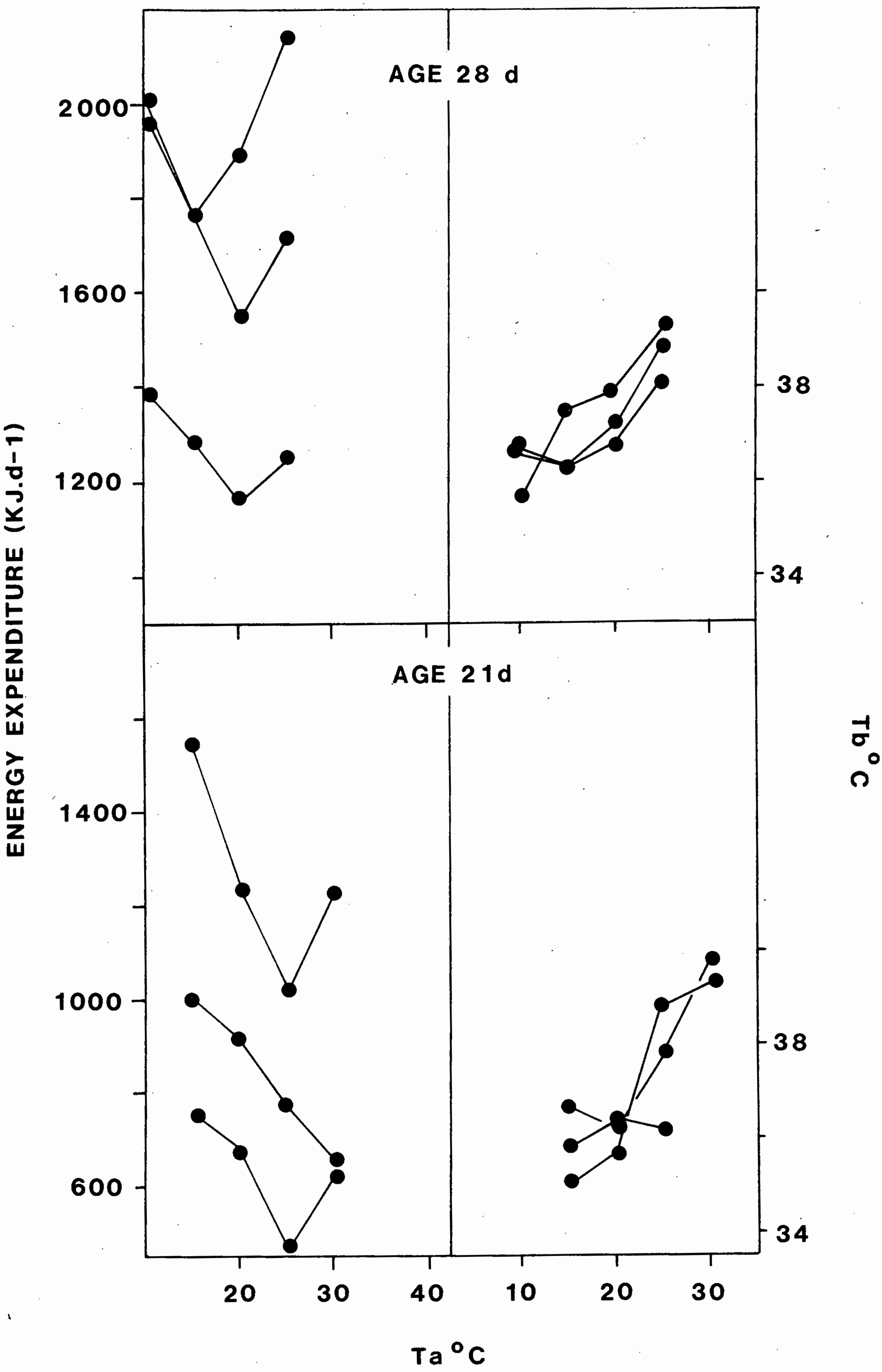

CULMEN (mm)
60
40
20
A CHICKS
B CHICKS
8
4
3
3
2
1
3
1
3
3
4
4
4
4
5
4
4
4
4
3
4
20
40
60
80
100
AGE (d)

FIGURE 4

Energy metabolism and body temperature of King Penguin chicks aged 7 to 28 d exposed to ambient temperatures from 35°C to 10°C. Data for three individual chicks are plotted.



AGE 14d
AGE 7d
ENERGY EXPENDITURE (KJ.d^{-1})
1000
600
500
100
1
2
3
38
34
Tb°C
20
30
40
10
Ta°C


AGE 28 d
AGE 21d
ENERGY EXPENDITURE (KJ.d-1)
2000
1600
1200
1400
1000
600
Tb °C
38
34
38
34
20
30
40
10
20
30
Ta °C

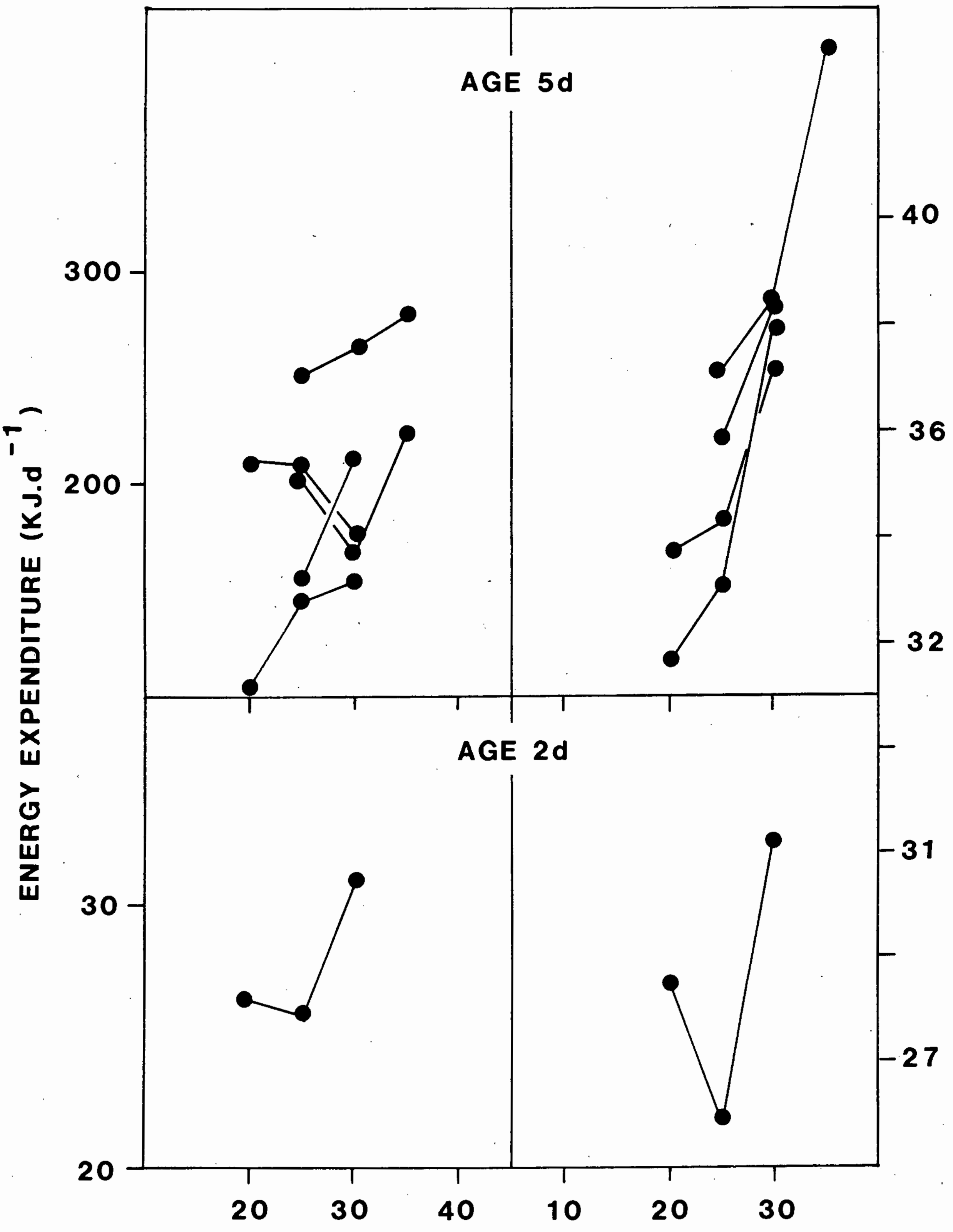
temperatures at ambient temperatures of 10^{o}C. Although data are variable and no clear pattern of oxygen consumption of individual chicks at specific temperatures is evident, the ambient temperature at which oxygen consumption is lowest drops with increasing age and improved ability to thermoregulate (Fig. 4). Data for Gentoo Penguin chicks show similar large variation in oxygen consumption of individual chicks (Fig. 5). However, by 15 d Gentoo Penguin chicks have developed the ability to regulate body temperatures within a relatively small range (Fig. 5).

Absolute and mass - specific energy expenditures, calculated from oxygen consumption of King Penguin chicks from hatching to independence are presented in Figs 6 & 7. Chicks are largely inactive throughout the growth period and I considered that these measurements were a reasonable estimate of the energy cost of existence. Absolute energy expenditure (Fig. 6a) was closely correlated with mass (Fig. 6b). Mass - specific metabolism (Fig. 7) of King Penguin chicks increased rapidly from 333 kJ.kg^{-1}.d^{-1} at two days to 867 kJ.kg.d^{-1} at 14 d and then decreased to hatchling values by about 55 d. Thereafter, until independence, values remained similar at 325 ± 40.8 kJ.kg.$^{-1}$, 1.94 x that of BMR measured for adults. Comparison of mass-specific energy expenditure of chicks from winter and summer (Table 1) showed no significant differences, although estimates based on mass loss suggest energy expenditure of large chicks approaching independence was considerably higher than that of fasting chicks in winter.

Energy metabolism of Gentoo Penguin chicks rose rapidly from

FIGURE 5

Energy metabolism and body temperate of Gentoo Penguin chicks aged 2 to 15 d exposed to ambient temperatures between 35°C and 10°C. Data are plotted for individual chicks.


AGE 5d
AGE 2d
ENERGY EXPENDITURE (KJ.d^{-1})
300
200
30
20
40
36
32
31
27
20
30
40
10
20
30

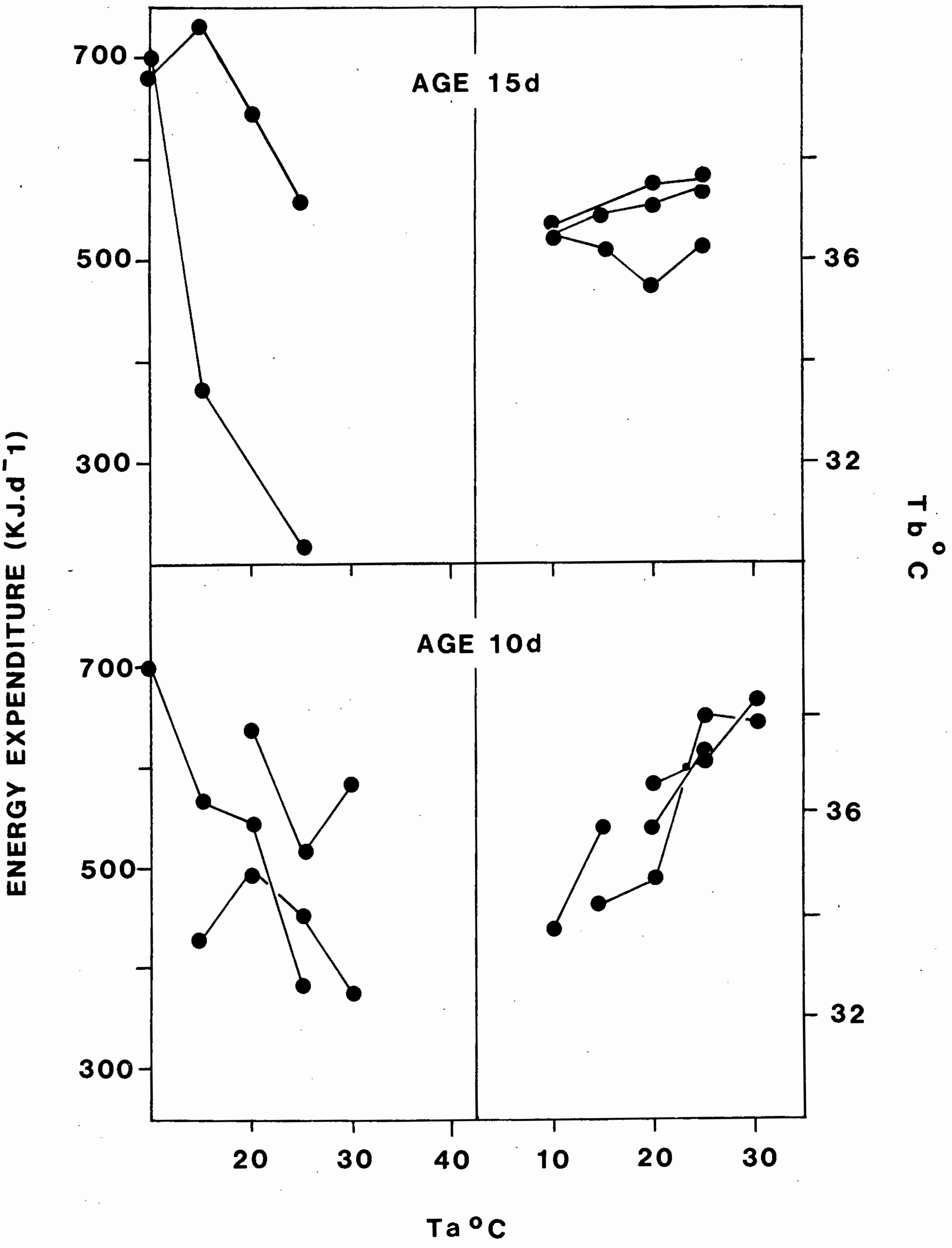

AGE 15d
AGE 10d
ENERGY EXPENDITURE (KJ.d⁻1)
700
500
300
700
500
300
36
32
36
32
Tb °C
20
30
40
10
20
30
Ta °C

FIGURE 6A

Absolute energy expenditure of King Penguins as a function of age. Bars indicate one SD.

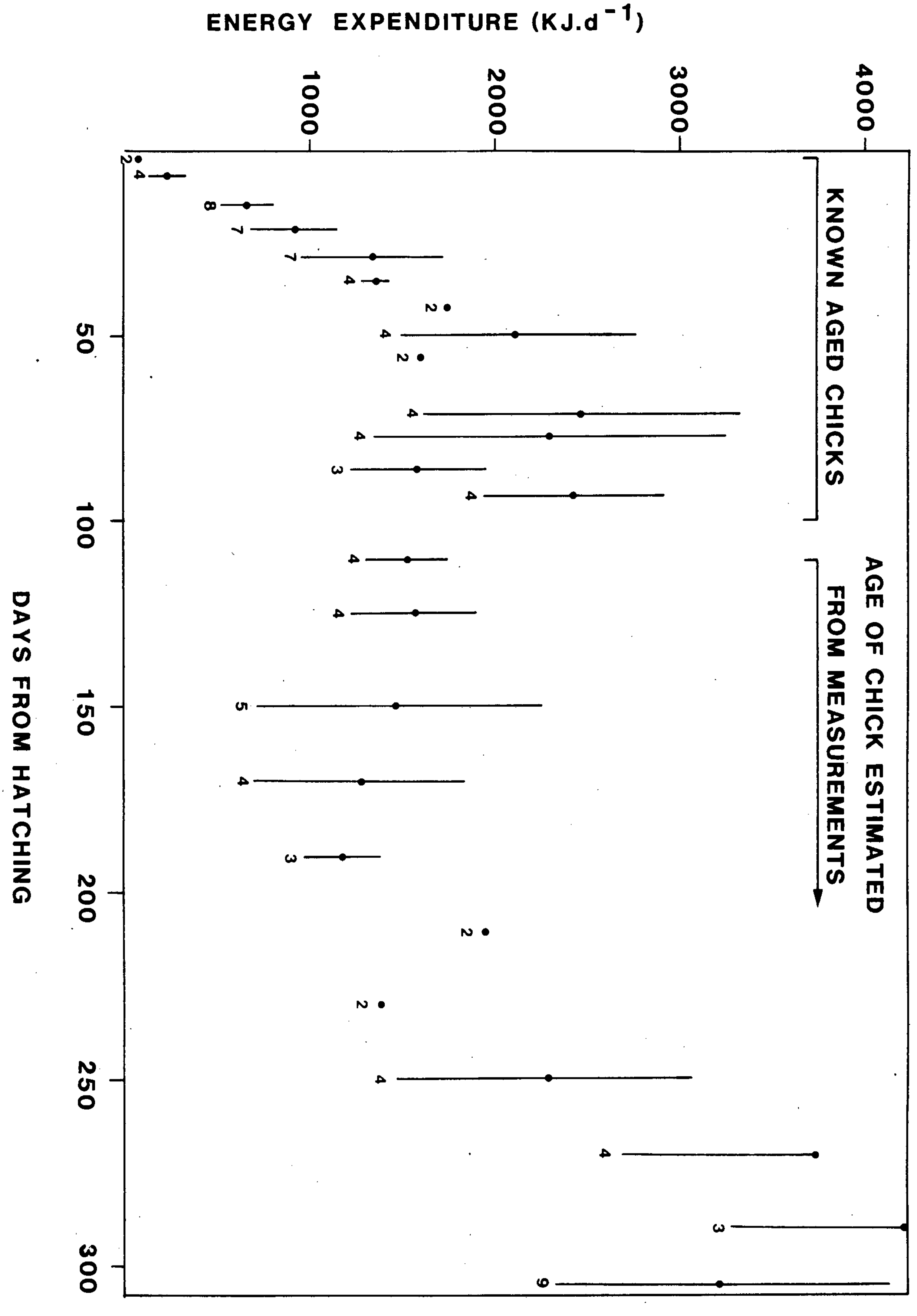

ENERGY EXPENDITURE (KJ.d^{-1})
1000
2000
3000
4000
DAYS FROM HATCHING
50
100
150
200
250
300
KNOWN AGED CHICKS
AGE OF CHICK ESTIMATED FROM MEASUREMENTS
2
4
8
7
7
4
2
4
2
4
4
3
4
4
4
5
4
3
2
2
4
4
3
9

FIGURE 6B

Masses of experimental King Penguin chicks.

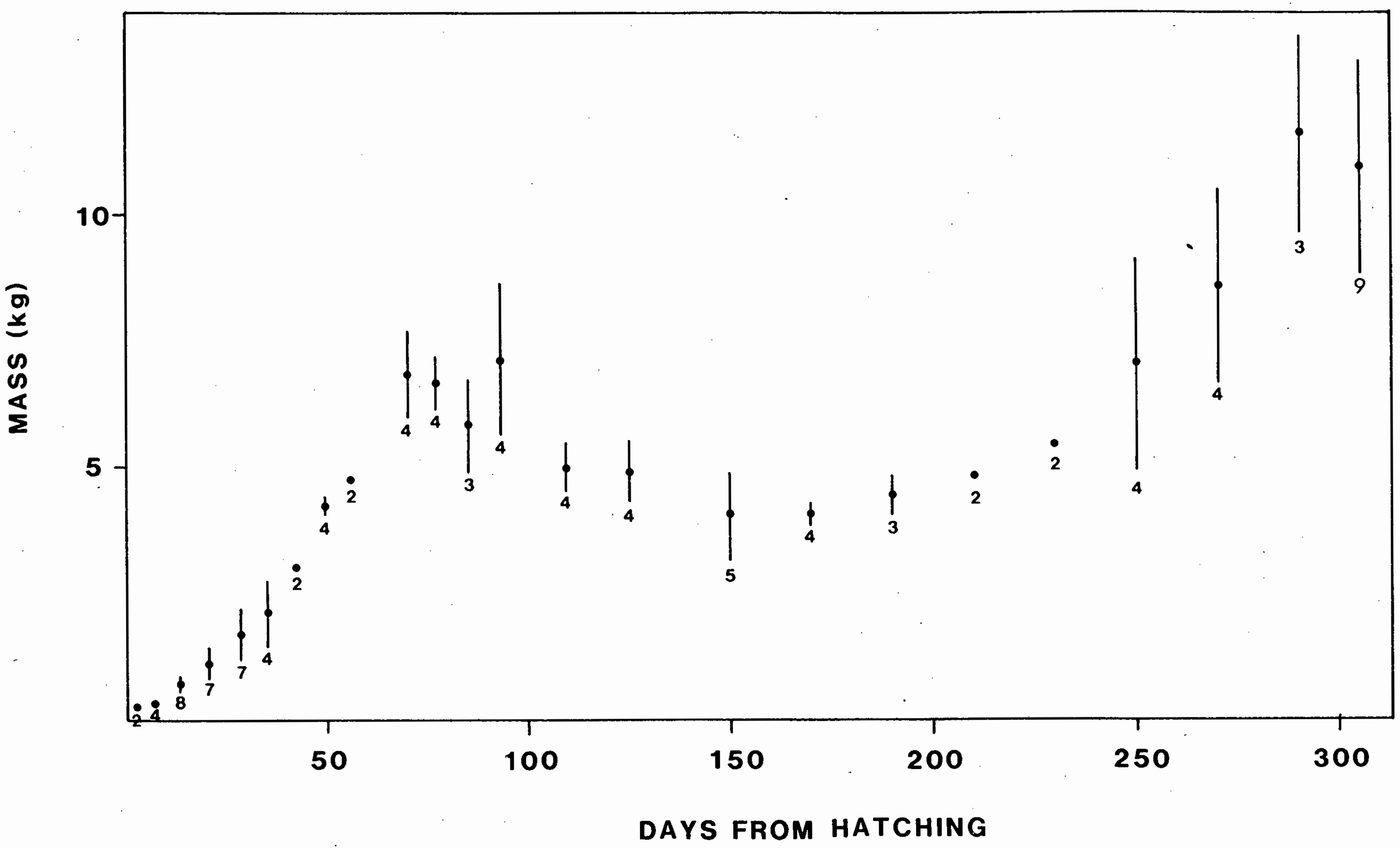

MASS (kg)
10
5
DAYS FROM HATCHING
50
100
150
200
250
300
2
4
8
7
7
4
2
4
2
4
4
3
4
4
4
5
4
3
2
2
4
4
3
9

FIGURE 7

Mass-specific energy expenditure of King Penguins as a function of age. Bars indicate one SD.

