

The food and energy intake rates of adult emperor penguins (*Aptenodytes forsteri*) rearing chicks

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Abstract: The food and energy requirements of adult emperor penguins parenting chicks were examined at Auster (about 11 000 pairs) and Taylor Glacier (about 2900 pairs) colonies during the winter, spring and summer of 1988. Tritiated water-derived estimates of food consumption trebled during the five-month period of chick care, ranging from 2.3 kg d⁻¹ in winter when chicks were <5% of adult mass, to 6.3 kg d⁻¹ in summer, when chicks represented 40–50% of adult mass. These food consumption rates were equivalent to the acquisition of 11.4 MJ d⁻¹ and 33.4 MJ d⁻¹ metabolizable energy in winter and summer respectively. Chick provisioning was not accompanied by a major increase in food consumption by adults. Adults assimilated 84–92% of their daily food intake themselves and retained the remainder for the chick. The food ration of chick for the three seasons (42 kg) constituted only about 9.5% of adult maintenance requirements during the same period. Adults consumed an estimated 482 kg of food (including the ration for the chick), which amounted to about 10 700 t and 2800 t of fish and squid consumed by the breeding populations at Auster and Taylor Glacier, respectively.

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Introduction

Quantitative assessments of the impact of seabirds on marine resources highlight the pre-eminent position of penguins among consumers of prey in Antarctic waters (e.g. Croxall *et al.* 1984, Croxall 1984). The large body mass of penguins, relative to those of flying seabird species, and their diving mode of hunting enable penguins to exploit a wide range of marine habitats and to take prey species that are also the target of commercial fisheries (e.g. Ichii 1990, Kailola *et al.* 1993). To assess the potential impact of commercial fisheries on Antarctic penguin populations it is important to understand not only the prey species complex taken by penguins but their annual food and energy requirements to maintain their populations.

The period of chick care is an important stage in the reproductive cycle of penguins, and is accompanied by an increased demand on marine resources as adults must forage for their chick in addition to feeding to maintain themselves. The Adélie (*Pygoscelis adeliae*) and emperor (*Aptenodytes forsteri*) penguins breed in the extreme high Antarctic and forage extensively in the waters of the pack-ice zone that flanks the Antarctic continent. The food and energy consumption of Adélie penguins during chick production has received considerable attention (Culik & Wilson 1992, Nagy & Obst 1992, Chappell *et al.* 1993), but the food requirements of emperor penguins have not yet been measured. The food requirements of emperor penguins are of particular interest because emperors are unique in their habit of raising young through the Antarctic winter and spring when the

birds foraging capacity is constrained by an extensive sheet of fast-ice over the continental shelf and limited daylight for hunting.

The main objectives of this paper are 1) to determine the food and energy intake rates of adult emperors throughout the entire chick rearing phase of their breeding cycle and, 2) in considering the food requirements of the chicks during their development (Robertson 1994), to determine the additional cost to adults of raising young during the Antarctic winter.

Methods

Salient features of the breeding cycle

The chick rearing period for the winter breeding emperor penguin commences in mid July when chicks hatch on the feet of adult males, and ends about five months later in mid December when fledglings leave the colony for open water. Hatching marks the end of a four month pre-nuptial and incubation fast for the male, and the commencement of brooding duties for the female, following her two-month winter absence at sea. For the first 50 days of the chick's life adults share the brooding and feeding duties, until about September when the chick is left in a crèche and both adults are free to commute between colony and ice edge to forage for themselves and their offspring. Many emperor penguin colonies lie great distances from open water (Jouventin 1975, Ancel *et al.* 1992) and after brooding ends chicks are fed large meals on relatively few occasions, as adults attempt to

balance their own food and energy requirements with those of their chick. In general, after completion of brooding, when the most intensive feeding begins, about six foraging trips are made by each parent (Mougin 1966, Isenmann 1971).

Adult selection and recapture

The study was conducted at Auster colony between July and late November 1988 after which it was transferred to the land-based colony at Taylor Glacier (due to decaying sea-ice at Auster) for the last three weeks of the breeding cycle. Auster (11 000 pairs) and Taylor Glacier (2900 pairs) lie 55 km east and 95 km west of Australia's Mawson station (67°36'S, 62°53'E), respectively. Adult penguins were studied at three different periods which were intended to reflect temporal changes in the breeding cycle and contrasting demands on adults during the five month chick development period (Table I). Variation in these demands was expected to arise from changes in the amount of food required by adults for self maintenance, changes in food required by growing chicks, and changes in the distance between colony and the waters where adults foraged. For birds in the three study periods the winter males were especially interesting because the isotope integration period spanned their first foraging trip after completion of their four-month pre-nuptial and incubation fast.

Penguins at both colonies were captured up to 1 km seaward of their colony to avoid selecting non-breeding adults which tended to reside close to the main mass of breeding birds. Adults used in the experiments were caught at random, except for the winter males, as they trekked back to sea having recently revisited the colony to feed their chick. With the winter males, only birds heavier than 22.5 kg, the lower critical body mass for emperor penguins (Dewasmes *et al.* 1980, Groscolas 1986, 1988), were used in the experiment. This selection procedure would have avoided males in a potentially weakened body condition (see Isenmann & Jouventin 1970) and would be expected to maximize the

recapture success of the males. In July the experimental birds were presumed to be males because they were leaving the colony *en masse* for the ice edge, were low in body mass and had soiled brood patches, having recently hatched their chick. The sex of the penguins captured in October and December was unknown and presumably included both males and females.

Upon initial capture the penguins were weighed and given a 1 ml injection of 1.85 GBq tritiated water (HTO) into the pectoral muscle. Following injection the birds were marked with a temporary flipper band and restrained in a 15 m diameter enclosure on the sea-ice for four hours to allow the isotope to equilibrate with the penguins' body water pools. A blood sample (2 ml) was taken from the radial vein and the penguins were released to continue their journey to the ice edge. Upon return to the colony the penguins were recaptured and a final blood sample taken. Six of the winter males were re-caught either brooding or guarding their chick (see below) and following withdrawal of blood samples these birds were allowed to re-unite with their chick inside the enclosure. At initial capture the 10 males caught in winter, the 14 birds caught in October and 19 of the 34 penguins caught in December were fitted with dive recorders as part of another study (Robertson 1994).

Emperor penguins are non-territorial and marked penguins returning from sea at unpredictable times were difficult to intercept before reaching the colony. All ten of the winter males returned to Auster and were recaptured and blood sampled. One male was captured after 49 days at sea and was probably returning after its second foraging trip, having been missed earlier when it returned to relieve the female of chick brooding; the foraging statistics of this bird were not included in the analyses. Of the other nine males six were caught attending chicks (the remaining three males were caught before reuniting with their partners) and five successfully rejoined their chick on release; the remaining adult abandoned its offspring. Of the 14 penguins injected in October, nine returned to Auster and were recaptured and blood sampled.

Table I. Outline of the experimental approach for feeding rate estimates of adult emperor penguins attending growing chicks.

Season	Sex	Colony	Sample size	Stage in breeding cycle		*Distance to ice edge (km)
				Adults	Chicks	
Winter (July)	Males	Auster	10	Post-fast (4 mo) foraging	Brooded, < 1 kg	70 (82)
Spring (October)	Males and females	Auster	14	Intensive chick feeding	Independent, mid-growth, < 6 kg	60 (70)
Summer (December)	Males and females	Taylor Glacier	34	Intensive chick feeding	Pre-fledging, < 15 kg	61 (50)

*Estimated from satellite pictures of the Mawson Coast. Figures in brackets represent the equivalent distances for either Auster or Taylor Glacier.

Table II. Prey components, water yield and energy density of the reconstructed diet used in the energy and food consumption calculations.