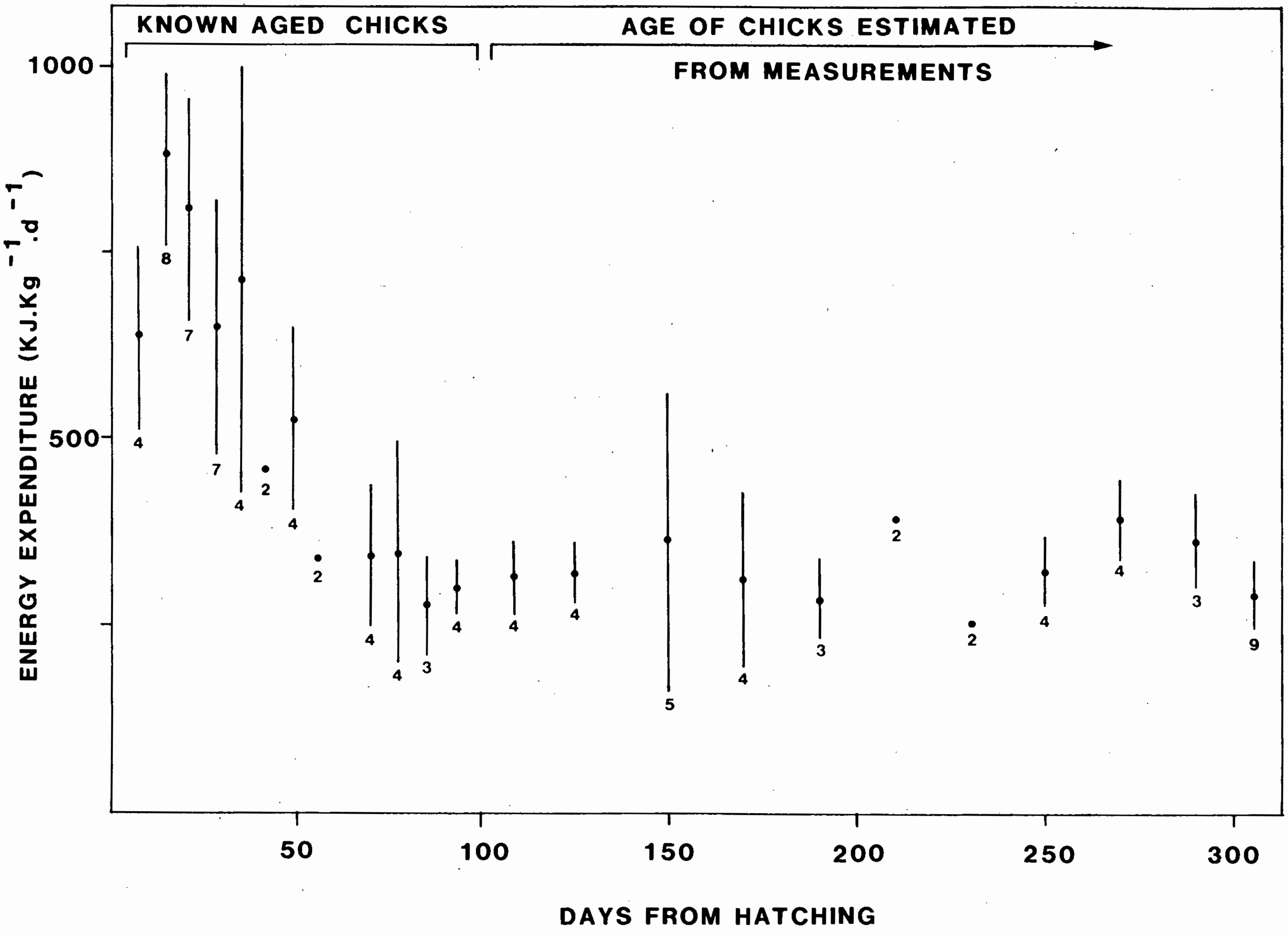

KNOWN AGED CHICKS
AGE OF CHICKS ESTIMATED FROM MEASUREMENTS
ENERGY EXPENDITURE (KJ.Kg $^{-1}$.d $^{-1}$)
1000
500
DAYS FROM HATCHING
50
100
150
200
250
300
4
8
7
7
4
2
4
2
4
4
3
4
4
4
5
4
3
2
2
4
4
3
9

TABLE 1

Energy expenditure of King Penguin chicks in summer and winter and between estimates based on rate of mass loss and oxygen consumption

	Mass loss $kJ.kg^{-1}.d^{-1}$	Oxygen consumption $kJ.kg^{-1}.d^{-1}$
Winter June-August	304 ± 87	327 ± 117
Summer October-December	653 ± 108	333 ± 69

181 $kJ.d^{-1}$ at hatching to 2 011 $kJ.d^{-1}$ at 40 d (Fig. 8). Between 40 d and independence at 104 d there was little change with energy metabolism values fluctuating around a mean of 2 177 ± 399 $kJ.d^{-1}$. Mass - specific metabolism of Gentoo Penguin chicks rose from 664 $kJ.kg^{-1}.d^{-1}$ at 5d to a peak of 888 $kJ.kg^{-1}.d^{-1}$ at 15 d before decreasing steadily to 451 kJ.kg-1.d^{-1} at 68 d (Fig. 9).

Body composition:

There was a general decrease in the total percentage water content of King Penguins with age from hatching until the end of the initial growth phase at 85 d (Table 2). Water content of birds close to minimum mass during winter fasting showed an increase over that at 85 d before finally decreasing slightly close to independence. Percent water in various body components followed the same pattern as above although percent water in integument (skin, subcutaneous fat and feathers) was generally lower than in other body components. Water content of integument showed the greatest decrease (Tables 2, 4). Energy content of King Penguin chicks (Tables 3, 5) increased with decreasing water content.

Water content of Gentoo Penguin chicks declined from 78 % at 10d to 64 % just before independence (Table 4). Consistent with the pattern described for King Penguins, relative water content of the integument decreased by the greatest amount from 77% at hatching, to 40 % at independence.

Total lipid content of King Penguin chicks, after a slow increase from 0 - 28d, increased rapidly during the initial growth phase (Fig. 10). Mass loss of chicks during winter

FIGURE 8

Absolute energy expenditure of Gentoo Penguins as a function of age. Bars indicate one SD.

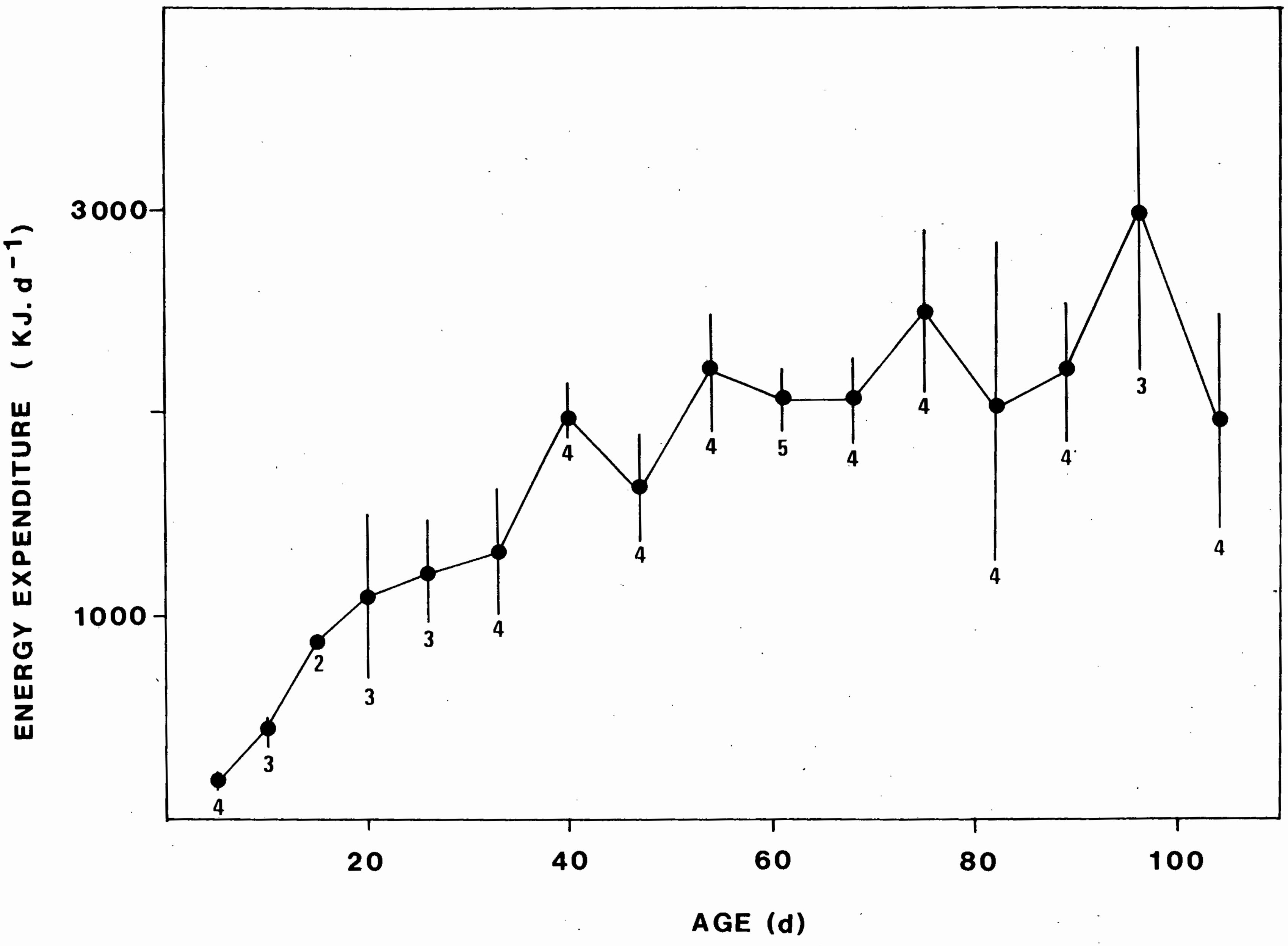

3000
1000
ENERGY EXPENDITURE (KJ. d^{-1})
20
40
60
80
100
AGE (d)
4
3
2
3
3
4
4
4
4
5
4
4
4
4
3
4

FIGURE 9

Mass-specific energy expenditure of Gentoo Penguins as a function of age. Bars indicate one SD.

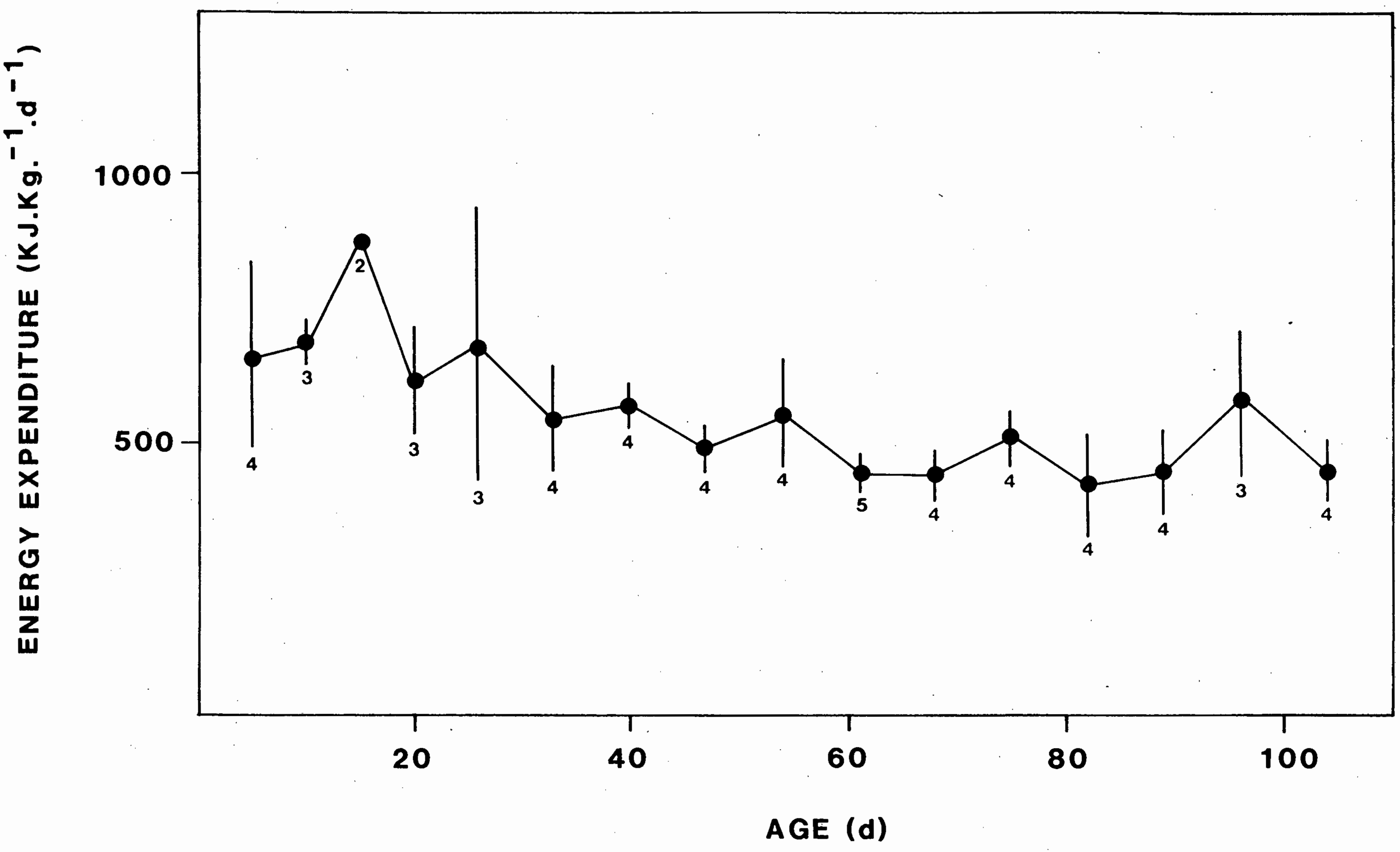

ENERGY EXPENDITURE (KJ.Kg.$^{-1}$.d^{-1})
1000
500
AGE (d)
20
40
60
80
100
4
3
2
3
3
4
4
4
4
5
4
4
4
4
3
4

TABLE 2

Water content of King Penguin chicks

Estimated age (d)	%H_2O Total	%H_2O Muscle	%H_2O Organs	%H_2O Integument	n
0	82.8 ± 0.3	83.4 ± 0.4	78.6 ± 0.8	83.7 ± 0.7	4
7	74.2 ± 0.8	78.4 ± 0.8	77.7 ± 0.9	63.9 ± 1.4	3
14	70.9 ± 1.7	75.4 ± 0.7	77.1 ± 1.4	59.2 ± 3.9	3
21	75.4 ± 2.0	80.7 ± 4.3	76.6 ± 1.0	63.9 ± 5.7	4
28	68.3 ± 3.2	73.5 ± 0.6	74.4a	58.1 ± 2.4	3
60	50.8	69.0	56.7	64.1	1
85	48.9 ± 1.6	67.3[a]	55.4 ± 2.4	[b]	3
190	65.2	72.0	74.7	54.0	2
290	53.4 ± 5.2	70.2 ± 1.0	61.4[a]	49.1[a]	3

[a] two samples analysed only

[b] samples lost

TABLE 3

Energy content (wet mass) of King Penguin chicks

Estimated age (d)	Energy content kJ.g^{-1}	Body mass (g)	n
0	4.2 ± 0.1	182.5 ± 12.6	4
7	4.9 ± 1.6	406.0 ± 82.2	3
14	6.4 ± 2.0	678.1 ± 37.3	3
21	6.4 ± 0.7	822.2 ± 90.5	4
28	8.6 ± 1.0	1 362.5 ± 185.3	3
60	15.2 ± 1.2	5 060.0 ± 639.7	3
85	16.6 ± 0.6	6 700.0 ± 318.0	3
190	9.4	4 455	2
290	14.7 ± 2.0	10 766.0 ± 702.0	3

TABLE 4

Water content of Gentoo Penguin chicks

Estimated age (d)	%H_2O Total	%H_2O Muscle	%H_2O organs	%H_2O integument	n
0	75.5 ± 1.4	81.3 ± 1.3	77.7 ± 2.8	77.5 ± 2.8	3
10	78.0	81.9	76.7	72.8	2
20	76.8	80.2	78.2	69.9	1
36	70.1 ± 2.4	74.1 ± 2.9	73.4 ± 2.9	61.2 ± 3.9	3
70	69.1	75.3	76.7	55.4	2
105	64.0 ± 3.7	70.8 ± 1.4	73.0 ± 3.3	40.3 ± 9.1	3

TABLE 5

Energy content (wet mass) of Gentoo Penguin chicks

Estimated age (d)	Energy content ($kJ.g^{-1}$)	Body mass (g)	n
0	4.9 ± 0.3	96 ± 26	3
10	5.3	585	1
20	5.9	1 300	1
36	7.4	2 730 ± 148	3
70	8.7	5 570	2
105	9.7 ± 2.3	4 667 ± 813	3

FIGURE 10

Total (A), lipid (B) and ash-free (C) mass of Gentoo Penguin chicks as a function of age.

FIG. 10a

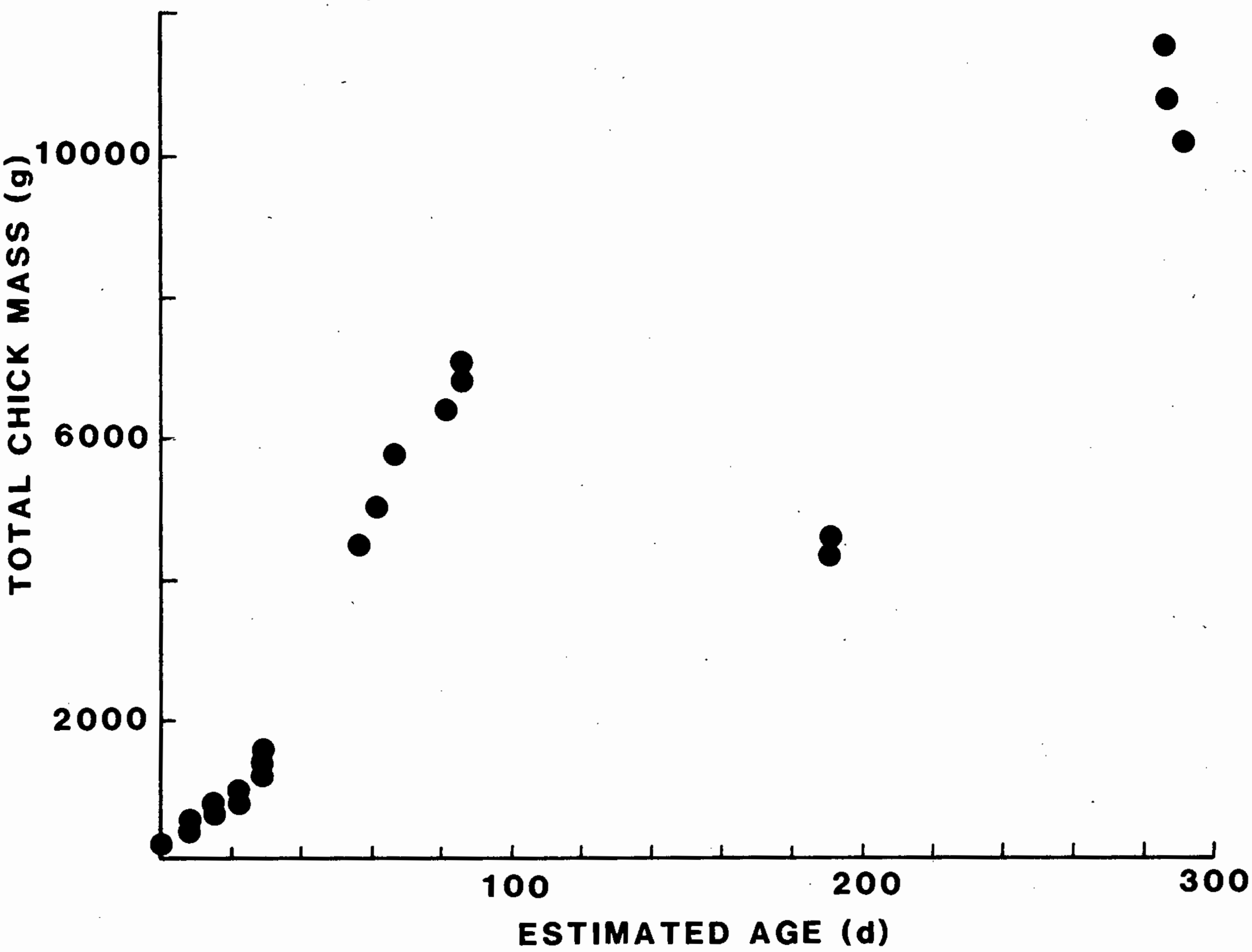

TOTAL CHICK MASS (g)
10000
6000
2000
100
200
300
ESTIMATED AGE (d)