Season	*Reconstructed diet		Free (ml g ⁻¹)	Water yield		bFood energy (fresh)	
	Fish (%)	Squid (%)		Metabolic (ml g ⁻¹)	Combined (ml g ⁻¹)	Gross (kj g ⁻¹)	Metabolizable (kj g ⁻¹)
Winter	79.9	20.1	0.74	0.15	0.89	6.14 (20)	4.95
Spring	59.0	41.0	0.75	0.14	0.89	6.15 (12)	4.89
Summer	37.6	62.4	0.75	0.13	0.88	6.79 (12)	5.32

*After Robertson *et al.* (1994).

^bGross energy determined by bomb calorimetry of food samples collected from penguin stomachs. Figures in brackets refer to the number of penguins sampled.

Of the 34 December penguins only three returned to Taylor Glacier and were recaptured for the withdrawal of blood samples.

Determining dietary water and food energy density

To convert estimates of water influx to estimates of food consumption and energy intake it is necessary to know the diet composition, its free and potential metabolic water content and its energy density during the isotope integration periods (Table II). The diet of adults was assumed to be the same as the diet available to chicks (Robertson *et al.* 1994); this was determined by water-offloading adults serially from July–December as they returned to the colony (along with the birds injected with isotope) to feed their chick. The chemical composition of the main prey species was determined from live caught fish (blunt scaly head *Trematomus eulepidotus* and Antarctic silver fish *Pleuragramma antarcticum*) and squid (*Alluroteuthis antarcticus* and *Psychroteuthis glacialis*), the dominant species in penguin stomach samples. The squid *Nototodarus gouldi*, a Tasmanian species, was analysed for water and chemical composition in place of Antarctic squid which proved impossible to catch. Metabolic water production was estimated by assuming each gram of fat and protein yield 1.07 ml and 0.5 ml water, respectively, and by assuming 0.028 ml water produced per kj metabolizable energy (Schmidt-Nielsen 1975). Although the former assumption took no account of water produced from phospholipids it resulted in a metabolic water production 7% higher than the latter assumption, a difference of only 0.9% when both free and metabolic water were considered. This is well within the 5% accuracy of the HTO method (Nagy & Costa 1980) and for the sake of consistency with other aspects of emperor penguin energetics research (see Robertson 1994) the former assumption was accepted. Free water content of prey was determined by desiccation to constant mass at 60°C in a forced air oven. Dried prey items were pulverized and lipid extracted from 1 g samples following immersion in a 1:1 ratio of diethyl ether and petroleum ether.

The de-fatted residue was then combusted in a muffle furnace at 550°C and protein content derived by mass difference between the sum of the lipid and ash contents.

The energy density of the diet mix was determined from samples taken from the stomachs of adults; the stomach contents were dried, pulverized and combusted in a ballistic bomb calorimeter. The conversion of gross energy yield of the diet mix to metabolizable energy for each of the three groups of birds was achieved using the energy assimilation efficiencies of 81.8% and 76.2%, respectively, for fish and squid (Robertson & Newgrain 1992), and calculated in proportion to their contribution to the diet.

Estimating water influx and feeding rate

In the laboratory water was extracted from the red cell fraction of the blood samples by vacuum sublimation in liquid nitrogen (Vaughan & Boling 1961). Aliquots containing 100 µl of this pure water were added to 3 ml of PCS scintillation cocktail and measured for tritium activity in a liquid scintillation spectrometer (Beckman LS 2800) to 1% accuracy. The total body water (TBW) of adults was determined by comparing blood isotope levels at equilibration with standard solutions made from 100 µl of solution used in the field diluted (1:5000) in distilled water.