FIG. 10b

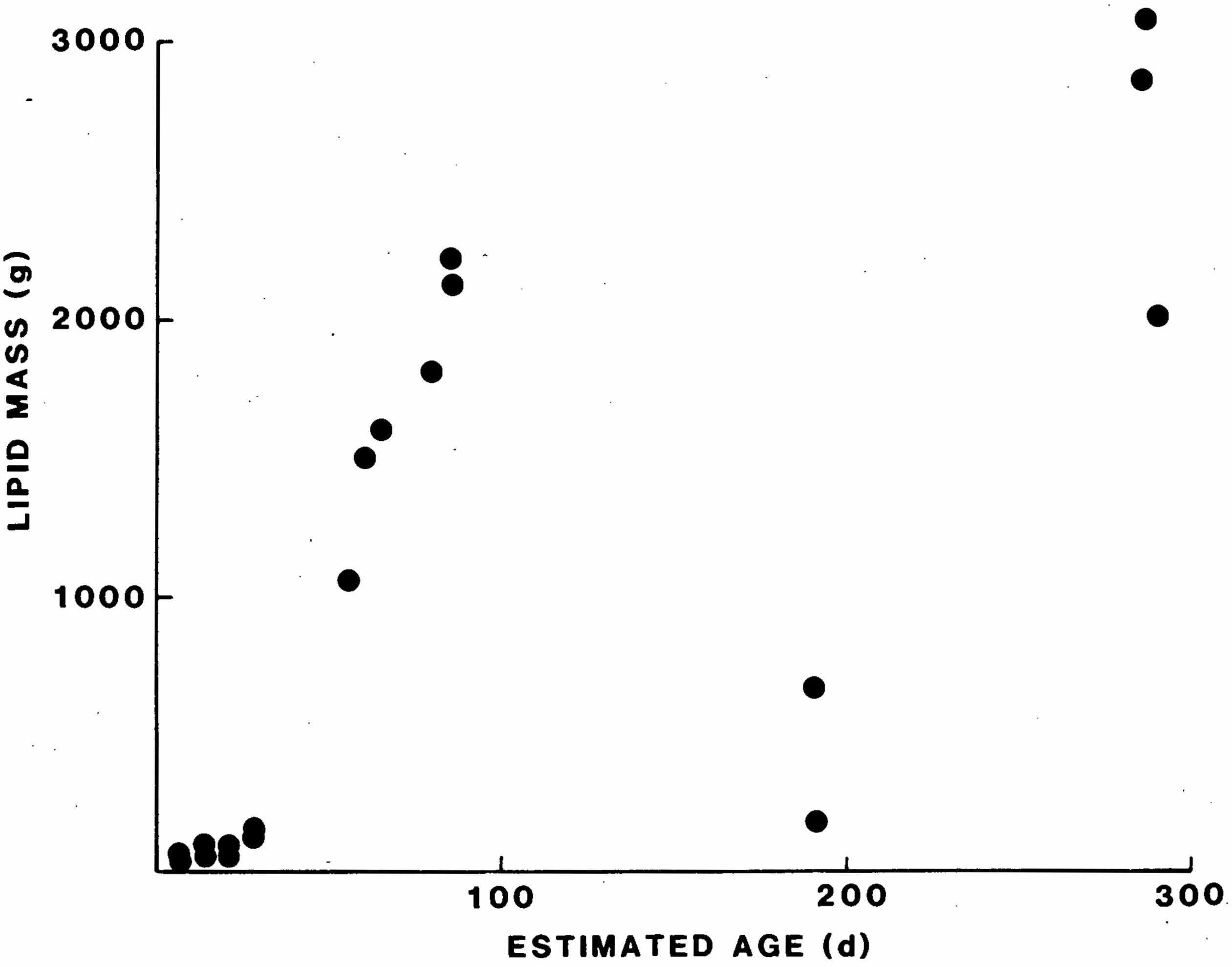
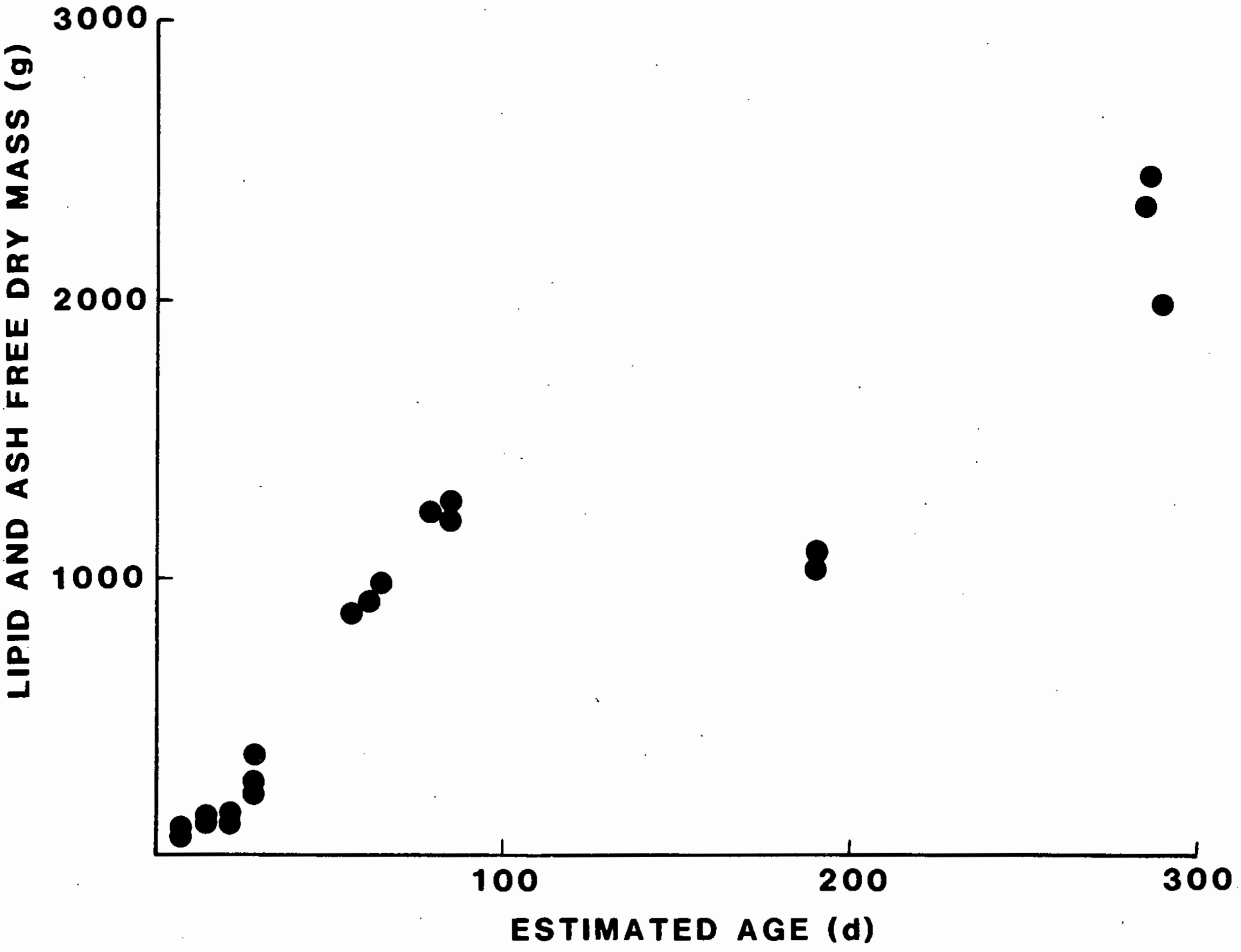


FIG. 10c



LIPID AND ASH FREE DRY MASS (g)
3000
2000
1000
100
200
300
ESTIMATED AGE (d)

starvation comprised largely lipid reserves. The subsequent increase in mass from the winter minimum to fledging was accompanied by renewed, rapid accumulation of lipids. Accumulation of protein (or lipid and ash-free dry mass) occurred at a slower rate during the initial stages of growth. Levels were maintained throughout the winter starvation period. The second growth phase was accompanied by further accumulation of protein. In contrast to King Penguins, Gentoo Penguins accumulated lipid and protein throughout the chick growth period, although rate of accumulation of lipid decreased with approach to independence (Fig. 11).

DISCUSSION

Chick growth:

The pattern of growth of King Penguin chicks at Marion Island is similar to that described for the species at South Georgia (54°55'S, 37°W) (Stonehouse 1960) and Possession Island, Crozet Islands (46°25'S,51°45'E) (Barrat 1976, Barre 1978). Mainly because of the winter hiatus in growth, the total fledging period of King Penguins is just over twice that of the considerably larger Emperor Penguin Aptenodytes forsteri, which however, attains independence at only 60% of adult mass (Croxall 1984). Initial growth of King Penguin chicks is fast with early hatched chicks attaining 90% of adult mass before the winter fast. King Penguins do not have a highly synchronized breeding season. At Marion Island chicks start hatching during the second week in January and continue to do so until April (pers. obs). The sudden decrease in growth rates (Fig. 2a,b,c) of King Penguins that occurs in mid April to early May appears to be largely independent of chick age

FIGURE 11

Total (A), lipid (B), and lipid and ash-free (C) mass of Gentoo Penguin chicks as a function of age.

FIG. 11a

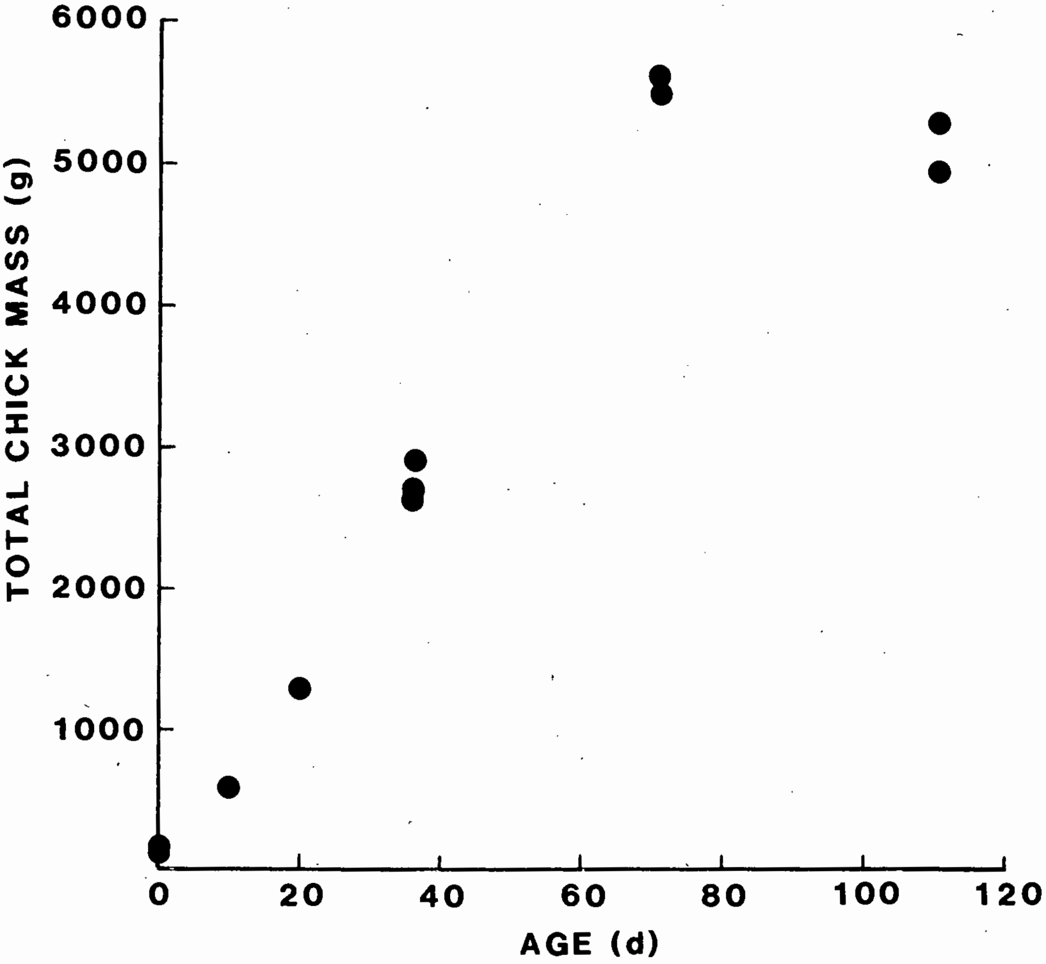

6000
5000
4000
3000
2000
1000
TOTAL CHICK MASS (g)
0
20
40
60
80
100
120
AGE (d)

FIG. 11b

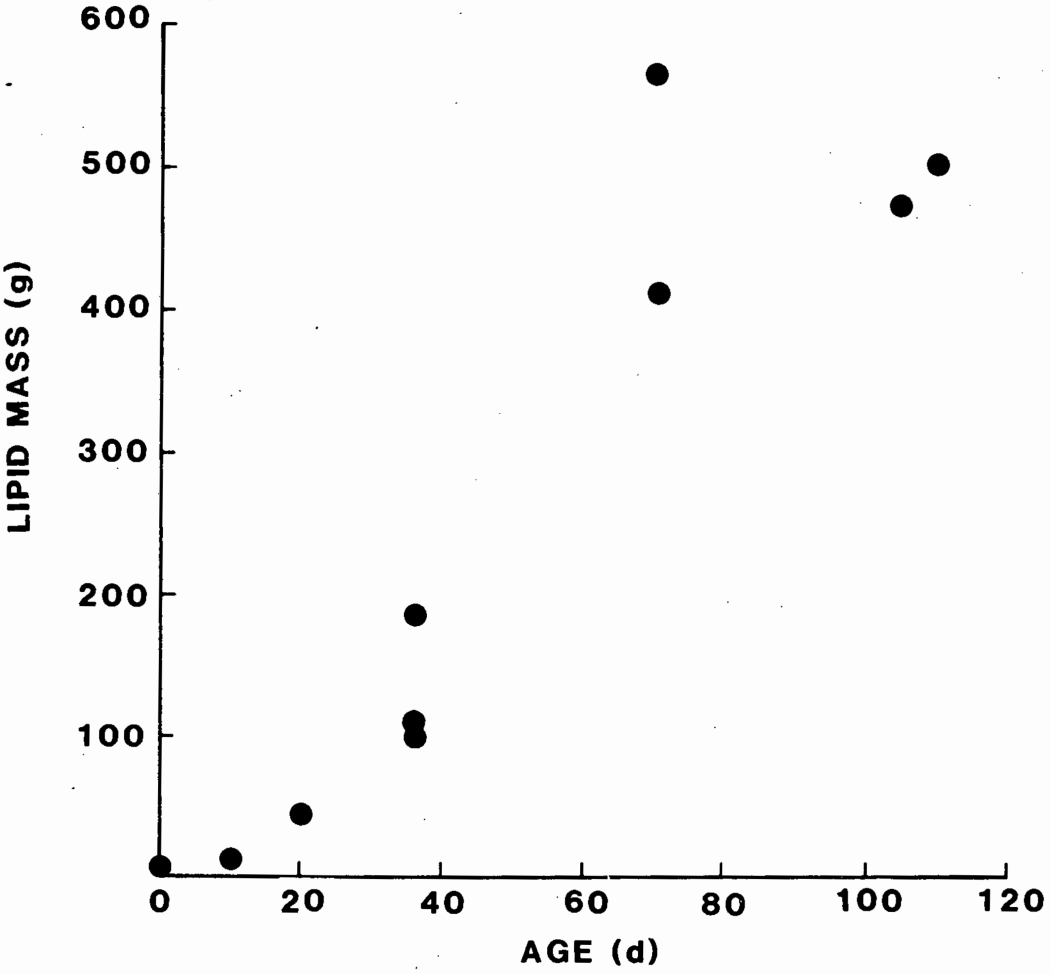
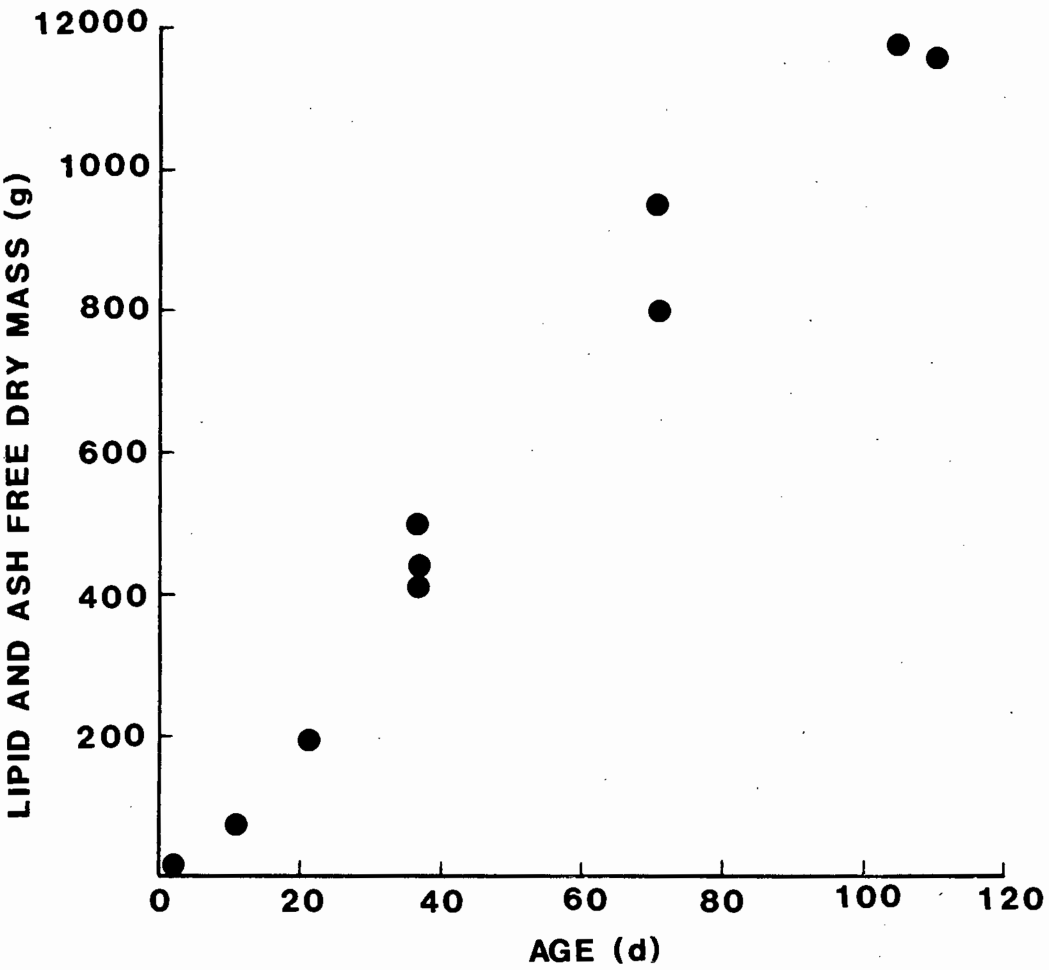


FIG. 11c


12000
1000
800
600
400
200
LIPID AND ASH FREE DRY MASS (g)
0
20
40
60
80
100
120
AGE (d)

and reflects initiation of the winter fast period (Cherel et al. 1987). At the Crozet Islands, at a similar latitude to Marion Island, initiation of the fast also occurs abruptly. The low asymptotic masses, after initial growth, of these late hatched chicks (Fig. 1) and their high mortality are a consequence of the rapid fall off in feeding rates. In September increased growth rates are concomitant with an increase in feeding rate (Adams 1987, Cherel et al. 1987). Timing of these events was similar for the two years in which data were collected (Fig. 2). King Penguin chicks eventually fledge at the beginning of the austral summer at a time of presumed high food availability of myctophid fish (Adams & Klages 1987).

Williams (1980) has previously described the growth of Gentoo Penguin chicks at Marion Island, noting that the chick-rearing period of Gentoo Penguins at Marion Island was considerably longer and growth slower than that of populations farther south (Volkman & Trivelpiece 1980). The faster growth rates and generally lower asymptotic masses of the higher latitude penguins are presumed to be advantageous in the reduced breeding season (Volkman & Trivelpiece 1980).

Development of homeothermy:

King Penguin chicks hatch with almost no down and are unable to regulate body temperature. The ability to thermoregulate develops as a function of down length (Barre 1978). Adjustments of metabolic rates also occurs prior to 28 d, but these are clearly inadequate to meet heat loss that would occur if chicks were unbrooded. Twenty-eight-day old King Penguin chicks are able to adjust metabolic rates in an attempt to maintain body temperatures in ambient temperatures from 25°C down to about 10°C (Fig. 4) (see also Barre 1978). Mean monthly ambient temperatures at Marion Island (Schultz 1971) during this time are 2 - 3°C below the experimental temperatures and unbrooded chicks would incur additional thermoregulatory costs at this age to maintain their body temperature. Although Gentoo Penguin chicks are also poikilothermic at 2 d old, the onset of homeothermy appears more rapid than in King Penguin chicks and by 15 d chicks are able to maintain body temperatures in air at 10°C. The erratic control of body temperatures in individual penguin chicks of similar age has been noted also for several petrel species and may be partly related to the nutritional status of the chicks (Brown & Prys-Jones 1988). In the main, however, the onset of endothermy corresponds to the length of the brooding period. A more detailed study of the development of thermoregulation in Gentoo Penguin chicks at King George Island, Antarctica suggests well developed cold acclimatization (Taylor 1985) in these high latitude birds by 25-27d. Lower critical temperature at this stage, was approximately -5°C (Taylor 1985). Limitations of equipment used here did not allow examination of metabolic response at temperatures below 10°C and it was not possible to determine if Gentoo Penguin chicks at Marion Island had similarily well developed cold acclimatization.

Although energy expenditure of King Penguin chicks expressed on a per bird basis (Fig. 6a) is similar to the pattern of mass through the growth period (Fig. 6b), mass-specific energy expenditure (Fig. 7) indicates changes in the relationship between metabolic rate and body mass during chick growth. The rapid rise in mass-specific energy metabolism from hatching to 14 d and subsequent fall by 55 d (Fig. 7) is similar to the pattern previously described for the species (Barre 1978). Barre (1978) attributed the decrease to growth of down resulting in improved insulation. Similar changes occur in mass - specific metabolic rates of Macaroni and Rockhopper Penguins (Brown 1987) but are not as marked. Brown (1987) suggested this pattern was consistent with the semi - altricial mode of development of penguin chicks and is in constrast to patterns of embryonic metabolism (Chapter 10).