Tritiated water turnover was determined from the decline in specific activity of isotope between the initial and recapture blood samples using equation 4 of Nagy & Costa (1980) which assumes that pool size remains a constant proportion of penguin body mass during the isotope integration period. HTO flux rates were adjusted according to the type of prey in the diet of the three groups of penguins to account for the degree by which HTO water flux underestimated actual water flux (Robertson & Newgrain 1992). Food consumption for each group of penguins was estimated by dividing the adjusted water influx by the combined (free + metabolic) water yields of the penguins' reconstructed diets.

Correcting estimates of water influx

Snow consumption and incidental seawater intake by adults when hunting would over-estimate water flux and feeding rate (Green & Gales 1990). Snow consumption by adults was rarely observed at Auster and Taylor Glacier, possibly because of the low deposition rate of snow typical of the Mawson Coast (Bromwich 1988, Streten 1990) and the prevalence of guano-stained, polished sea-ice at both colonies. Snow consumption by penguins away from the colonies is open to conjecture and for the purpose of the calculations was assumed to be negligible. To account for incidental seawater consumption 35 adults caught at various stages throughout the chick rearing season were given intramuscular injections of 2.4 MBq ^{22}Na in addition to HTO and their seawater intake estimated using the iterative method of Green & Brothers (1989). This technique depends on knowledge of the water and sodium contents of the diet, water and sodium influxes of penguins and the Na content of seawater. Serum (200 μl) was drawn from the blood samples, bleached with concentrated hydrogen peroxide (to de-colourize tritium residues), oven dried, mixed with 3 ml PCS cocktail and assayed for ^{22}Na activity by liquid scintillation spectro-photometry. Serum sodium contents were determined by atomic absorption spectrophotometry. A standard solution containing 100 μl of ^{22}Na used in the field was mixed with 500 ml distilled water and counted with the blood samples to enable calculation of the penguins' exchangeable sodium pool sizes at isotope equilibration. Seawater was assumed to contain 470 mmol l^{-1} Na.

The sodium content of the main prey species was determined by atomic absorption spectrophotometry after digesting 1 g samples in concentrated nitric acid and subsequent dilution in deionized water. Sodium influx rates were estimated using the equation of Green *et al.* (1985) assuming a linear relationship between pool size and body mass during the isotope integration periods. Flux rates were corrected upwards, according to the prey types and proportion in the diet, to accommodate errors associated with the ^{22}Na turnover method (Robertson & Newgrain 1992).

Results

Seawater consumption

The exchangeable sodium pool sizes of the 35 penguins at initial capture averaged $39.8 \pm 4.7 \text{ mmol kg}^{-1}$. Only 21 of the adults injected with ^{22}Na returned to their colonies and were recaptured and bled, and only six of these yielded ^{22}Na blood levels sufficiently greater than background levels to calculate sodium fluxes. The mean sodium influx rate for the six penguins was $7.8 \pm 3.8 \text{ mmol kg}^{-1} \text{ d}^{-1}$. Estimated seawater intake for these birds ranged from 0–9.3 $\text{ml kg}^{-1} \text{ d}^{-1}$ and averaged $2.4 \pm 4.3 \text{ ml kg}^{-1} \text{ d}^{-1}$, which was deducted from the

HTO-derived water influx estimates before converting them to estimates of food consumption.

Body masses, mass gains and cycle times

The mean body masses at initial capture were $24.7 \pm 1.4 \text{ kg}$, $23.2 \pm 1.8 \text{ kg}$ and $23.9 \pm 1.6 \text{ kg}$ for the 10 winter males, the 14 adults caught in October and the 34 penguins sampled in December, respectively; these masses were statistically indistinguishable (ANOVA: $F_{2,59} = 2.8$; $P > 0.1$). In each season penguins increased in mass while at sea. The winter males accrued $2.9 \pm 1.7 \text{ kg}$, the October birds $1.3 \pm 1.2 \text{ kg}$ and the December penguins $3.5 \pm 1.0 \text{ kg}$. Except for the three December adults, which were captured prior to chick feeding (and therefore had full stomachs), the mass increases include unknown quantities of food in adults' stomachs because most adults were captured and weighed attending chicks. In addition, the birds would have presumably catabolized fat to fuel their journey back to their colonies. For these reasons the mass increases during foraging bouts at sea would be underestimated by an unknown amount. The mean foraging trip durations were $27.7 \pm 5.3 \text{ days}$, $23.0 \pm 6.2 \text{ days}$ and $17.7 \pm 10.2 \text{ days}$ for the July, October and December penguins respectively (Table III).