Although there was some indication of a peak in mass - specific metabolic rates of Gentoo Penguin chicks at about 15 d, there was little subsequent change over the remainder of the development period (Fig. 9). Mean metabolic rates never fell below 400 $kJ.kg^{-1}.d^{-1}$. In contrast, Taylor (1985) demonstrated a drop from 531 $kJ.kg^{-1}.d^{-1}$ at 25-27 d to 208.2 $kJ.kg^{-1}.d^{-1}$ at 70-75 d of age. The result for the difference is not clear, but may reflect superior cold acclimatization of the higher latitude chicks.

Lower mass - specific metabolic rates determined from a combination of oxygen consumption and rates of mass loss of King Penguin chicks in winter compared to summer at the Crozet Islands indicated winter cold acclimatization (Barre 1984). No such significant differences between mass-specific metabolic rates calculated from oxygen consumption of resting chicks at Marion Island measured during winter and summer were noted (Table 1). Estimates of energy expenditure based on mass loss intergrate costs over the measurement period and were higher in summer than in winter. Since these summer estimates were made on chicks approaching independence they are likely to include an increased activity component in addition to the cost of maintenance and are not a consequence of cold acclimatization of metabolism. In addition, I may have overestimated such estimates of energy expenditure (see Groscolos 1988). Cherel et al (1987) has demonstrated increased rates of mass loss of King Penguin chicks during the initial stages of longterm fasts that are not directly related to increased rates of energy expenditure.

Body composition:

The decrease in water content of King and Gentoo Penguin chicks from hatching is similar to the pattern described for other penguins (Myrcha & Kaminski 1982, Brown 1987) and occurred for all three body components analysed. The greatest reduction in water content occurred in the integument layer and reflects the low water content of the subcutaneous lipid reserves. The decrease in water content of chicks with age has been ascribed to functional maturation of muscle and other tissues (Ricklefs & White 1981). For King Penguins much of this decrease takes place during the initial growth phase and at the age of 85d water contents are lower and energy density higher than chicks approaching independence (Tables 2 & 3). Values of energy density of King Penguins at or close to independence were similar to the 13 $kJ.g^{-1}$ of Northern Gannets <u>Sula bassana</u> (Montevecchi et al. 1984), but considerably higher than the 5.79 $kJ.g^{-1}$ and 6.53 $kJ.g^{-1}$ for Macaroni and Rockhopper Penguins (recalculated from data in Brown 1987). The differences are accounted for by the generally higher water contents of these two penguin species at fledging.

Energy content of Gentoo Penguins increased from 4.9 kJ.g^{-1} at hatching to 9.1 kJ.g^{-1} at independence, similar to the 9.2 kJ.g^{-1} for Gentoo Penguins at Antarctica (Myrcha & Kaminski 1982). This is lower than that determined for King Penguins in this study and is an indication of the smaller lipid reserves of Gentoo Penguins (see below). The decrease in rate of increase in energy value demonstrated for Gentoo and Chinstrap Pygoscelis antarctica Penguins at King George Island (Myrcha & Kaminski 1982) was not evident in this study but this may merely reflect the smaller sample size.

Large fluctuations in the lipid reserves of King Penguins are evident through growth. The ability of King Penguin chicks to survive long periods of winter fasting is dependent on their ability to accumulate lipid rapidly and subsequently utilize these reserves (Fig. 10b). The small decrease in absolute amounts of protein (Fig. 10c) suggests efficient protein sparing during this winter fast (see Cherel et al. 1987). In this respect, King Penguin chicks are very different from other chicks of pelagic feeding species that accumulate lipid reserves. These reserves are retained throughout the growing period (Ricklefs et al. 1980, Ricklefs & White 1981, Montevecchi et al. 1984, Simons & Whittow 1984) and it is only during the period of mass recession, immediately before independence, that substantial proportions of these reserves maybe utilized.

In contrast to the patterns described for King Penguins (this study) and Macaroni and Rockhopper Penguins (Brown 1987), lipid and lipid-free dry mass of Gentoo Penguin chicks accumulated at approximately the same rate (Fig. 11). The daily feeding schedule of Gentoo Penguins at Marion Island (Adams & Wilson

1987), presumably makes it unneccessary for chicks of this species to accumulate large amounts of lipid.

Energetics of chick growth:

Energy budgets of King and Gentoo Penguins were constructed by combining information on rates of accumulation of lipid and nonlipid dry material and oxygen consumption. Estimates were corrected for cost of biosynthesis according to Ricklefs et al. (1980) (see Table 6). Accumulated energy in body tissues was calculated from rates of lipid and lipid-free accumulation converted to energy equivalents. Maintenance energy requirements were estimated from oxygen consumption measurements corrected for biosynthesis. Such measurements take no account of any additional thermoregulatory component or activity costs. However, it is unlikely that ambient temperatures at Marion Island fall below the thermoneutral zone of Gentoo or King Penguin chicks for extended periods. Mean monthly temperatures at Marion Island ranged from 3.5-8.0^{o}C (Schultz 1971). The lower critical temperature of large King Penguin chicks at the Crozet Islands was -10 ^{o}C in winter increasing to 4.8 ^{o}C in summer (Barre 1984). Potential thermoregulatory costs to King Penguin chicks during winter may be further reduced by the huddling behaviour of this species (Barre 1984). Gentoo Penguin chicks at King George Island, Antarctica have a lower critical temperature of between -4 and -6.5^{o}C at the end of brooding decreasing to between -13^{o}C and -15.5 ^{o}C by 40 d (Taylor 1985). Energy costs of moulting from down to feathers and general activity may, however, represent a significant component of the energy budget prior to independence, representing between 72 % and 107 % of resting metabolism (Table 1, Barre 1984) and total energy costs will be underestimated. However, given the long fledging period and generally inactive nature of penguin chicks during most of the growth period, such costs will be a smaller proportion of the total energy budget. The energy budget of nestling Savannah Sparrows Passerculus sandwichensis calculated, in part, from laboratory measurements of oxygen consumption, underestimated that determined from the doubly labelled water technique by 25 % (Williams & Prints 1986).

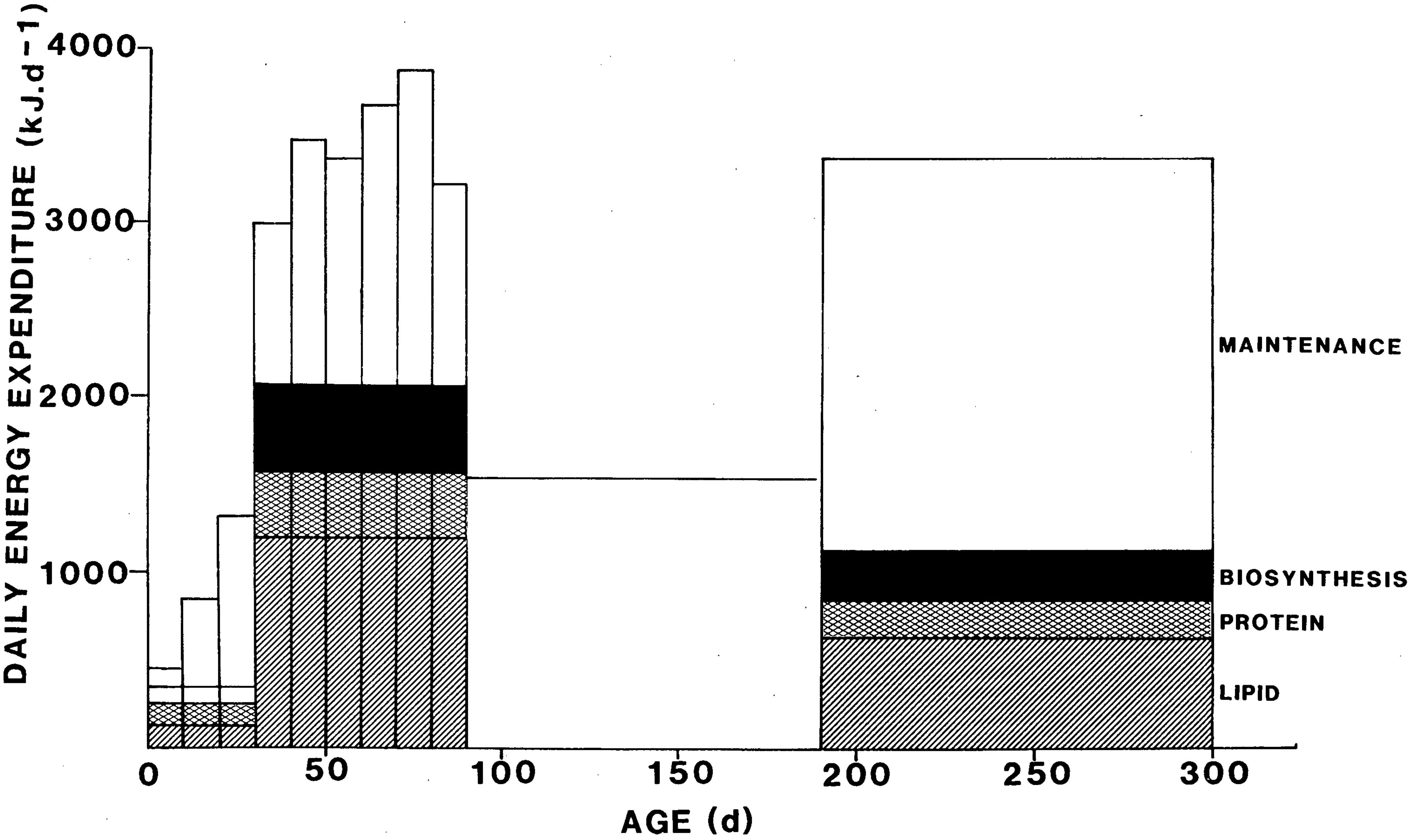
The energy budget of King Penguin chicks is characterized by large changes in the proportional allocation of energy requirements to growth and maintenance (Table 6, Fig. 12). Total energy requirements increased rapidly to a maximum of 3 900 kJ.$^{-1}$ between 70 and 80 d. Growth requirements including lipid accumulation, generally form just over 50% of the total energy requirement. During winter, growth ceased and energy requirements were allocated solely to maintenance with a consequent drop in total energy requirements. Total lipid reserves of King Penguin chicks at 85 d of age, prior to the winter fast, were 1 799 g. Assuming no growth and limited activity and a utilization efficiency of 100%, these reserves could maintain a chick for 46 d. Winter-acclimatization and huddling in creches may lower the metabolic rate of chicks below resting levels and allow extension of the length of the fasting period. Mean feeding frequencies of King Penguin chicks at the Crozet Islands during May to August ranged from one feed every 88.3 d to one feed every 27.9 d (Cherel et al. 1987). This suggests that King Penguin chicks at Marion Island may be fed more frequently than those at the Crozet Islands, although it is possible that birds analyzed for lipid content had yet to reach

TABLE 6

Energy budget of King Penguin chicks

Age interval (d)	1	2	3	4	5	6	7	8	9
0 -10	3.4	5.2	135.1	122.9	258.0	343.1	191	106	449
11-20	3.4	5.2	135.1	122.9	258.0	343.1	572	487	830
21-30	3.4	5.2	135.1	122.9	258.0	343.1	1 131	1 046	1 304
31-40	30.2	15.0	1 200.1	345.6	1 554.7	2 068.0	1 425	912	2 980
41-50	30.2	15.0	1 200.1	354.6	1 554.7	2 068.0	1 903	1 390	3 458
51-60	30.2	15.0	1 200.1	354.6	1 554.7	2 068.0	1 781	1 268	3 336
61-70	30.2	15.0	1 200.1	354.6	1 554.7	2 068.0	2 122	1 609	3 677
71-80	30.2	15.0	1 200.1	354.6	1 554.7	2 068.0	2 313	1 800	3 868
81-90	30.2	15.0	1 200.1	354.6	1 554.7	2 068.0	1 656	1 143	3 211
91-190	-14.3	-4.1					1 538	1 538	1 538
191-300	15.8	9.6	627.8	266.9	854.8	1 137.0	2 526	2 244	3 381

1. Lipid accumulation g.d^{-1}
2. Protein accumulation g.d^{-1}
3. Energy equivalent of lipid accumulation kJ.d^{-1}
4. Energy equivalent of protein accumulation kJ.d^{-1}
5. Energy equivalent of tissue accumulation kJ.d^{-1}
6. Total energy required for growth kJ.d^{-1}
7. Energy equivalent of oxygen consumption kJ.d^{-1}
8. Energy equivalent for maintenance kJ.d^{-1}
9. Total energy growth and maintenance kJ.d^{-1}


DAILY ENERGY EXPENDITURE (kJ.d - 1)
4000
3000
2000
1000
0
50
100
150
200
250
300
AGE (d)
MAINTENANCE
BIOSYNTHESIS
PROTEIN
LIPID

peak pre-fast mass. With the approach to independence, regular feeding was again initiated, growth recommenced and total energy requirements rose sharply. Allocation to growth was, however, proportionally less than that during the first 80 d. There were no data available during the period of mass recession to allocate energy requirements to growth and maintenance.

Energy requirements of Gentoo Penguins increased from 555 $kJ.d^{-1}$ in the first 10 d of age to 1 703 $kJ.g^{-1}$ between 70 and 80 d (Table 7, Fig. 13). With the increase in total energy requirements, the relative proportion allocated to growth decreased to about 40% by 90-100 d (Fig. 13). Linear accumulation of lipid and protein between 0 and 40 d was assumed. Accordingly the proportion of energy requirements allocated to growth during the first 0-10 d may have been underestimated. It is probable that lipid accumulation rate decreased towards the end of growth (Fig. 11). However, there were few data and it was assumed also that accumulation was linear from 40 to 105 d.

The total energy requirements for growth and maintenance of King and Gentoo Penguins were 756 840 kJ and 137 575 kJ, respectively. The mass proportionate energy costs of the King Penguin chicks expressed as a function of mass of fledgling chicks, was 74.9 $kJ.g^{-1}$, approximately double the 30.6 $kJ.g^{-1}$ calculated for Gentoo Penguins and for the other species of naturally reared penguins (Brown 1987). The high cost for King Penguins reflected the long growth period and consequent high maintenance costs combined with two phases of tissue accumulation.

TABLE 7

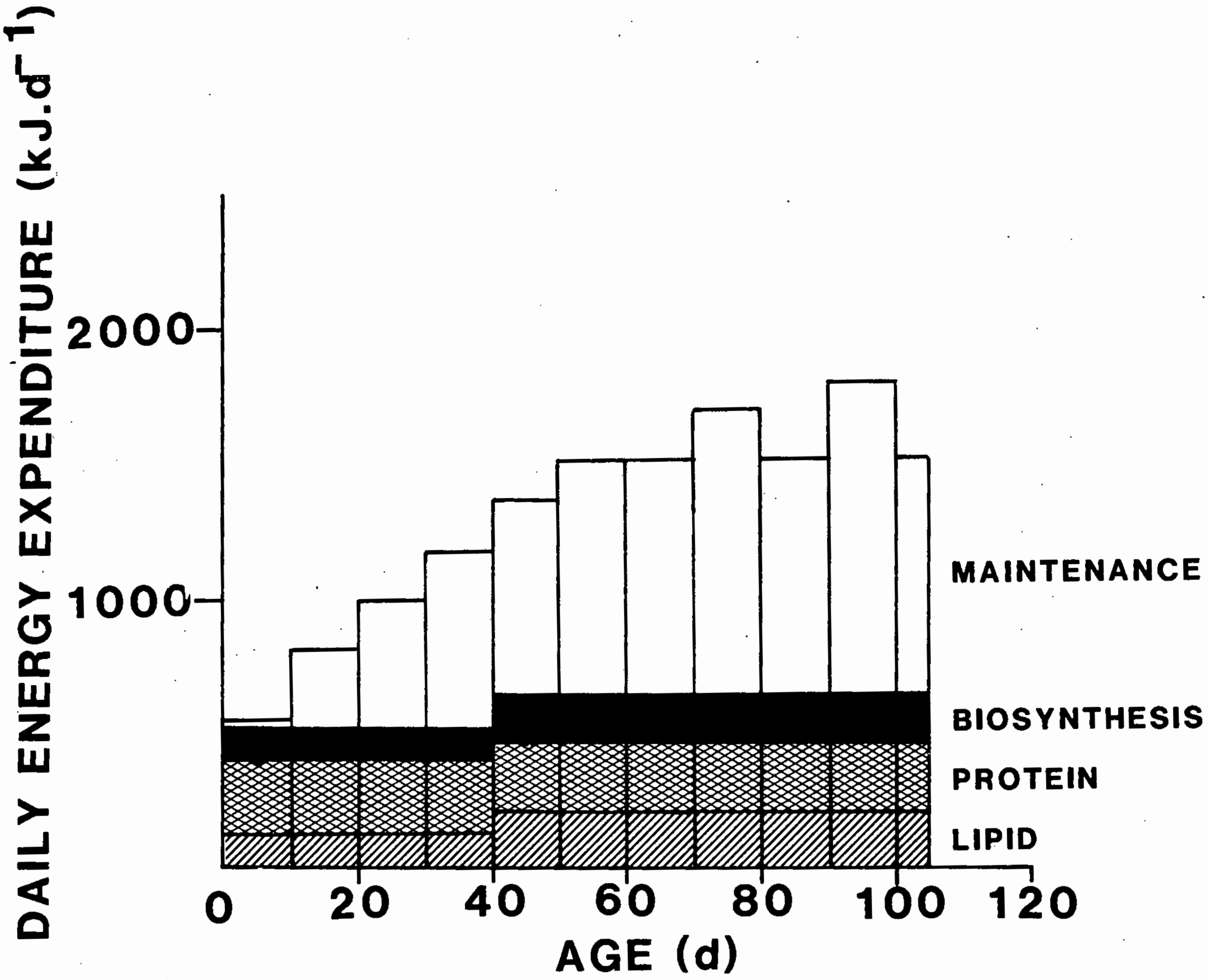
Energy budget of Gentoo Penguin chicks

Age Interval (d)	1	2	3	4	5	6	7	8	9
0 -10	3.6	11.3	143.1	267.1	410.2	545.6	144	9	555
11-20	3.6	11.3	143.1	267.1	410.2	545.6	401	266	812
21-30	3.6	11.3	143.1	267.1	410.2	545.6	589	454	1 000
31-40	3.6	11.3	143.1	267.1	410.2	546.6	771	636	1 182
41-50	5.3	11.3	210.6	267.1	477.7	635.3	886	728	1 363
51-60	5.3	11.3	210.6	267.1	477.1	635.5	1 041	883	1 518
61-70	5.3	11.3	210.6	267.1	477.1	635.5	1 038	880	1 515
71-80	5.3	11.3	210.6	267.1	477.1	635.5	1 226	1 068	1 703
81-90	5.3	11.3	210.6	267.1	477.1	635.5	1 056	898	1 533
91-100	5.3	11.3	210.6	267.1	477.1	635.5	1 333	1 175	1 810
101-105	5.3	11.3	210.6	267.1	477.1	635.5	1 056	898	1 533

Column codes as for Table 7

FIGURE 13

Energy budget of Gentoo Penguin chicks.


DAILY ENERGY EXPENDITURE (kJ.d⁻¹)
2000
1000
0
20
40
60
80
100
120
AGE (d)
MAINTENANCE
BIOSYNTHESIS
PROTEIN
LIPID

Total growth costs of King Penguins are 33% of total energy requirements compared to the 46% for Gentoo Penguins. Allocations to growth of Macaroni and Rockhopper Penguins were 38 % and 28 %, respectively (Brown 1987). Brown (1987) suggested that the relatively greater energy requirement for growth and the smaller requirement for maintenance in Macaroni Penguins to be related to differences in body size. Inclusion of data from this study demonstrates no consistent relationship between proportional allocation of energy to growth and body mass.

Lipid reserves of the inshore feeding species of terns accumulated more slowly than for pelagic foragering terns and peaked at lower levels (Ricklefs & White 1981, Ricklefs 1983). The similarly high allocation of total energy requirements to lipid accumulation by the offshore foraging King Penguins compared to the three other more inshore foraging penguin species at Marion Island, is evident (Table 8). This value is high in spite of the relatively small proportion (33 %) allocated to growth. If we consider the first 50 d of growth before lipid accumulation rates decrease, the proportional allocation energy requirement to lipid accumulation of King Penguins increases still further. In contrast, inshore foraging seabirds have little need to accumulate lipid reserves. Although percent allocation of the energy budget to growth is high in Gentoo Penguins, that specifically allocated to lipid accumulation is low (Table 8). It is of note that the feeding ranges of Macaroni Penguins are intermediate between those of King and Gentoo Penguins (Adams & Brown 1989) and similarly, so is the relative allocation of energy to growth and

TABLE 8

Relative allocation of energy budget to growth and lipid accumulation in four species of penguins

Species	% allocation to growth	% allocation to lipid accumulation	% allocation to lipid accumulation in first 52 days
King	33	26	41
Gentoo	46	19	21
Macaroni*	38	21	27
Rockhopper*	28	14	20

* Data from Brown (1987)

lipid accumulation. The large allocation of energy maintenance costs and consequently low growth and lipid accumulation of Rockhopper Penguin chicks reflect their small size and hence high mass specific metabolism.

Lipid reserves accumulated by seabird chicks provide important energy stores to be utilized when feeding conditions are poor (e.g. Lack 1968, Montevecchi et al. 1984), although it is now questioned that this is their primary function for volant seabirds (Ricklefs et al. 1980, Ricklefs et al. 1985, Taylor & Kanazewski 1989, Schaffner 1990) this appears not to be the case for King Penguins. The cessation of growth associated with the long winter fasting period of King Penguin chicks is unique amongst the developmental patterns of seabird chicks and the acquisition of lipid reserves to sustain chicks through this period is critical for their survival. The differences in allocation of energy for growth and maintenance between King and Gentoo Penguins may be understood largely on this basis.

ACKNOWLEDGEMENTS

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CHAPTER 12

IMPACT OF PENGUINS ON THEIR PREY AT THE PRINCE EDWARD ISLANDS

Four species of penguins, King Aptenodytes patagonicus, Gentoo Pygoscelis papua, Macaroni Eudyptes chrysolophus and Rockhopper E. chrysocome, make up approximately 98 % of the surface breeding seabird biomass at the Prince Edward Islands. I assessed the potential impact of these penguins on marine resources around the islands on an annual and seasonal basis. Total annual consumption was estimated at 880 000 tonnes, of which King Penguins accounted for 74 %, Macaroni Penguins 21 %, Rockhopper Penguins 5 % and Gentoo Penguins, less than 1 %. Pelagic fish, almost entirely myctophids, were the most important prey (70 % of total prey biomass), followed by pelagic crustaceans (18 %) and cephalopods (11 %). Demersal fish and benthic crustaceans accounted for less than 1 % of total consumption being consumed only by Gentoo Penguins. Peak demands of between 2 and 3.3 x 10^6 $kg.d^{-1}$ occurred during October to December when three of the four species of penguin were breeding, including the two demi-populations of King Penguins. Food demand decreased to 1.2 x 10^6 $kg.d^{-1}$ during winter when only King and Gentoo Penguins were resident at the islands. Much of this consumption is presumed to occur within 300 km of the island. Assuming an even distribution of foraging effort by penguins within their respective foraging ranges, rates of food transferred to penguins in November ranged from 4.1 x 10^{-3} $g.m^{-2}.d^{-1}$ for Macaroni Penguins to 1.24 x 10^{-2} $g.m^{-2}.d^{-1}$ for King Penguins. In mid July, transfer rates to King and Gentoo Penguins were 3.9 x 10^{-3} $g.m^{-2}.d^{-1}$ and 6.7 x 10^{-3} $g.m^{-2}.d^{-1}$, respectively. In contrast to waters south of the Antarctic Polar Front, where Antarctic Krill Euphausia superba forms the basis of the food web, the importance of pelagic myctophid fish to penguin populations at Prince Edward

Island is clear. In the absence of information from research trawling or commercial fisheries, the information provided here represents the best knowledge currently available on the relative abundance of the prey resources and their potential production in the area.

INTRODUCTION

Concentrations of breeding seabirds, constrained by the need to return regularly to feed young, may have a significant impact on marine resources, especially at a local scale. Studies in two Northern Hemisphere marine ecosystems have suggested that seabirds may consume between 22 and 29 % (Wiens & Scott 1975, Furness 1978) of estimated annual pelagic fish production. Estimates of the impact of Southern Ocean terrestrially breeding marine predators are available for the suite of predators at South Georgia (Croxall & Prince 1982, Croxall et al. 1984) the Scotia Sea area as a whole (Croxall et al. 1985) where Antarctic Krill _Euphausia superba_ is the most important prey, and on pelagic volant seabirds in the African sector of the Southern Ocean (Abrams 1985), and over the Argentine shelf and near the South Orkney Islands (Hunt 1985). These predator impact models have generally underlined the importance of Antarctic Krill in these high latitude marine food webs and also have suggested that provisional acoustic surveys for Antarctic Krill around South Georgia have underestimated krill stocks in the area (Croxall et al. 1984). However, in the Southern Indian Ocean, at least, fish may be as important a prey of avian predators as pelagic crustaceans (Adams & Klages 1987, Adams & Brown 1989, Brown & Klages 1987, Hindell 1988).

The Prince Edward Islands have a seabird assemblage of some 27 breeding species and an estimated population at Marion Island of perhaps six million seabirds (Cooper & Berruti 1989). The four species of penguins, King Aptenodytes patagonicus, Gentoo Pygoscelis papua, Macaroni Eudyptes chrysolophus and Rockhopper E. chrysocome account for 98 % of the biomass of surface - nesting birds. Brown (1989) noted that although total food consumption of Macaroni and Rockhopper Penguins amounted to some 165 000 tonnes during the seven-month breeding and moulting seasons, King Penguins were probably the single most important avian consumer of marine resources in the seas surrounding the Prince Edward Islands.

I present here estimates of the daily food consumption of the King Penguin and Gentoo Penguin populations at the Prince Edward Islands, using a similar approach to that of Croxall et al. (1984). Along with Rockhopper and Macaroni Penguins, these two species complete the penguin community at the Prince Edward Islands. Estimates of the combined consumption of all four species are computed. I have restricted estimates of food consumption to penguins because, except for Wandering Albatrosses Diomedea exulans, insuffecent data exist to undertake similar analyses for the other members of the seabird assemblage at the Prince Edward Islands.

METHODS

The model developed here is a modified version of that presented by Croxall et al. (1984). Information on the sizes and activities of the non-breeding populations is sparse (see also

Croxall et al. 1984 and Brown 1989) and the model computes the impact of breeding populations only.

Breeding cycle and population sizes:
King Penguins at South Georgia may breed successfully twice in three years (Stonehouse 1960), but only once every two years at the Crozet Islands (Barrat 1976). Recent data collected at Marion Island suggest a similar cycle to that reported for the Crozet Islands (FitzPatrick Institute unpubl. data). The total moult and breeding cycle of King Penguins at Marion Island extends over some 14 months. Most birds commence their prenuptial moult in October with chicks eventually attaining independence in December the following year. In winter, the number of adults at colonies decreases dramatically and chicks are fed infrequently (Cherel et al. 1987). I assumed there were two demi - populations of King Penguins present during September to February, but at different stages of breeding.

Gentoo Penguins at Prince Edward Islands have a five - month breeding cycle with egg laying commencing in the austral winter. Failed breeders will relay, but breeding success is low (Williams 1980). The whole population is assumed to be resident at the islands throughout the year. The breeding and moult cycle of Macaroni and Rockhopper Penguins extends over six - seven months. The cycles are similar for the two species although Macaroni Penguins commence breeding three to four weeks earlier than do Rockhopper Penguins (Brown 1989).

Energy costs (see below) were allocated to eight defined activities: pre-laying attendance at the nest, laying fast, incubating, brooding and guarding chicks, at - sea foraging for chicks, chick growth, at - sea foraging for self, and moulting. During winter (June to August), when King Penguins chicks ceased growth (Chapter 11), I assumed breeding adults were only foraging for themselves, but remained within 300 km of the islands. Although egg laying by King Penguins at Marion Island was spread over four months (pers. obs.) and Gentoo Penguins will relay (Williams 1980), the model assumed the activities of breeding birds were synchronized and that eggs were not replaced (see Croxall et al. 1984). Recently fledged chicks and adults were assumed to feed in the vicinity of the islands for a week before and after the breeding and moulting season. Failed breeders were assumed to remain at sea in the vicinity of the islands, only departing at the end of the breeding and moulting cycle.

Population sizes of all four penguin species breeding at Prince Edward Islands were from Watkins (1987), Cooper & Berruti (1989) and unpublished records of the FitzPatrick Institute. Figures for King and Gentoo Penguins were based on earlier counts presented in Siegfried et al. (1978) and Adams & Wilson (1987), respectively. Estimates of population size of King Penguins are more than a decade old and may now be in error. Recorded increases in the numbers of adults breeding at small colonies, (FitzPatrick Institute unpubl. data) suggest that the breeding population of King Penguins at Marion Island may have increased over the past decade.

Egg loss and chick mortality from laying to independence were obtained from Williams (1980) and from unpublished data (FitzPatrick Institute). Breeding success of Macaroni and Rockhopper Penguins at Marion Island has been recorded annually from 1981/82 and 1983/84, respectively (FitzPatrick Institute unpubl. data). Data for King and Gentoo Penguins were considerably more fragmentary. In the absence of data, the model assumed egg loss and chick loss decay linearly from laying to hatching and hatching to independence, respectively (Appendix 1).

Diet:

The diets of all four species of penguin breeding at Marion Island have been described quantitatively (Adams & Klages 1987, 1989, Brown & Klages 1987). In contrast to the situation at high latitudes (Croxall & Lishman 1987), there were considerable seasonal and annual changes in the diets of penguins at Marion Island. Dietary data were considered for 1984/85 only (Appendix 2), but monthly changes in diet were incorporated into the model. The presence of King and Gentoo Penguins throughout the year allowed sampling for 12 months. Samples from King Penguins were obtained from adults returning to feed chicks or from large chicks immediately after feeding. Gentoo Penguins attend chicks from July to December. During the remainder of the year I sampled non-breeding adults. Diet sampling of Macaroni and Rockhopper Penguins was restricted to the chick - rearing period only. I assumed the proportion of different prey prior to chick rearing was similar to that in the diet of the first month sampled. Similarly, diet subsequent to chick rearing was assumed to be the same as the last month sampled. Diet composition was specified as 1) pelagic fish, 2) demersal fish, 3) pelagic crustaceans, 4) benthic crustaceans, and 5) cephalopods. Relative proportions were extracted from Adams & Brown (1989). Prey types comprising less than 1 % of the diet by mass were ignored.

Energy content of prey:

Information on the energy content of the main prey species taken by penguins at the Prince Edward Islands is meagre. I used values for energy content of prey (wet mass) given by Brown (1987a) for crustaceans (4.68 $kJ.g^{-1}$) and cephalopods (3.25 $kJ.g^{-1}$). These values are close to the 4.35 and 3.57 $kJ.g^{-1}$ given by Croxall et al. (1984). Energy content of fish was taken as 3.97 $kJ.g^{-1}$ wet mass (Clarke & Prince 1980). I did not account for any seasonal changes in energy content, although such changes have been demonstrated for Antarctic Krill (Clarke 1984). Measured assimilation efficiencies of King and Gentoo Penguins fed on fish averaged 75.5 %. King Penguins assimilated squid with a mean efficiency of 73 % (Adams 1984, unpubl. data). Assimilation efficiency of Gentoo Penguins fed Antarctic Krill _Euphausia superba_ was 71.7 % (N.J. Adams unpubl. data). I assumed Macaroni and Rockhopper Penguins assimilated the various prey types at similar efficiencies.

Energy costs:

Daily energy costs of various activities (see above) were determined largely from empirical measurements presented in preceding chapters and from the literature (Appendix 3).

Energy requirements of male adult King, Macaroni and Rockhopper Penguins attending breeding sites (prelaying attendance) were assumed to be equivalent to Average Daily Metabolic Rates (ADMR) of resting penguins (Chapter 7, Brown 1984). Average energy cost of egg formation was estimated to be 7.2 % of Basal Metabolic Rate BMR (Chapter 10) and was added to ADMR to determine energy cost of prelaying attendance of female penguins. During this period male and female Gentoo Penguins continue to go to sea regularly and energy costs were taken from Davis et al. (1989). Similarly, during incubation, both Gentoo and King Penguin partners alternate shifts and regularly go to sea (pers. obs., Chapter 9). Integrated energy costs over the incubation period of King Penguins were determined from measurements of oxygen consumption of birds incubating in the colony (Chapter 9) and at-sea costs (see below). Corrections were made for differences in activity budgets between male and female penguins. Energy costs of Gentoo Penguins during incubation were taken from Davis et. al. (1989). Macaroni and Rockhopper penguins divide incubation duties into two shifts only (Brown 1989). Energy expenditure at the nest was taken from rates of oxygen consumption measured over 24 h (Brown 1984). King and Gentoo Penguins alternate brood and guard shifts in a similar way to their incubation duties (Stonehouse 1960, pers. obs.). Energy costs to King Penguins were determined by combining measurements of ADMR (Chapter 7) and at-sea costs. Energy costs to Gentoo Penguins were again taken from Davis et al. (1989). Brooding and guarding duties of Eudyptes penguins were undertaken exclusively by males. Energy costs to Macaroni Penguins were from Davis et al. (1989). Costs to Rockhopper Penguins were calculated from this on a mass-specific basis. Measurements of at - sea energy costs have been measured for King Penguins (Kooyman et al. 1982), Macaroni and Gentoo Penguins (Davis et al. 1989). Costs to Rockhopper Penguins were calculated from mass-specific equivalents measured for Macaroni Penguins. Measurements of the energy cost of feeding chicks of Gentoo and Macaroni Penguins account for species - specific activity budgets during chick rearing. King Penguins are assumed to spend negligible time ashore while feeding large chicks and costs are taken directly from Kooyman et al. (1982). Male and female penguins are assumed to divide foraging effort equally once they begin feeding large chicks. Measurements of at - sea costs of King Penguins were measured using tritiated water whereas those of Gentoo and Macaroni Penguins were based on dilution rates of doubly labelled water. Comparison of results of studies on these latter two species using both techniques (Davis et al. 1983, 1989) suggested that the tritiated water technique may underestimate at - sea costs. Results for King Penguins (Kooyman et al. 1982) await validation. Energy costs of failed breeders were assumed to be equivalent to at - sea energy expenditure of penguins foraging for themselves. Total food requirements during chick rearing were calculated from the addition of food required to meet at - sea energy costs and that required to meet the cost of growth and maintenance of surviving chicks (Chapter 11) corrected for assimilation efficiency. Moult costs were determined as average daily energy expenditure during moult measured from rates of oxygen consumption (Brown 1985, Chapter 7). To account partly for accumulation of fat reserves prior to moult, I assumed a feeding rate during moult commensurate with these energy costs. Normally during moult, penguins are restricted to land and no feeding takes place. Masses of male and female penguins vary through the breeding season as a consequence of fast and periods of food accumulation. Energy expenditures during different breeding activities take into account these changes in body mass.

Foraging range:

The potential mean maximum foraging ranges of all four species of penguins during chick rearing at Marion Island have been estimated using time-speed meters (Adams 1987, Adams & Wilson 1987, Brown 1987a). Measurements of foraging ranges of Macaroni and Rockhopper Penguins were for adults feeding large and small chicks, respectively.

Gentoo Penguins at the Prince Edward Islands are inshore foragers (Adams & Wilson 1987). During early chick - rearing, Rockhopper Penguins feed at intermediate distances from the islands, but may feed farther offshore during late chick - rearing (Brown 1987b). King and Macaroni Penguins are assumed to be offshore feeders throughout chick rearing (Adams 1987, Brown 1987b). I have no data on the distribution of foraging effort of penguins within these zones, other than circumstantial evidence which suggests foraging zones are to some degree mutually exclusive (Adams & Brown 1989). To calculate prey transfer rates, I assume the foraging effort of penguins was distributed uniformly within their exclusive foraging zones.

Total food requirements of the penguin community at the Prince Edward Islands were estimated by summing food requirements for all four species. I may have overestimated the energy consumption of the breeding populations in the area. At - sea energy requirements of failed breeders are likely to be less than those of birds attending chicks. In addition, I have assumed failed breeders remain feeding in the vicinity of the island. This may not be true, particularly for King Penguins, since during winter, reduced chick feeding rates suggest limited availability of prey in waters surrounding the islands. However, I have not considered the impact that the pre - population has on marine resources. Sub - Antarctic penguins begin breeding at between two and five years of age, depending on the species

(Croxall 1984). Immature penguins return to breeding sites to moult and are presumably in the surrounding waters feeding for some time before and after moult. Pre - breeders of some penguin species may comprise up to 40 % of the breeding penguin population (Croxall & Prince 1982) and, therefore, will have a substantial impact. Other errors are likely to arise because maximum foraging ranges quoted here probably overestimate actual foraging ranges. In addition, it is unlikely that penguins distribute their foraging effort uniformly around the islands. For instance, Gentoo Penguins may feed largely in shallow waters that lie between Marion and Prince Edward Islands (Adams & Wilson 1987).

RESULTS AND DISCUSSION

I did not conduct any formal sensitivity tests to determine confidence limits around food consumption estimates. On the basis of Monte Carlo simulations on a model developed to determine the food consumption of the seabird community at Foula, Shetland Islands, Furness (1978) indicated that changes in input values of existence metabolism equations, population size, flight or swimming activity levels and their energy costs had a large effect on output values. Because actual measurements of the energy costs of many activities are now available, greatest errors are likely to arise from use of varying population size inputs. The importance of obtaining better estimates of breeding and especially non - breeding populations has been stressed (Croxall et al. 1984, Brown 1989).

Total food consumption:

Total annual food consumption of the breeding penguin community at the Prince Edward Islands (Marion and Prince Edward) was close to 800 000 tonnes. Pelagic fish (mainly myctophidae) account for 70% of the total consumption, pelagic crustaceans 18% and cephalopods 11%. Benthic crustaceans and demersal fish were consumed almost exclusively by the small Gentoo Penguin population and accounted for considerably less than 1% of total consumption (Table 1). Much of the pelagic fish was consumed by King Penguins which took 74% of total consumption. Macaroni Penguins accounted for 21% of consumption and Rockhopper Penguins, 5%.

The importance of pelagic fish as prey for penguins at the Prince Edward Islands was in marked contrast to the situation south of the Antarctic Polar Front where energy flux to top predators is primarily through krill, principally _Euphausia superba_ (Croxall et al. 1984, 1985). The absence of significant populations of fish in diets of seabirds at South Georgia has been ascribed to the dominance of small fish species in the area and the absence of obligate pelagic shoaling species (Croxall et al. 1985). Sub-Antarctic seabird assemblages breeding at localities north of the Antarctic Polar Front may be operating generally as higher order predators than is the case for krill dominated food webs farther south. This may partly explain the lower avian biomass in the area compared to more southerly sites. Diet studies of the large marine mammal populations that breed at the Prince Edward Islands have yet to be completed, but it is probable that they also have a considerable impact on local fish resources. Such studies merit attention.

TABLE 1

Estimated annual food requirements of the penguin community at the Prince Edward Islands

		Food consumption (tonnes per annum)					
Species	Population size	Pelagic fish	Demersal fish	Benthic crustaceans	Pelagic crustaceans	Cephalopods	Total
Macaroni Penguin	422 084	30 176	0	0	120 833	34 769	185 778
Rockhopper Penguin	172 652	3 111	0	0	41 368	933	45 412
Gentoo Penguin	1 543	96	674	397	310	28	1 505
King Penguin	220 230	583 630	0	0	0	64 523	648 153
Total	815 509	617 013	674	397	162 511	100 253	880 847

Seasonal food consumption: Predators

During October to April, three of the four penguin species breed or moult, and peak food demand at the Prince Edward Islands occurred (Fig 1). Food consumption rates over this period ranged from about 1.9 to 3.3 x 10^6 kg.d^{-1} decreasing to 1.1 x 10^6 kg.d^{-1} during winter.

Daily consumption rates compared here are considerably higher than those presented by Adams & Brown (1989) which were calculated from predictive equations relating body mass to feeding rate (Nagy 1987). However, the pattern of penguin population consumption rates decreasing with decreasing average foraging range of the respective species, was consistent (see Adams & Brown 1989).

Consumption remained high for individual species during chick rearing when adults were collecting food for their chicks and failed breeders were assumed to be in the vicinity of the islands (Fig. 2a-d). Peak demands coincided with premoult foraging excursions (see Chapter 8) and the presence of recently fledged chicks feeding in the vicinity of the islands and were a consequence of the model assuming synchrony of activity. Such peaks are unlikely to be as high in the natural situation. Periods of reduced consumption occurred when the population or a proportion of the population was confined to land, for example, during incubation or moult.