Water influxes and feeding rates

Estimates of TBW at injection ranged from 574 ml kg^{-1} to 821 ml kg^{-1} and averaged $689 \pm 53 \text{ ml kg}^{-1}$ for the 59 penguins sampled. There was a weak but significant inverse relationship between TBW and body mass, lighter birds generally having higher mass-specific pool sizes: (TBW [ml kg^{-1}] = $978.3 - 12.12 \text{ mass [kg]}$); $r^2 = 0.15$; $F_{1,55} = 9.6$; $P < 0.01$). Pool sizes were $613 \pm 35 \text{ ml kg}^{-1}$, $692 \pm 62 \text{ ml kg}^{-1}$ and $710 \pm 26 \text{ ml kg}^{-1}$ for the winter males, October and December birds respectively. Analysis of variance performed on transformed (\log_e) data showed these differences to be statistically significant ($F_{2,56} = 27.1$; $P < 0.0005$) with TBW differing significantly for all comparisons ($P < 0.001$; Newman-Keuls multiple range test). Mean water influxes, estimated feeding rates and metabolizable energy intake for the three groups of penguins are shown in Table III. Water influxes showed strong seasonal variation (ANOVA: $F_{2,19} = 26.2$; $P < 0.0005$) with mass-specific rates increasing greatly as the chick rearing period progressed (all comparisons $P < 0.001$; Newman-Keuls multiple range test).

As a significant portion of each foraging trip was spent commuting to and from the ice edge, the estimates in Table III include an adjustment according to the penguins' estimated travelling speed and distance to open water to enable at-sea determinations of water, food and energy influxes. This adjustment is made to enable comparison between emperors and other species of penguin which generally breed close to the open ocean and potential foraging waters. Assuming the penguins commuted by walking (they probably walked and

Table III. Mean masses during release periods, foraging trip cycle time, estimated travelling time from colony - ice edge - colony, water influx, feeding rate and metabolizable energy consumption of adult emperor penguins for three stages during chick rearing. Water influx, feeding rate and energy intake estimates are adjusted according to the estimated total transit times to allow at-sea determination of these parameters (see text).

Season	Sample size (n)	Mean mass (kg)	Foraging duration (days)	Travel time (days)	^b Water influx		^b Feeding rate		^{b,c} Metabolizable energy intake	
					Overall (ml kg ⁻¹ d ⁻¹)	At sea (ml kg ⁻¹ d ⁻¹)	Overall (g kg ⁻¹ d ⁻¹)	At sea (g kg ⁻¹ d ⁻¹)	Overall (kJ kg ⁻¹ d ⁻¹)	At sea (kJ kg ⁻¹ d ⁻¹)
Winter (July)	9	26.0 ± 1.4	27.7 ± 5.3	2.9	72.8 ± 15.1	78.8 ± 16.3	82.2 ± 17.0	88.9 ± 18.3	406.9 ± 84.1	440.5 ± 91.0
Spring (Oct.)	9	24.6 ± 1.7	23.0 ± 6.2	2.5	127.9 ± 11.6	140.9 ± 12.7	144.5 ± 12.8	159.1 ± 14.1	706.6 ± 62.6	778.3 ± 69.1
Summer (Dec.)	3	24.2 ± 1.3	17.7 ± 10.2	2.1	203.7 ± 76.7	228.3 ± 85.9	231.15 ± 87.4	259.1 ± 97.9	1229.7 ± 465.0	1378.5 ± 565.8

^aEstimated from distances between Auster colony and ice edge (Table I) and assuming 2 km h⁻¹ travelling speed (G. Robertson, personal observation).

^bMeans for water flux, feeding rate and energy intake have been weighted according to the length of the isotope integration periods.

^cFeeding rate x metabolizable energy density of diet in Table II.

tobogganed, but there are no data on the energy cost of the latter), that fat was the primary metabolite of commuting emperors and that each gram of fat yielded 39.4 kJ (Groscolas *et al.* 1991) and 1.07 ml metabolic water (Schmidt-Nielsen 1975), the 20.2 MJ d⁻¹ expended in locomotion by the winter males (estimated from fig. 4 in Dewasmes *et al.* 1980) would have required the oxidation of about 1490 g fat and the production of about 1590 ml metabolic water for the trip to and from open water. This amount of water was subtracted from the water influx of the winter males and the new value divided by the estimated at-sea time to determine water influx, feeding rate and metabolism at sea. A similar calculation was performed for the penguins in the other two groups.

Discussion

Effects of experiments

The abandonment rate of adults increased during the chick rearing period and the trend did not follow the pattern of chick deaths (Robertson 1992), implicating experimental effects as a likely factor. This trend in abandonment rate most likely reflects the gradual diminution in the tolerance of the adults to the trauma of capture and handling as the chick rearing season progressed (see Wilson *et al.* 1989).

The experimental procedure may also have affected the penguins' foraging trip durations. In Adélie penguins back-mounted devices increased the time adults were away, because of the extra work required for swimming, about 40% more than non-instrumented birds (Culik & Wilson 1991, 1992). Penguins compensated by staying at sea longer to rest, and did not increase their daily field metabolic rate (FMR) because of the extra energy cost of transporting devices. Proportionate to the size of the penguin the frontal area (1.4–2.1%) of the device used on Adélie was less than that

of the dive recorder used on the emperors, which corresponded to 2.7% of the cross-sectional area (590 cm²) of a 24 kg emperor penguin. This dive recorder would have caused substantial drag and protracted cycle times would be expected.

Feeding rates and energy expenditure

Mean TBW (% of body mass) for the three groups of penguins were 61% in winter, 69% in spring and 71% in summer (note that these values were probably over-estimated by about 5% (Robertson 1994)). Since penguins in each group had similar body masses, and since TBW varies as the inverse of body fat content (Groscolas *et al.* 1991) the trend in TBW indicates a decrease in adiposity of penguins as the breeding season progressed. This means that the winter males were either dehydrated or that their fat store, even after their extensive fast, was proportionally larger than the fat store of adults foraging later in the year.

With the estimation of the at-sea foraging statistics, the travel times shown in Table III assume penguins traversed the fast ice without stopping (i.e. they had no rest or feeding stops), that they traveled day and night (e.g. Ancel *et al.* 1992) and in all weather conditions. The route the penguins took to open water was surveyed from a light aircraft in mid November and no substantial tide cracks or congregations of birds were found, so it seems likely that feeding *en route* may not have been an important factor in determining the time the penguins took to reach the ice edge. Regarding rest time, each rest day by the winter males would have required the production of about 114 ml metabolic water (assuming about 4200 kg d⁻¹ expended (Le Maho *et al.* 1976), and 39.4 kJ and 1.07 ml water produced for each gram of fat metabolized), which amounts to only 0.2% of the total water influx (about 52 l) of the males. Thus an error with the travel times should have only a minor effect on the accuracy of the at-sea foraging values. Even so it is impossible to be sure of the time and

energy spent by penguins travelling to and from the ice edge and for this reason the at-sea determinations of food consumption and energy intake shown in Table III are provisional. As mentioned previously mass-specific estimates of energy expenditure should not be affected by this uncertainty.