Patterns of food consumption of the two congeneric species, the Macaroni and Rockhopper Penguins, were similar, reflecting their similar activity patterns (Fig. 2). Consumption rates were highest during February and March immediately after chicks attained independence (Fig. 2a & b). Values for food

FIGURE 1

Seasonal variation in the daily food consumption of all four species of penguins at the Prince Edward Islands

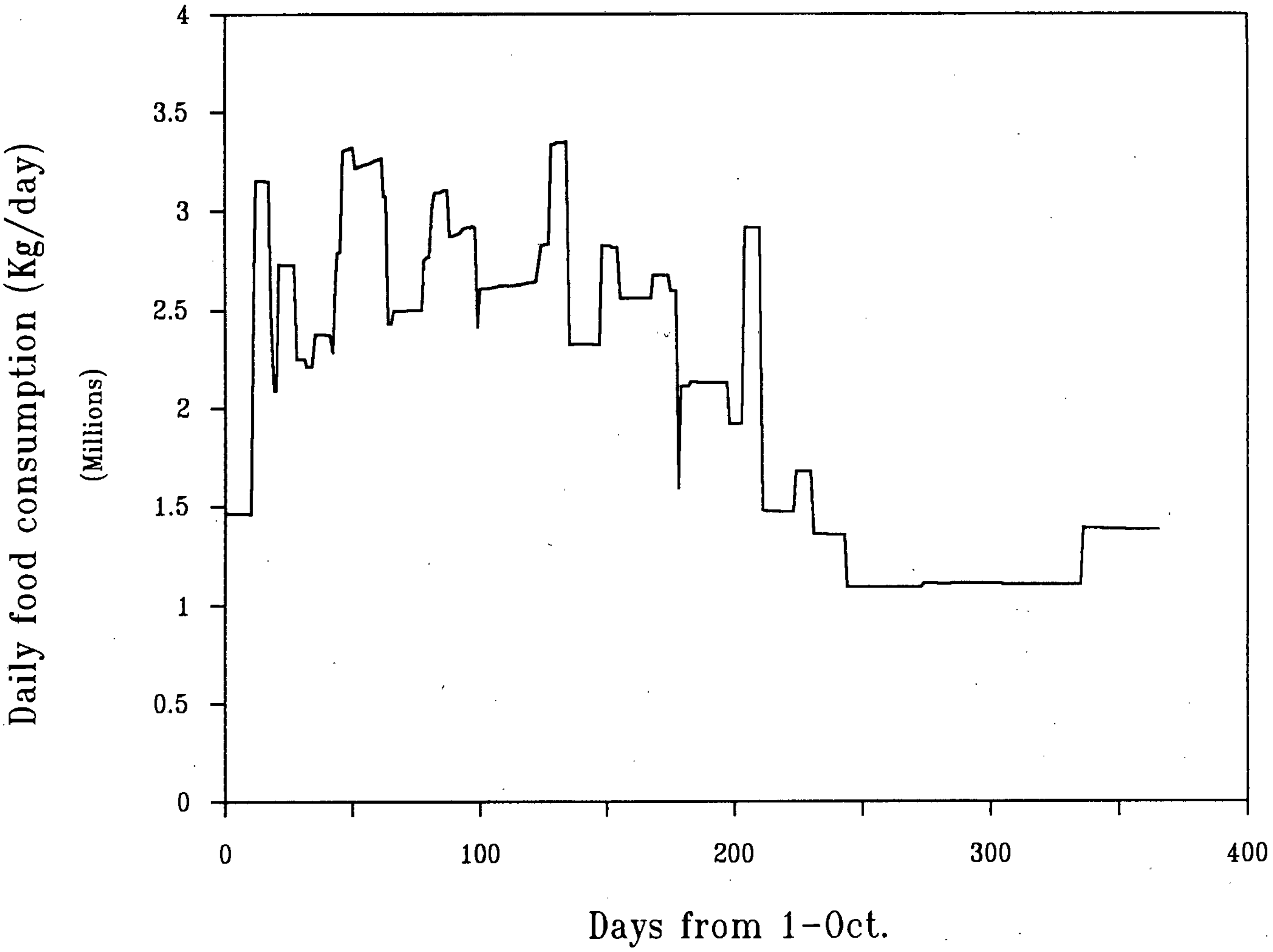
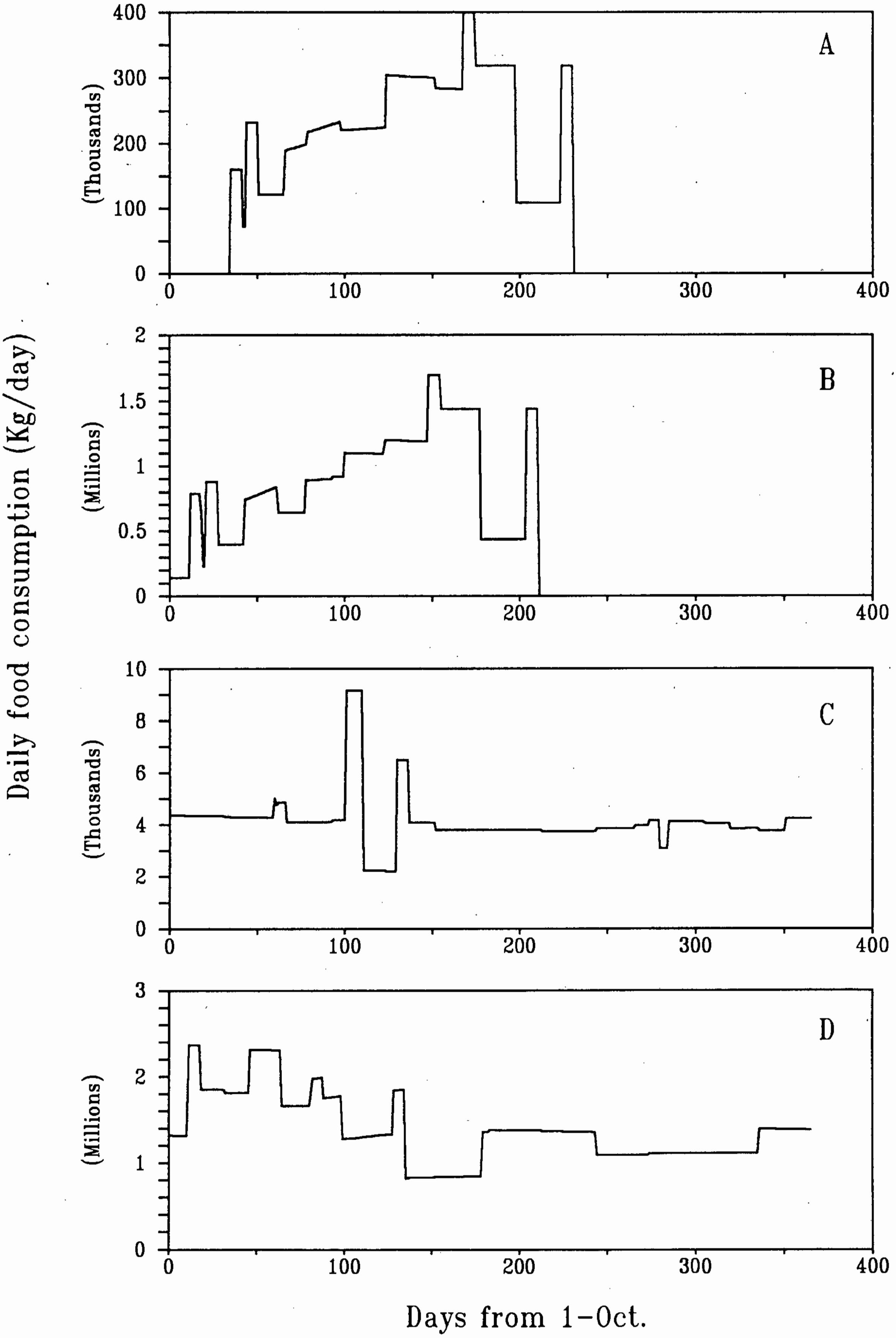

Daily food consumption (Kg/day)
(Millions)
4
3.5
3
2.5
2
1.5
1
0.5
0
0
100
200
300
400
Days from 1-Oct.

FIGURE 2

Seasonal variation in the daily food consumption of Rockhopper (A), Macaroni (B), Gentoo (C) and King (D) Penguins at the Prince Edward Islands.


A
B
C
D
Daily food consumption (Kg/day)
(Thousands)
(Millions)
(Thousands)
(Millions)
400
300
200
100
0
2
1.5
1
0.5
0
10
8
6
4
2
0
3
2
1
0
0
100
200
300
400
Days from 1-Oct.

consumption of Macaroni and Rockhopper Penguins from this study were 49 % and 11 % higher, respectively, than those presented by Brown (1989) for the same site. The differences were partly accounted for by the higher at-sea costs used here. Previous estimates based on dilution of tritiated water (Davis et al. 1983) and used by Brown (1989) may have underestimated actual costs. The closer coincidence of consumption figures for Rockhopper Penguin in the two studies were due to the use of revised population estimates. Croxall & Lishman (1987) and Trivelpiece et al. (1987) have stressed the importance of differences in timing of breeding of sympatric congeneric species pairs as a mechanism to ensure staggering of food demands by chicks. However, the relatively long chick - rearing period is nearly three times the length of the differences in the timing of breeding. This coupled with the observation that energy requirements of chicks accounted for only between 9 % and 4 % of the total energy budget of <u>Eudyptes</u> penguins (Brown 1989), such an argument is unconvincing. Energy constraints on individual breeding penguins may be most severe during brooding and guarding when chicks require frequent feeds, but potential foraging time is halved by the necessity of one adult having to remain at the nest site. It may be that the interspecific staggering of brooding is the more important factor in trophic segregation.

Total food consumption of the Gentoo Penguin population was small compared to the other three penguin species. Consumption rates of Gentoo Penguins were highest during the beginning of January when adults were at sea immediately prior to moult (Fig. 2c). In contrast to their activities during the remainder of the year, Gentoo Penguins spend this period at sea continuously and may feed away from the immediate vicinity of the islands. For the remainder of the year, there was little variation in food consumption rates which vary between 3 000 and 5 000 kg.d^{-1}.

The high food demands of King Penguins can be ascribed to their large size and high consequent energy demands and long breeding season. King Penguins had their greatest impact on marine resources during the first part of summer when the breeding activities of the two demi-populations overlapped (Fig. 2). Consumption was lowest during January and February when adults were incubating, and during July and August when it was assumed that adults remain in the vicinity of the islands, but do not attempt to feed chicks.

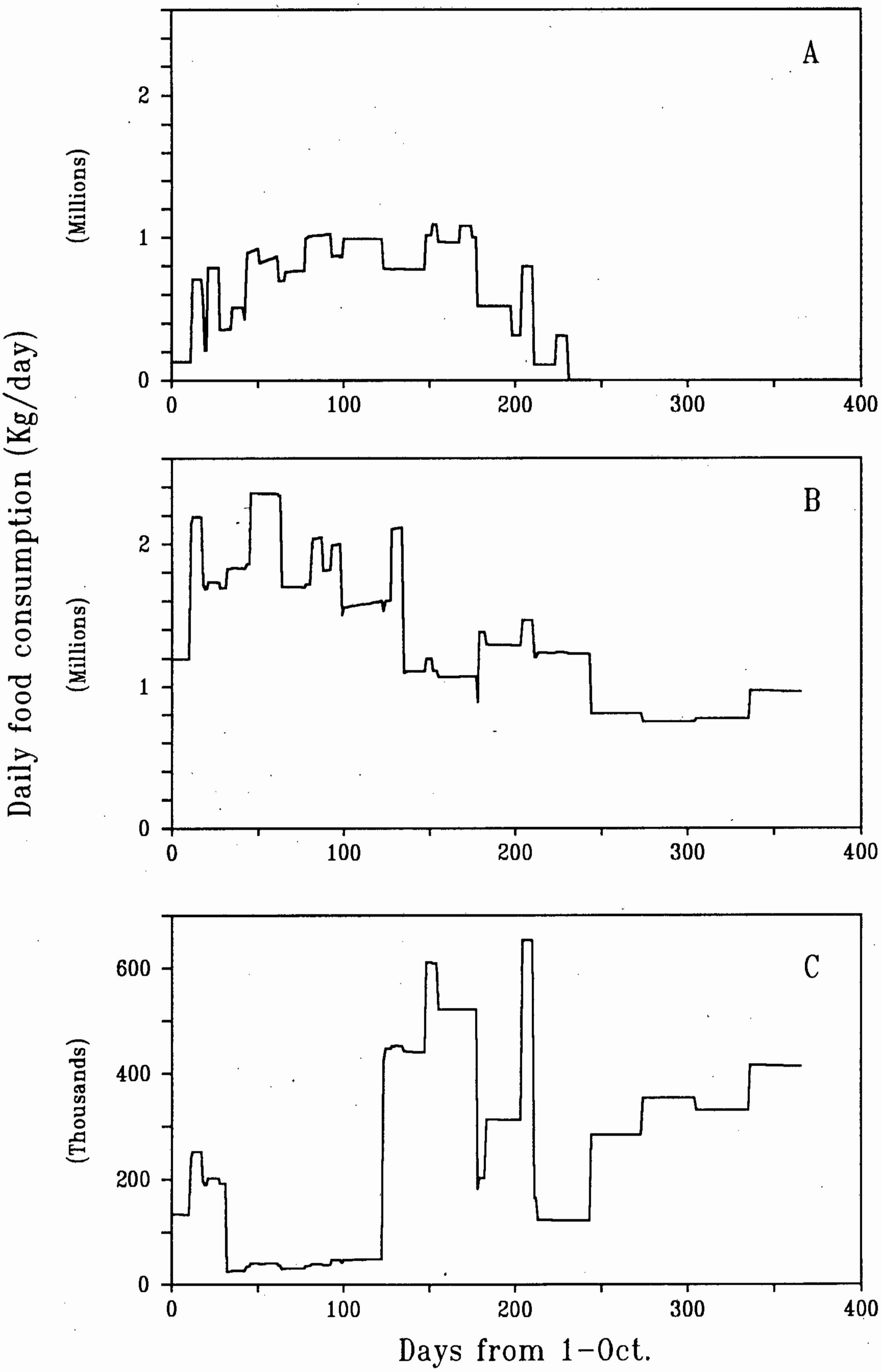
Seasonal food consumption: Prey

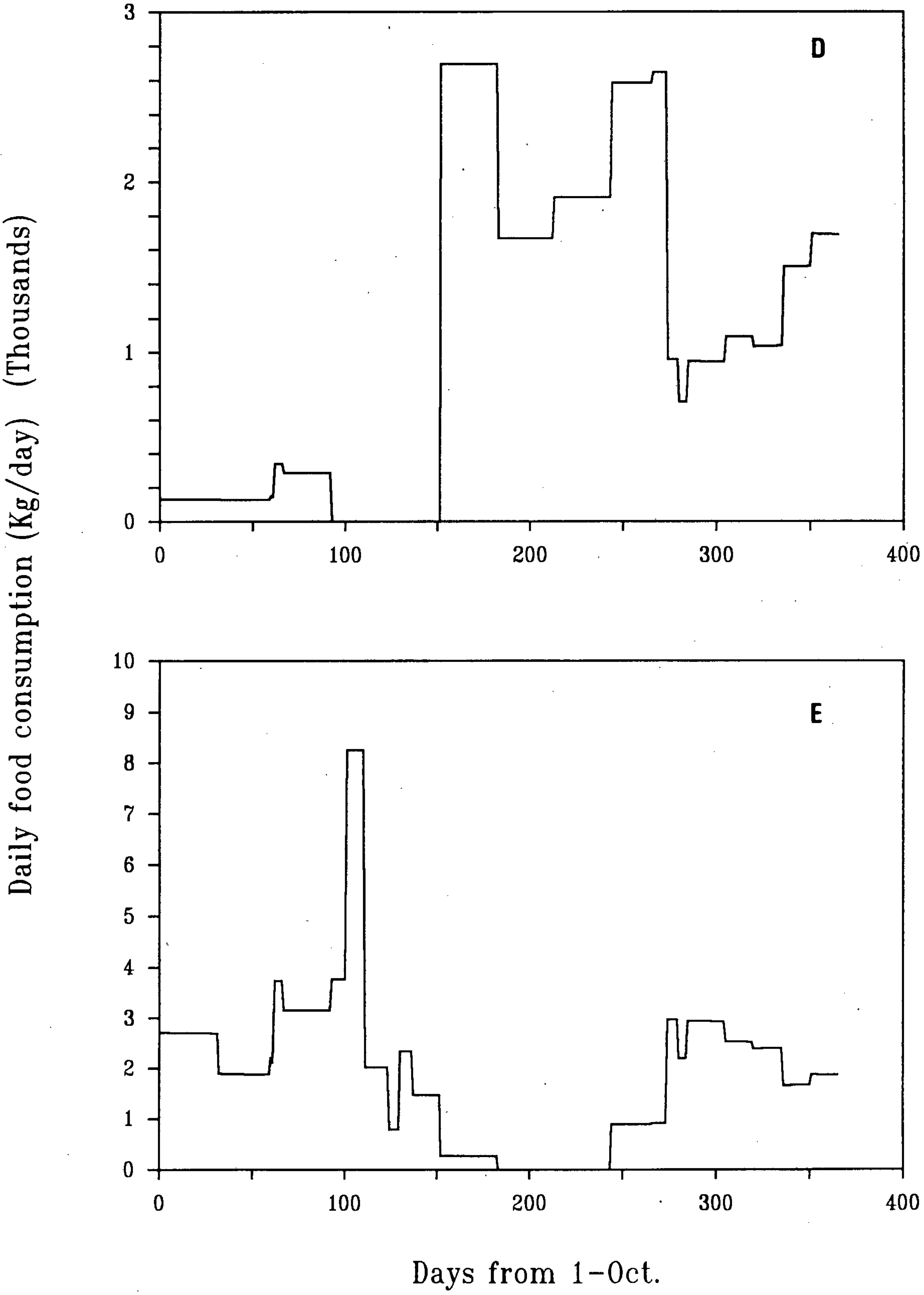
Daily consumption rates of benthic crustaceans, mainly the shrimp <u>Nauticaris</u> <u>marionis</u>, ranged from zero to 2 600 kg.d^{-1} during March when it accounted for over 70 % of the diet of Gentoo Penguins (Fig. 3a). Consumption rates of the other dietary component restricted to Gentoo Penguins, demersal fish and mainly juvenile Antarctic Cod (Nototheniidae), peaked at 8 000 kg.d^{-1} for 10 d coinciding with the end of the premoult foraging excursion when I assumed Gentoo Penguins were at sea continuously (Fig. 3b). During March to May consumption fell to zero. Consumption rates during the remainder of the year were close to 2 000 kg.d^{-1}.

Impact on pelagic crustaceans was confined mainly to summer, largely reflecting the presence of their major consumers, Macaroni and Rockhopper Penguins (Fig 3c). Consumption rates

FIGURE 3

Seasonal variation in daily food consumption of pelagic crustaceans (A), pelagic fish (B), cephalopods (C), benthic crustaceans (D) and demersal fish (E) by penguins at the Prince Edward Islands.


Daily food consumption (Kg/day)
A
(Millions)
2
1
0
0
100
200
300
400
B
(Millions)
2
1
0
0
100
200
300
400
C
(Thousands)
600
400
200
0
0
100
200
300
400
Days from 1-Oct.


D
E
0
1
2
3
4
5
6
7
8
9
10
0
100
200
300
400
Daily food consumption (Kg/day) (Thousands)
Days from 1-Oct.

averaged around 7.0 x 10^5 kg.d^{-1} and peaked at 1.1 x 10^6 kg.d^{-1}. In 1984/85, the most important crustaceans consumed were the euphausiids Euphausia vallentini and Thyssanoessa vicina (Brown & Klages 1987).

Daily consumption of pelagic fish, largely myctophids, averaged 1.7 x 10^6 kg.d^{-1}. In late summer the consumption by Macaroni Penguins increased, but rates were still less than during early summer when two demi-populations of King Penguins were present (Fig. 3d).

Highest consumption rates of cephalopods occurred during February and March when the proportion of cephalopods in the diet of Macaroni Penguins increased sharply. Intake consisted almost entirely of small Kondakovia longimana. Consumption of this species was sustained through winter by King Penguins at around 3.5 x 10^6 kg.d^{-1} before falling to less than 1.0 x 10^6 kg.d^{-1}, from November to January.

Prey transfer rates to populations of the different penguin species in November ranged from 9.6 x 10^{-3}g.m^{-2}.d^{-1} for King Penguins feeding offshore to 5.69 x 10^{-2}g.m^{-2}.d^{-1} for Rockhopper Penguins feeding closer to shore (Table 2). These values were considerably less than the 2.5 g.m^{-2}.d^{-1} calculated for the very large Macaroni Penguin population at South Georgia, although the difference partly reflected the different assumptions regarding distribution of foraging effort. By mid - July only King and Gentoo Penguins remain at the Prince Edward Islands and a far more even distribution of foraging effort is suggested with maximum transfer rates to King Penguins of 3.9 x 10^{-3}.g.m^{-2}.d^{-1} and 6.6 x 10^{-3} g.m^{-2}.d^{-1} to Gentoo Penguins.

TABLE 2

Food transfer rates to penguins at the Prince Edward Islands assuming mutually exclusive foraging ranges

Species	Foraging range km	Daily consumption Nov (Day 36) $g.d^{-1} \times 10^{6}$	Daily consumption Nov (Day 36) $g.m^{-2}.d^{-1} \times 10^{-3}$	Daily consumption July (Day 288) $g.d^{-1} \times 10^{6}$	Daily consumption July (Day 288) $g.m^{-2}.d^{-1} \times 10^{-3}$
King Penguin	300	1755	9.5	1104	3.9
Macaroni Penguin	178	397	4.1	-	-
Rockhopper Penguin	33	160	56.9		
Gentoo Penguin	14	4	7.0	4	6.7

Diets of penguins at breeding sites south of the Antarctic Polar Front show little seasonal or interannual variation (Croxall & Lishman 1987). This is in marked contrast to the situation at Marion Island (Adams & Klages 1987, 1989, Brown & Klages 1987). In an important departure from earlier models I have attempted to account for seasonal variations in diet. However, I have not addressed the problem of year to year variation in diet composition and consumption rates (see Brown, Klages & Adams in press). Large changes in the annual food consumption of seabirds have occurred in the Benguela and Humboldt upwelling regions (Duffy & Siegfried 1987). Large fluctuations in breeding success of particularly krill - eating seabirds at South Georgia (Croxall et al. 1988) and Macaroni Penguins at Marion Island (FitzPatrick Institute unpubl. data) suggested similar year to year variability in population energy consumption rates in higher latitude waters.

Brown (1989) noted that primary production in the vicinity of the Prince Edward Islands is sufficient to support at least the populations of Macaroni and Rockhopper Penguins. However, there are other substantial populations of marine predators at the islands. In addition, a large proportion of primary production in marine ecosystems is known to sink or be taken up by microzooplankton and thus appears to be unavailable to higher order consumers (Miller et al. 1985). In fact, as Brown (1989) pointed out, offshore penguins appear to rely to a large extent on the importation of prey from outside their foraging ranges while breeding. Based on prey - transfer rates alone, the region around the Prince Edward Islands appears considerably less productive than do South Georgia waters where the seabird populations are sustained by very large populations of Antarctic Krill.

In the absence of any systematic research or commercial trawling in the region, there are no independent estimates of the abundance of the main prey species of penguins at the Prince Edward Islands. Consequently, it is impossible to evaluate the significance of the level of consumptions calculated in this chapter in terms of total prey populations. In fact, the data presented represent the best estimates available for the relative abundance of marine resources in the area. Predator independent assessments of prey populations in the vicinity of the Prince Edward Islands remain the challenge for the future.

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APPENDIX 1

Estimated population figures of penguins during various stages of breeding at the Prince Edward Islands

Species	Population at laying (pairs)	Population at hatching (pairs)	Population at fledging (pairs)
King	220 230	140 947	101 482
Gentoo	1 543	846	570
Macaroni	422 084	198 379	150 768
Rockhopper	172 652	122 583	88 259

APPENDIX 2

Monthly prey species composition by percent mass of penguins at the Prince Edward Islands

Month	Pelagic fish % mass	Demersal fish % mass	Benthic crustaceans % mass	Pelagic crustaceans % mass	Cephalopods % mass
King Penguin					
September	90	0	0	0	10
August	70	0	0	0	30
July	68	0	0	0	32
June	74	0	0	0	26
May	91	0	0	0	91
April	88	0	0	0	12
March	96	0	0	0	4
February	99	0	0	0	1
January	99	0	0	0	1
December	99	0	0	0	1
November	99	0	0	0	1
October	90	0	0	0	10
Gentoo Penguin					
September	0	44	40	16	0
August	2	62	27	9	0
July	1	71	23	4	1
June	0	23	67	8	2
May	1	0	51	48	0
April	14	0	44	42	0
March	7	7	71	15	0
February	10	36	0	43	11
January	7	90	0	2	0
December	2	77	7	13	1
November	23	44	3	30	0
October	9	62	3	25	1
Macaroni Penguin					
April	18	0	0	48	34
March	18	0	0	48	34
February	18	0	0	48	34
January	26	0	0	71	3
December	8	0	0	90	2
November	8	0	0	90	2
October	8	0	0	90	2
Rockhopper Penguin					
May	2	0	0	98	0
April	2	0	0	98	0
March	2	0	0	98	0
February	24	0	0	67	9
January	4	0	0	95	1
December	4	0	0	95	1
November	4	0	0	95	1

APPENDIX 3

Energy expenditure and duration of defined activities of penguins at the Prince Edward Islands. Values for males and females are given separately where relevant

Activity	King		Gentoo				Macaroni				Rockhopper			
	Energy kJ.d^{-1}	Duration d	Energy kJ.d^{-1}		Duration d		Energy kJ.$^{-1}$		Duration d		Energy kJ.d^{-1}		Duration d	
			F	M	F	M	F	M	F	M	F	M	F	M
Moult	3 605	57	2 180	2 180	19	19	1 519	1 519	26	26	1 056	1 506	26	26
At sea	7 009	141	8 902	8 902	10	17	5 032	5 032	61	62	3 081	3 081	63	57
Prelay	2 632	18	4 208	4 121	14	19	1 296	1 816	15	24	943	1 404	15	24
Incubate	4 781	55	4 121	4 121	35	35	753	1 109	19	17	570	895	13	19
Guard	4 820	42	3 736	3 736	31	31	-	1 707	-	22	-	1 159	-	26
At sea (Chick)	7 009	176	4 066	4 066	251	244	3 513	4 370	70	48	2 227	2 729	70	44
Chick growth	3 471	176	655	655	75	75	715	544	70	48	581	424	70	44
Lay	-	-	2 036	-	5	-	-	-	-	-	-	-	-	-

APPENDIX 1

EFFECT OF MEAL AND PREY SIZES ON STOMACH EVACUATION RATES OF KING PENGUINS _APTENODYTES_ _PATAGONICUS_

INTRODUCTION

Many seabirds feed dependent young by regurgitating prey accumulated in their stomachs. Quantitative analysis of such seabird diets have been based largely on examination of stomach contents of adults returning to feed chicks at terrestrial breeding sites. The potential biases of such an approach, due to differential digestion of the main prey classes (fish, cephalopods and crustaceans) have been investigated (e.g. Wilson et al. 1985, Jackson & Ryan 1986, Gales 1987, Jackson & Cooper 1988). I investigate here the influence of meal size and prey size on stomach evacuation rates of King Penguins (Aptenodytes patagonicus). Previously, comparisons between digestion rates and stomach evacuation times had not considered these effects. Foraging trips of King Penguins feeding large chicks at sub-Antarctic Marion Island, are on average eight days long (Adams 1987). These trips are the most extended of any sub-Antarctic seabird (Croxall 1984) and the potential for large biases may be high.

MATERIALS AND METHODS

Adult King Penguins at a colony at Marion Island (46°52'S, 37°51'E) were captured, stomach flushed (Wilson 1984) to ensure the stomach was empty, and then confined to wooden crates for the duration of the experiments. To obviate the effects of stomach flushing, birds were fasted for at least 24 h before commencement of experiments.

Mesopelagic myctophid fish are the major component of the diet of King Penguins at Marion Island (Adams & Klages 1987).

Supplies of these fish were not available and I used three species (see below) of pelagic shoaling fish caught in temperate waters off the coast of South Africa. Fish were frozen after capture and subsequently thawed before being fed to King Penguins.

Meal size and stomach evacuation rate:

Nine birds were fed similarly-sized pilchards Sardinops ocellatus (mean total length: 206.2 ± 10.9 mm) in a total of 21 meals split into portions that averaged 540 g, 938 g or 1 402 g, representing 4.1 %, 7.1 % and 10.6 % of average body mass, respectively (13.1 kg). Individual birds were fed at least twice but were fasted for 24 h between feeds. For each experimental run involving nine birds, I attempted to stomach flush two birds at intervals of approximately 3 h, 7 h, 14 h and 26 h for each meal size. Because there were limited supplies of fish, this was not always possible. Recovered material was drained, excess water removed by placing on absorbant paper towelling and then weighed.

Prey size and stomach evacuation rate:

Four birds were fed approximately a 500 g meal of anchovy *Engraulis japonicus* (mean total length: 128.1   5.2 mm, mean mass: 11.5   1.7 g) and four birds were fed light fish *Maurolicus muelleri* (mean total length: 47.4 ± 3.9 mm, mean mass: 0.7 ± 0.2 g). The average length of natural prey consumed by King Penguins at Marion Island is 49.8 mm (calculated from data in Adams & Klages 1987), similar to the 42.0 mm of light fish but considerably smaller than anchovy (128.0 mm). After 7 h birds were stomach flushed repeatedly (Wilson 1984, Gales 1987) until only clear water was regurgitated. Food recovered was drained and weighed. Because meals fed to individual penguins were of different sizes, comparisons of evacuation times were based on recovered mass relative to mass of the original meal.

RESULTS

Arcsine transformed fractional digestion by mass was plotted against time from ingestion and linear regression performed on data for each meal size (Fig. 1). Due to limited data I was not able to estimate the length of time required to empty stomachs. Accordingly, I estimated the time required to pass 50 % of the meal through the stomach for each meal size from Fig. 1. The increase in evacuation time with meal size is readily apparent. For meals of 522 g, 938 g, and 1402 g time taken to evacuate 50 % of the meal was estimated at 5.9 h, 8.4 h, 14.1 h respectively.

After 7 h only 15 % of a meal of 535 g of light fish remained in the stomach compared to 58 % of a meal of larger anchovy (Table 1). The differences were significant (Mann Whitney U-test, $U_{0.05(1)4,4} = 15$, $P < 0.05$). However, the rate of digestion of a meal of the largest fish, pilchard, was intermediate between the above two meals; 39.5 % of the original meal being retained. The small sample size did not allow statistical comparisons.

DISCUSSION

Although, Gales (1987) has validated the use of stomach flushing for obtaining the stomach contents of penguins,

FIGURE 1

Digestion rates of fish meals of differing sizes fed to King Penguins. Arcsine transformed fractional digestion is indicated: for 522 g meal; for 938 g meal and for 1 402 g meal. Regression equations are $y = 4.1x - 20.5$ ($r = 0.96$, $P < 0.02$), $y = 1.7x - 29.7$ ($r = 0.92$, $P < 0.002$) and $y = 1.8x - 20.1$ ($r = 0.73$, $0.2 > P > 0.1$) for 522 g, 938 g and 1 402 g meals respectively. Data points reflecting complete digestion were not used in determination of regression equations.

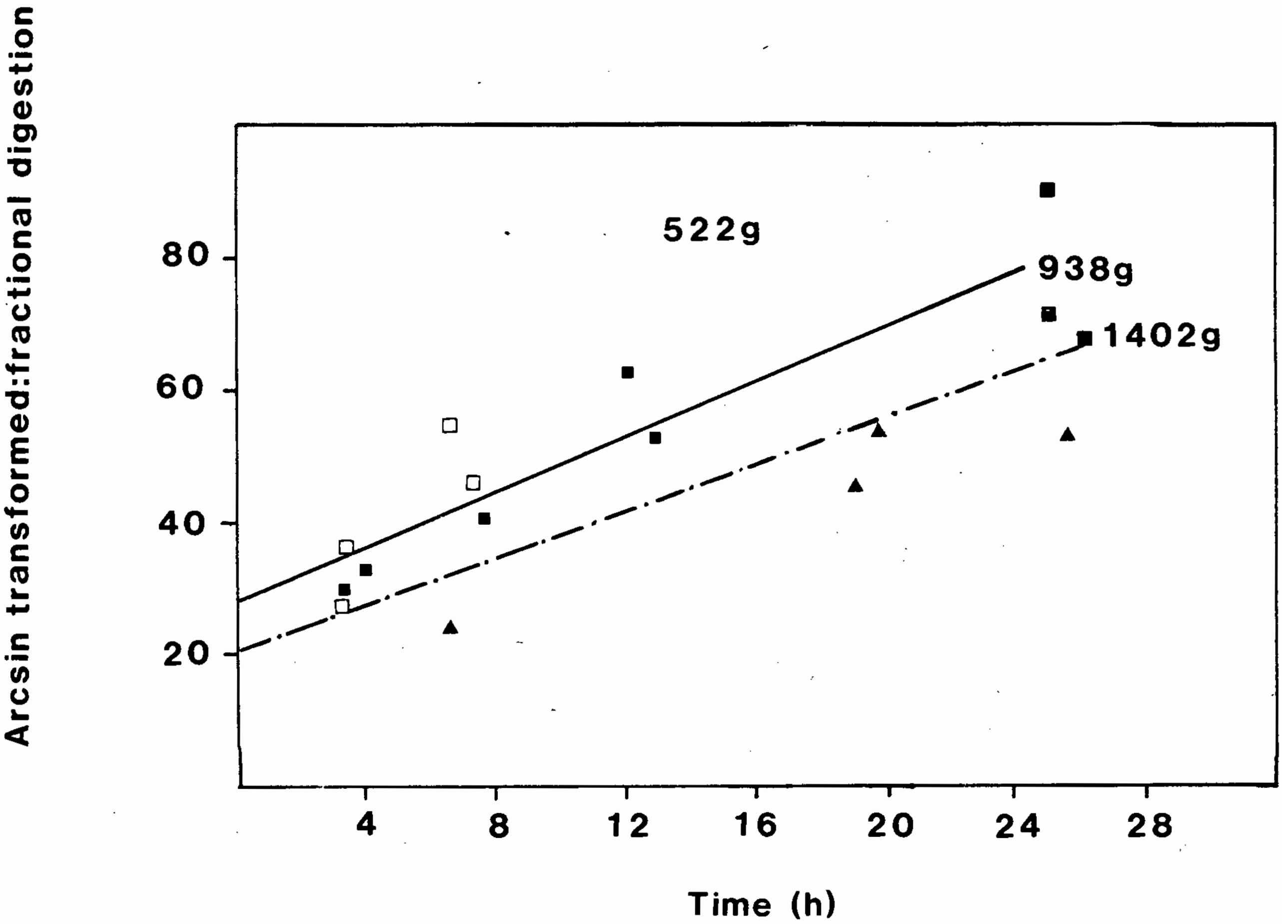
Arcsin transformed:fractional digestion
80
60
40
20
4
8
12
16
20
24
28
Time (h)
522g
938g
1402g

TABLE 1

Mass and proportion of fish digested by King Penguins 7 hours after ingestion

	n	Mass of initial feed g	Mass recovered g	Amount digested %
Pilchard	2	516	204	61
Anchovy	4	535	310	42
		± 12	± 29	± 6
Light fish	4	501	76	85
		± 14	± 9	± 2

several potential sampling biases have been identified. Retrieval rate decreases as digestion progresses and the number of flushes required to empty the stomach increases with meal size (Gales 1987). I did not note the number of flushes I performed on each individual. However, flushing was repeated until clean water was obtained and it is likely that most, if not all, undigested material was recovered. No comprehensive validation of the technique has been completed for the King Penguin (but see Hindell 1988). However, no effect on recovery rate of ingested meals of penguins varying in body mass from 1 kg to 5.8 kg was evident (Gales 1987). I assumed the technique is just as efficient with King Penguins as with smaller penguins. Mass of ingested food may increase due to absorption of water during stomach flushing (Jackson & Ryan 1986, Wilson et al. 1985). This effect is small, particularly for fish (Wilson et al. 1985) and I ignored this potential error.

In contrast to King Penguins, there are no obvious differences in evacuation rates between Jackass Penguins Spheniscus demersus fed different sized meals (Wilson et al. 1985). However, these meals were relatively small (1.7 % and 3.5 % of body mass) and the effect of meal size on evacuation rate increases with increased meal size (Fig. 1).

King Penguins digest small fish at a faster rate than they do larger fish. With increased size the pattern is less clear and bears further investigation with larger sample sizes. Differences in the tissue structure of prey of different classes are undoubtedly important in causing differences in evacuation rate of individual prey items (Jackson & Ryan 1986, Jackson & Cooper 1988). However, for similarly structured tissue (in this case pelagic or epipelagic teleost fish) digestion rate is presumably related to surface area of food exposed to enzyme and chemical attack. The larger surface area to volume ratio of small prey items presumably results in their faster digestion in comparison to larger items. In addition, small meals are probably restricted to the pyloric region of the stomach. The potential biases in analyses of stomach contents of adults returning to feed chicks with both large and small prey are evident.

In order to maximize resident time of food in stomachs of adult King Penguins, so that food can be delivered to chicks after long foraging trips, both meal size and prey item size should be relatively large. The recovery of over 60% of an original meal of 1 402 g from the stomach of an experimental bird 26 h after ingestion indicates a retention time considerably longer than the maximum of 12-16 h recorded for Whitechinned Petrels Procellaria aequinoctialis (Jackson & Ryan 1986), Jackass Penguins (Wilson et al. 1985) and Little Penguins Eudyptula minor (Gales 1988). Average natural meal size fed to large King Penguin chicks, determined from regular weighings, was 1 650 g (maximum size: 2 190 g) (Adams & Klages 1987) considerably heavier than the maximum experimental meal size. These larger meals may well have longer resident times.

It is pertinent to note that in seabirds it is the largest birds, with a high full stomach volume to surface area ratio, which have the most extended foraging trips (e.g. King Penguin and Wandering Albatross Diomedea exulans at Marion Island). Gales (1987) has noted a decrease in stomach evacuation rate with increasing penguin size; an effect that may be related to the above.

I may have underestimated stomach evacuation time of naturally foraging birds. Bigg and Fawcett (1985) noted that activity in seals increased variability in digestion and passage rates. Muscular activity associated with birds returning over long distances to feed chicks may reduce evacuation rate. In addition, fresh fish may be digested at a slower rate than thawed fish (Jackson et al. 1987). Birds may feed continuously over the foraging period. The presence of food in the intestine may further reduce evacuation rates.

Based on the observation that pelagic seabirds bring back meals to chicks after extended foraging trips Murphy (1936) and Ashmole & Ashmole (1967) suggested that they may delay digestion. However, resident times of food in full King Penguin stomachs may be well over 24 h. If most of the foraging time is spent replacing the adult's own energy reserves, perhaps no factor other than large meal size and intense muscular activity need be invoked to explain the ability of King Penguins to bring back large meals after long periods at sea.

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APPENDIX 2

THE USE OF THALLIUM AS A RADIOACTIVE SOURCE IN AUTORADIOGRAPHIC DEVICES FOR PENGUINS AT SEA

Published with R.P. Wilson and C.A.R. Bain as junior co-authors in J. Field Ornith. (1988). 59: 43-45.

INTRODUCTION

The difficulty of observing penguins at sea has precipitated the development of new radiotelemetry techniques (Trivelpiece et al. 1986) and remote sensing devices (Wilson & Bain 1984a, 1984b) for studying their behaviour at sea. The remote sensing devices of Wilson & Bain record data autoradiographically. Recently, one such device has been used to estimate foraging ranges of four species of penguins at sub-Antarctic Marion Island (46°52′ S, 37°51′ E) (Adams 1987, Adams & Wilson 1987, Brown 1987). This appendix describes a modification that may be useful in such remote areas.

These devices work on the principle of ionizing radiation from a point source, fixed on the indicator of the gauge, exposing film immediately adjacent to this source. Previously, the radioactive source used was phosphorus 32 (^{32}P), a pure beta emitter (E_{max} 1.71 MeV) with a half-life of 14.3 d, in the form of the insoluble salt barium orthophosphate. The optical density of blackening of the film can be used to calculate the exposure time and the location of blackening can be used to determine the magnitude of the parameter being measured, e.g. speed.

For a film response (optical density of blackening) that is linearly related to the irradiation dose, the error incurred due to exposure sometime during a known wearing period of X half lives is approximately:

$$100 \;.\; A\, e^{-0.69x}/A \quad \%$$

where A is the activity of the isotope when the device was first put on the bird. Radioactive decay from such an isotope will thus result in large errors if measurements are made over a significant proportion of the isotope half-life.

Moreover, the half-life limits the storage life of the source prior to deployment, that is, for a short half-life there is a limited period over which the bead is viable for field use. The use of thallium 204 (^{204}Tl) as an alternative isotope is therefore suggested in situations where devices may be worn for long periods of time or fresh supplies of ^{32}P are not readily available. ^{204}Tl fulfills the requirements of a suitable radioactive source for autoradiography, having both pure beta emission (E_{max} 0.77 MeV, with associated mercury X-rays of 0.7 % occurrence) and a high specific activity, but a half life of 3.8 yrs.

MATERIALS AND METHODS

The radioisotope was obtained in the form of thallium sulphate ($TlSO_4$) in 0.5 m H_2SO_4 with an activity better than 1 microcurie per milligram ($uCi.mg^{-1}$: 3.7×10^4 radioactive disintegrations per second per milligram) (supplier: Amersham International Ltd., Amersham, Buckinghamshire, U. K.). Thallium iodide was precipitated (solubility at 20°C: 0.0006 $mg.cm^3 x 10^2$) by adding potassium iodide. Beads were prepared by dipping the tip of a fine glass rod into epoxy glue (Wilson & Bain 1984a). This in turn was dipped into the dried thallium iodide. A further application of glue was used to seal the radioactive salt. Once dry the tip was coated with polyurethene and the glass rod broken off flush with the surface of the bead. By maintaining the glass rod in a vertical position while drying, the bead attained a spherical shape.

The radioisotope was field tested on speedmeters (Wilson & Bain 1984b) consisting of the radioactive bead mounted in wax on a bung attached to a spring and encased in a cylindrical tube. A lightproof, waterproof plastic sachet, containing a strip of X-ray sensitive film, taped along the length of the tube recorded the position of the bead at various speeds (Wilson & Bain 1984b). The accuracy of time-based data is critically dependent on film to bead separation (Wilson & Bain 1984a). This is particularly the case with ^{204}Th because of its lower energy radiation relative to ^{32}P. It is therefore important to insure the X-ray film is placed as close as possible to the radioisotope and that the bead to film distance is kept constant.

Four speedmeters were attached to the dorsal feathers of Gentoo Penguins Pygoscelis papua resident at Marion Island using hose clamps and recovered the birds when they returned after foraging.

RESULTS AND DISCUSSION

The results from one field trial indicated that a nonbreeding Gentoo Penguin travelled for 18 h at 8.0 $km.h^{-1}$, covering an estimated total of 144 km (for trace analysis techniques see Wilson & Bain 1984a, 1984b). The speedmeter was on the penguin for a total of 24 d, the bead having been fabricated seven months previously. The maximum error due to decay during the time the meter was on the bird was 1.2% (assuming the unlikely event of all travelling taking place at the end of the wearing period), far less than the 70% error that would have occurred using ^{32}P. Moreover, after seven months the activity of ^{204}Tl was reduced by only 10% of the original activity, whereas the activity of ^{32}P would have been reduced by 99.997% over the same period and probably would not have been usable. Activity loss due to leaching while the device is in water may be a consideration when used in depth gauges (see Wilson & Bain 1984a) and additional tests should be conducted to determine the extent of this. However, radioactive beads used in speedmeters are encased in wax and the problem does not arise here.

Activities of individual beads are low and, in view of the low beta energy, constitute a very minor health hazard; an unshielded 3.7 kilobecquerel ^{204}Tl source (kBq: one thousand radioactive distintegrations per second) results in a dose rate of less than 6 microgray per hour (uGy.h^{-1}: energy absorbed in microjoules per unit mass of absorber in kilograms per hour) at a depth of 5 mm in tissue (Birkoff 1967). This is less than the 18 uGy.h^{-1} for an equivalent ^{32}P source. The total dose received will of course be greater for the longer wearing period. However, in practice the shielding provided by the device and water layer will considerably reduce the dose to the skin from the beta radiation, but as an added precaution a thin (~ 0.1 mm) layer of copper foil may be inserted between the device and the bird.

The remoteness and consequent difficulty of obtaining regular supplies at isolated sites such as Marion Island and the potential for leaving autoradiographic devices attached for extended periods (e.g. the chick-rearing period) make the use of a radioisotope with the extended half-life of ^{204}Th particularly appropriate.

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CONCLUSIONS

Penguins (Sphenisciformes) are a specialized group of seabird predators confined almost exclusively to the cool or cold marine ecosystems of the Southern Ocean. Local densities of these birds reach their highest levels close to breeding sites in Antarctic or sub-Antarctic regions where they account for the largest proportion of the avian biomass. In view of the potentially large impacts of penguins on local marine resources in these regions, their interactions with their prey warrant attention. The diets of the pelagic feeding King Aptenodytes patagonicus and the inshore feeding Gentoo Pygoseclis papua at the Marion Island were assessed in terms of measured foraging parameters and mechanisms important in causing dietary differentiation between the species.

Feeding biology

It is likely that the diving ability of penguins may make available a suite of prey species not readily accessible to surface feeding seabirds. The diet of King Penguins at Marion Island was dominated by three species of myctophid fish which were partly replaced by a single species during winter (Chapter 2). Both these prey groups are considered to be largely mesopelagic, consistent with the deep diving ability of King Penguins. Since the presence of shoaling marine prey within the foraging range of breeding penguins may be essential for successful fledging of chicks, the importance of myctophid fish in King Penguin diets suggests that such aggregations are common. Prior to this study the presumed absence of fish as an important prey for pelagic predators had been attributed to the paucity of obligate shoaling fish in Antarctic and sub-Antarctic waters. Seasonal changes in the relative proportions of prey species are considered to reflect similar fluctuations in primary and secondary productivity which in turn influence the distribution and hence availability of prey. Although not as extreme as in the maritime Antarctic, such changes are probably the most important factor determining the timing of breeding in sub-Antarctic penguins.

During chick rearing adult seabirds must go to sea for varying periods to collect food for growing chicks. Based on the frequency and duration of such trips, seabirds may be classified as pelagic, offshore or inshore feeders. Mean provisioning rates to King Penguin chicks during September to December were on average 0.25 meals. day^{-1} (Chapter 3). Adult birds at sea were estimated to travel, on average, 74 $km.day^{-1}$, while feeding large chicks. Foraging range from the island was probably no more than 175 km. Based on these estimates, King Penguins are the most pelagic of all penguins and share the single egg clutch and long chick development characteristic of such birds. Also typical of pelagic seabirds, meal delivery rates of King Penguins were more variable within individuals than between individuals presumably reflecting large variations in foraging distance associated with the unpredictable nature of prey distribution.

In marked contrast to King Penguins, the diet of Gentoo Penguins at Marion Island was dominated by demersal fish and benthic crustaceans, especially in winter (Chapter 4). Pelagic crustaceans were more common during summer. These changes appear unrelated to potential interactions with sympatric penguins but, as in the case of King Penguins, reflected changes in local availability of prey. However, the dietary differences between the two species suggest major differences in foraging. Gentoo Penguins are inshore foragers, with 80 % of foraging trips less than 40 km (Chapter 5). Provisioning rates to chicks during the brooding period were in the order of 1 meal.day^{-1}. Data from simultaneous sampling of diet and travelling distances suggested differences in the availability of specific prey at different distances from the island. In addition, significant intercolony differences in travelling distances while foraging and the non-random distribution of breeding colonies suggested use of specific foraging areas. The ability of Gentoo Penguins to feed close to the seabed and to exploit demersal and benthic prey which occur in close proximity to the island may allow these birds to commence breeding during the austral winter when the abundance of pelagic prey is low.

It is clear that prey-size selection and differing diving capabilities among the penguin species at Marion Island have a role in causing diet differentiation. However, differences in the distribution of foraging effort reflected in differences in their foraging ranges were concluded to be the most important factor (Chapter 6). In particular, it is suggested that the availability of specific prey in the apparently differing and distinct foraging zones is the reason for the clear separation in diet among the three penguin genera at Marion Island.

Energetics

Such differences in species' foraging ranges and consequently meal delivery rates are also likely to influence the allocation of energy within annual energy budgets of individual penguins.

The low reproductive rates of many seabirds, including penguins, are considered to reflect energy constraints on breeding productivity that arise from limits on the ability of adults to supply food to chicks (Lack 1968, Ricklefs 1983). Although the large biomass of penguins suggests that their adaptations for deep diving have increased potential food availability compared to volant seabirds in the region, this is at the apparent cost of the energetically efficient mode of locomotion of many of the volant seabirds (Birt-Friesen et al. 1989). At high latitudes breeding seabirds have to cope with additional constraints, including low ambient temperatures, seasonal changes in the behaviour and productivity of prey. The penguins' energy requirements for breeding and moult are assessed in the light of potential constraints on breeding.

In spite of the low core body temperatures of penguins, usually considered to reflect low metabolic rates, the basal metabolic rates of sub-Antarctic penguins were similar to or higher than values predicted from general allometric equations for non-passerine birds (Chapter 7). The ability of both King and Gentoo Penguins to maintain body temperatures at ambient temperatures as low as -15°C indicated well developed adaptation to cold conditions. In addition, King Penguins ,at least, did not require any metabolic adjustments to maintain body temperature in conditions normally occurring at Marion Island. In contrast, immersion of King Penguins in water at the average sea temperature in the region resulted in an increase in metabolism. Heat generated by swimming activity at sea may be sufficent to maintain thermal balance. In comparison to species breeding in the high latitudes .pa of continential and maritime Antarctica, there are fewer physical constraints on breeding in the milder climates of the sub-Antarctic.

The annual activity budgets of especially offshore feeding seabirds are characterized by periods of fasting ashore and extended periods at sea. Such a strategy reduces the number of energy costly communting trips between nest site and offshore feeding areas and allows adult birds to maximize energy delivery to the nest site. While ashore, birds are easily approached and good candidates for metabolic studies. All measurements of onshore activities were conducted on birds constrained within the confines of metabolic chambers or by metabolic masks (Chapters 7,8,9 & 11). This procedure restricts the activity of penguins including that associated with social interactions. However, because penguins ashore are relatively inactive, I considered these measurements to be a reasonable approximation of actual field costs. The energy costs of moult, incubation and chick production were measured in this way.

The intense moult of penguins involves the production of new tissue and changes in the thermal conductance of the integument. Accordingly, the process incurred additional energy expenditure above that required for normal maintenance. Mass-specific metabolism was maintained at high levels through most of moult, presumably in response to the changes in thermal conductance (Chapter 8). Moult costs averaged about one-and-a-half times basal rates. The apparent constraints on timing of moult may rather be a consequence of the high cost of the premoult foraging period when penguins must accumulate large lipid reserves to be utilized during the moult fast. Similarily energy costs of incubation of King Penguins are relatively low, not being significantly different from those of resting non-incubating birds (Chapter 9). However, incubation fasts may last as long as three weeks, and any energy constraints are also likely to arise during foraging periods at sea when accumulating lipid reserves (see below).

Aspects of the feeding and breeding biology which characterize penguins as pelagic or inshore feeders are reflected in hatchling compositions and production efficiences. The greater yolk reserves of King Penguin, compared to Gentoo Penguin, hatchlings were consistent with their longer feeding interval (Chapter 10). The low production efficiency of King Penguin embryos reflected the small hatchling size and relatively long incubation period with consequently high total maintenance costs. Long incubation periods, reflecting slow development, are characteristic of pelagic feeding seabirds. However, energy cost of yolk production, estimated from analyses of egg composition and duration of egg formation, was less than 10 % of basal metabolism and insignificant compared to the costs of other activities. Consequently energy limitations are unlikely to affect egg production per se.

During chick rearing, and in contrast to other activities, relatively undigested food must be delivered to terresterial nest sites. Energy constraints on breeding seabirds are likely to arise from having to feed dependent young, regularly, for extended periods coupled with the need to commute from feeding grounds at sea to terresterial breeding sites. Detailed development of the King Penguin chick, which includes two periods of tissue accumulation, results in considerably higher total energy requirements over the growth period than is the case for Gentoo Penguins. Mass proportionate energy costs of rearing King Penguin chicks were more than double that of Gentoo Penguins. The disadvantage of adult King penguins having to invest large amounts of energy in chick rearing may be offset by higher chick survival due to birds fledging at a time of improved food availability.

Relative energy requirements at the nest site

Evaluation of the relative energy demands on penguins at the nest during different stages of the breeding cycle may allow identification of times of potential energy constraints on breeding penguins. Based on measurements of the energy costs of the various activities (Chapters 7,8,9,11) the daily energy requirements at the nest through breeding can be determined (Fig. 1). Energy costs of incubating Gentoo Penguins and brooding birds at the nest have not been measured but were assumed to be equivalent to the average daily metabolic rate of birds in metabolic chambers. Incubation and brooding duties are shared between adult partners and are split between foraging at sea and attendance of eggs or small chicks. If penguins are to maintain overall energy balance during each breeding activity birds must arrive at the nest site after foraging with energy to supply energy requirements while ashore. During incubation, adults need only return to the nest with energy to meet the daily energy requirements for maintenance alone. During brooding, additional food is required to meet the energy requirements of the chick and maximum daily requirements at the

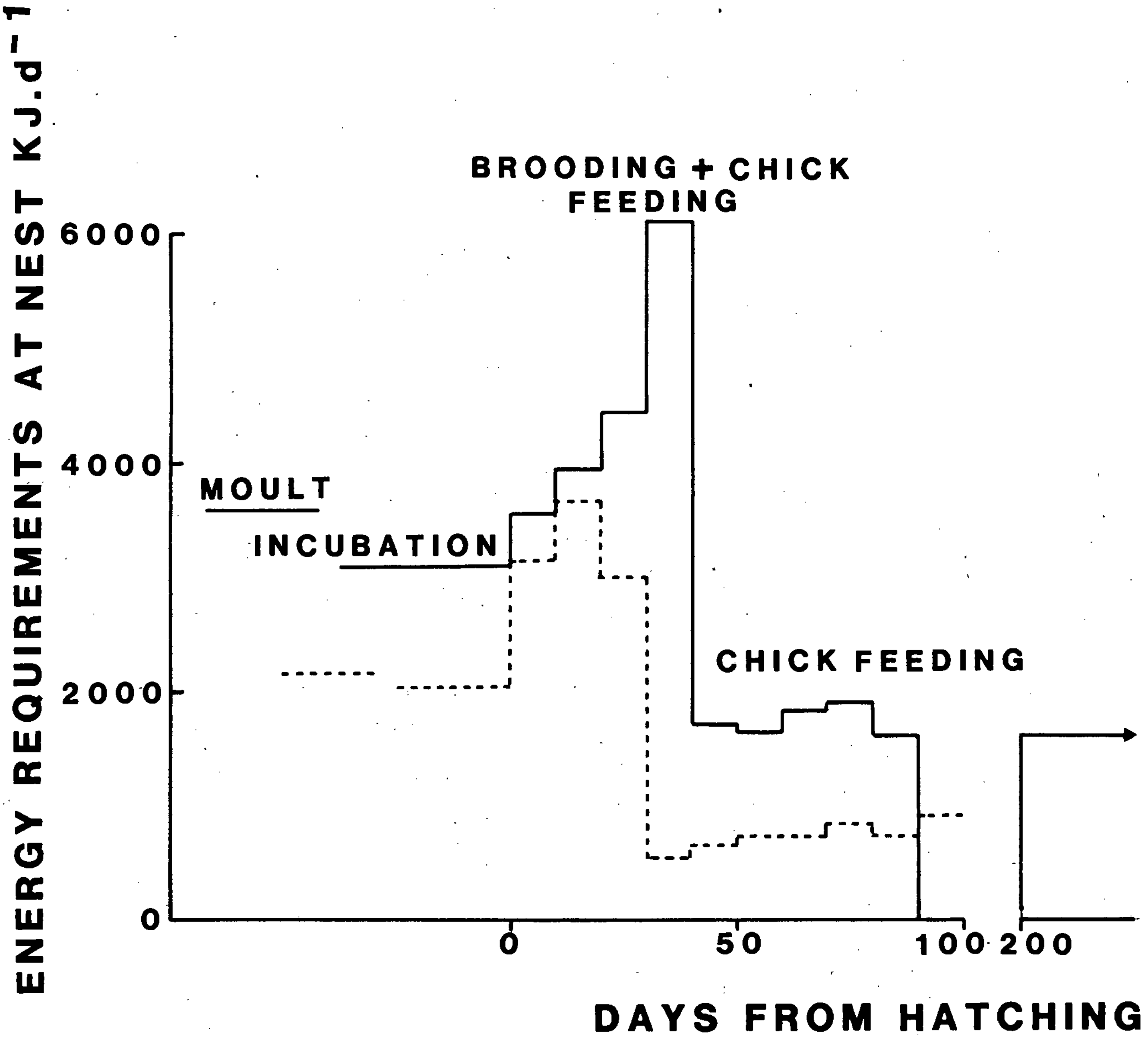

ENERGY REQUIREMENTS AT NEST KJ.d^{-1}
6000
4000
2000
0
BROODING + CHICK FEEDING
MOULT
INCUBATION
CHICK FEEDING
0
50
100
200
DAYS FROM HATCHING

FIGURE 1

Daily energy requirements at nest during breeding and moult for King (solid line) and Gentoo (dashed line) Penguins.

nest occur. Peak daily energy costs for King Penguins attempting to raise one chick only occurred immediately prior to the end of the brood period at around two-and-a-half times basal metabolism. The pattern was similar for Gentoo Penguins, but their maximum energy requirements occurred mid-way through brooding at the time adults were feeding two chicks. At Marion Island, all second chicks had starved by 20d at which point energy requirements decreased by 17 %. At the end of brooding both adults are free to forage. Consequently, only half the chick energy requirements need to be provided by any individual adult at the nest. Energy requirements of King and Gentoo Penguins at the nest dropped by some 70% and 80%, respectively, to values below that of incubating birds.

This analysis indicates that, after brooding and assuming food availability remains constant during breeding, adult penguins can potentially gather enough food to meet the daily food requirements of at least single and probably double chick broods (see also Ricklefs 1983). However, the consistent failure of one of the two Gentoo Penguin chicks, presumably of starvation (Chapter 11), at the time of peak energy demand, is circumstantial evidence that there are constraints on the ability of adult penguins to gather sufficent food to feed two chicks during brooding at Marion Island. Given the markedly different diet and breeding schedule of Gentoo Penguins compared to the other breeding species at the island it may be unwise to conclude there are similar constraints on King Penguins, at least during summer when pelagic prey is abundant. However, the increased foraging ranges of pelagic penguins results in a decrease in feeding frequency compared to inshore feeding birds.

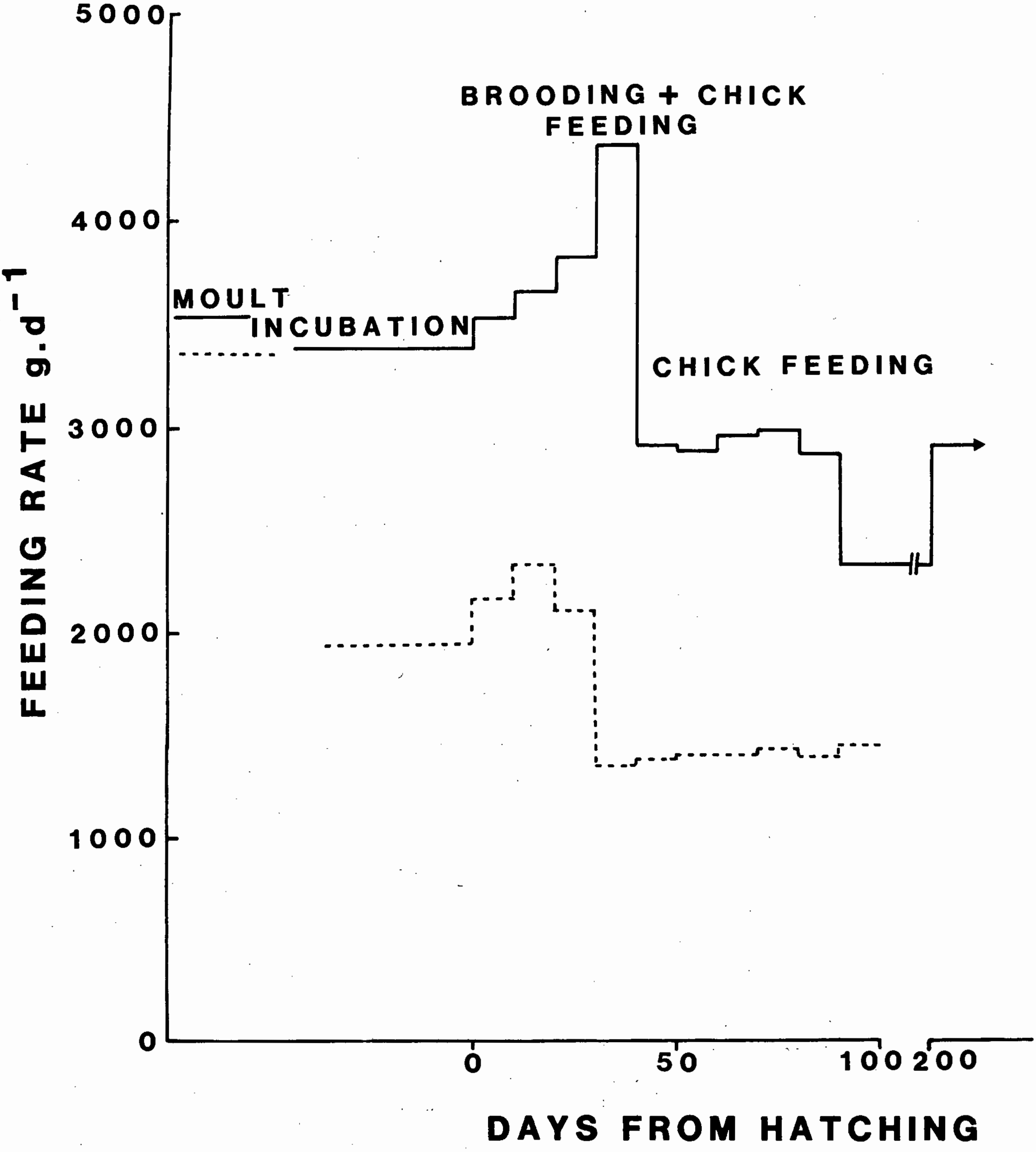
Because there are apparent limits on the relative size of meals transported by adults (approximately 20 % of body mass) (Prince & Harris 1988) there are severe limits on energy delivery rates of pelagic seabirds. Penguins are unable to increase the energy density of meals fed to chicks by retaining the lipid fraction of digested prey as is the case for Procellariiformes (Warham et al. 1976). Given these limits on energy delivery rates, it is of note that the pelagic feeding King Penguin is also the largest species at Marion Island with the consequently lowest mass-specific metabolism. A meal consisting of a given percentage of adult body mass will therefore sustain individuals of larger species longer than individuals of smaller species.

Feeding rates at sea

The above approach has not considered whether feeding rates at sea may approach some limiting factor. At sea, penguins must accumulate energy reserves to be utilized while fasting ashore. Such reserves were assumed to be accumulated at the rate they were utilized ashore. Additional food to satisfy maintenance requirements at sea must also be collected and processed. At-sea feeding rates of penguins engaged in breeding and moult can be determined by converting energy requirements of such activities to feeding rates based on prey energy content corrected for assimilation efficiencies (Chapter 12). These figures were added to feeding rates for maintenance of adults foraging at sea (Davies et al. 1989, Kooyman 1982) and, where relevant, food required by growing chicks (Fig. 2). Maximum food demands on King Penguins while at sea occurred during the brooding period and required an intake of 33 % of adult body mass daily of which 944 g (7.2 % of body mass) was delivered to the chick. Although

FIGURE 2

Daily feeding rates required at sea to maintain energy balance over moult and brooding and to meet chick energy demands for King (solid line) and Gentoo (dashed line) Penguins.


5000
4000
3000
2000
1000
0
FEEDING RATE g.d^{-1}
MOULT
INCUBATION
BROODING + CHICK FEEDING
CHICK FEEDING
0
50
100
200
DAYS FROM HATCHING

relative food requirements of Gentoo Penguins during the brooding period were similar at 36 % of adult body mass with 518 g delivered to chicks (8.1 % of body mass), peak demands occurred during the premoult foraging trip (Fig.2). This largely reflects the high at-sea costs estimated for these premoult birds combined with their higher mass-specific metabolism (Davies et al. 1989). It unlikely that Gentoo Penguins are able to sustain daily intakes equivalent to 50 % of body mass. This suggests that at-sea costs of premoult Gentoo Penguins at sea have been overestimated. Estimates were based on foraging costs at sea which included energy required for commuting between feeding areas and nesting sites (Davis et al. 1989). Nevertheless, the results indicate that penguins at sea have to maintain high feeding rates during premoult foraging as well as during breeding. These rates may approach their physiological limits to process such food intake. For example, adult King Penguins required 14 h to digest 50 % of meals approaching the average meal size of large chicks (Appendix 1).

It is the requirement for such high prey encounter rates that restrict penguins, with their relatively short foraging ranges compared to volant seabirds, to breeding adjacent to productive marine ecosystems with, at least, seasonally resident populations of shoaling prey. More particularly, it may explain why King Penguins do not attempt to feed chicks on a regular basis through winter when prey availability is low.

Penguins at the Prince Edward Islands occur in large numbers and it is clear that they may have a considerable impact on prey populations. Based on estimates of the feeding rates of individual penguins during breeding and moult, coupled to dietary information and population counts, the magnitude of this impact was estimated. That breeding and moult, and hence peak food demands, of the three abundant species occurred during summer supports earlier conclusions that there is a strong seasonal peak in the abundance of, especially, pelagic prey. The total food requirement of the small Gentoo Penguin population which commences breeding during winter and includes a significant proportion of non-pelagic prey in its diet, was less than one per cent of the total requirements of the whole population which approached a million tonnes per annum. Within the summer breeding season at Marion Island the timing of breeding within penguin species was synchronized to a lesser or greater extent. Since the breeding schedule of each penguin species was different, the timing of brooding and accompanying high food demands were staggered. It is of note that the two penguin species that show the least temporal separation of breeding have the more synchronized breeding, and the interval between breeding peaks is of similar length to the brooding period .

Three quarters of the total consumption of prey taken by penguins at the Prince Edward Islands was ascribed to King Penguins. This was attributable to their large numbers and size and long breeding season. Because of their pre-eminent role as consumers in the penguin community, the main prey of King Penguins, myctophid fish, proved to be the most important single prey group consumed in the region. In this respect the marine food webs of the sub-Antarctic are very different from those of Antarctic waters which are dominated by krill, mostly Euphausia superba. In the absence of fishery data on the quantity of food consumed by penguins represents the best estimate currently available on the relative abundance and potential production of marine prey in the area. Based on prey transfer rates alone the region around the Prince Edward Islands appears considerably less productive than South Georgian waters where seabirds are sustained by very large populations of krill. The mean foraging range of penguin species at the Prince Edward Islands was positively correlated with population food requirements. In contrast to the sedentary nature of much of the prey exploited by the small population of inshore feeding Gentoo Penguin, prey of pelagic origin utilized by offshore foraging penguins may be more easily replenished by prevailing local ocean circulation patterns. Such a situation may explain the differences in food availability that account for the differences in total population sizes between these two groups of penguins.

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