Adult feeding rates almost trebled during the period of chick care, ranging from 2.3 kg d⁻¹ in winter, when chicks weighed <5% of adult mass, to 6.3 kg d⁻¹ in summer when chicks represented 40–50% of adult mass. These rates of food consumption are equivalent to the acquisition of 11.4–33.4 MJ d⁻¹ metabolizable energy. This seasonal trend in food and energy intake paralleled seasonal changes in hourly dive occurrence (9 h d⁻¹ in winter; 24 h d⁻¹ in summer (Robertson 1994)), reduction in the extent of the fast-ice (Table I) and changes in the mean mass of adult stomach contents intended for the chick (1.6 ± 0.5 kg in winter; 2.7 ± 0.6 kg in summer (G. Robertson, unpublished data)). The feeding rates of adults in summer seems remarkably high and may reflect feeding to fatten in preparation for the forthcoming moult prior to the cessation of chick feeding. Energy expended at sea by adults during the brood and late crèche stages (c. 440–778 kJ kg⁻¹ d⁻¹) was less than doubly-labelled water derived FMRs for Adélie penguins at the comparable stages of chick care (1150–1218 kJ kg⁻¹ d⁻¹, Culik & Wilson 1992; 1455 kJ kg⁻¹ d⁻¹, Nagy & Obst 1992), but similar to the FMR of king penguins (*A. patagonicus*) brooding small chicks (864 kJ kg⁻¹ d⁻¹, Kooyman *et al.* 1992). Higher mass-specific FMRs for the smaller Adélie penguin would be expected because metabolic rate varies as a function of body mass, and scales in penguins at less than unity (0.74, Croxall 1982). Proportionate to basal metabolic rate (BMR, Le Maho *et al.* 1976), energy expenditure by emperors for the brood and late crèche stages (2.7–4.5 x BMR) was similar to that predicted (Lasiewski & Dawson 1967) for both Adélie penguins (5.4 x BMR, Nagy & Obst 1992; 3.4–3.6 x BMR, Chappell *et al.* 1993) and king penguins (4.6 x BMR, Kooyman *et al.* 1992) for the corresponding stages in the reproductive cycle. In summer, when feeding big chicks, energy acquisition rates by the emperors were 7.8 times BMR.

The emphasis placed by adults on provisioning themselves compared to their chick can be assessed by comparing adult and chick feeding rates. Isotope dilution estimates of chick feeding rates showed that chicks consumed about 0.182 kg d⁻¹, 0.546 kg d⁻¹ and 1.0 kg d⁻¹ during the winter, spring and summer stages respectively (estimated from Robertson 1994). Compared to the feeding rates of the adults for the corresponding times shown above, each adult retained for the chick only 8%, 14% and 16%, respectively, of its average daily food intake during the three seasons examined. Thus the adults would have assimilated 84–92% of their daily food intake themselves, and could have satisfied their chick's food requirements in the equivalent of less than one day's hunting time. This indicates the adults' priorities on a foraging trip

were to satisfy their own food requirements first and then to gather the extra food required for the chick.

It is apparent that chick provisioning by the emperors was not accompanied by a substantial increase in food consumption above requirements for maintenance. Similar results have been reported in Adélie penguins, which operate below their maximum capacity when raising chicks (Chappell *et al.* 1993), and in some other bird species (e.g. Weathers & Sullivan 1989). In light of this observation it is unclear how energetically demanding chick provisioning is for adults. Emperor penguins are capable of consuming far greater amounts of food above maintenance levels than recorded in this study. For example, as fuel for the four month pre-nuptial and incubation fast, adult males must accumulate about 850 MJ metabolizable energy in body tissue (assuming a post-moult mass of 24 kg, 40 kg at the onset of the breeding fast and 53 kJ g⁻¹ fat and protein deposited (Pullar & Webster 1977)), which is equivalent to about 125 kg of food (at 6.79 kJ g⁻¹, Table II) above that required for maintenance. This is almost three times the amount of food each adult delivered to the colony to raise its chick (≈ 42 kg, Robertson 1994), and is gathered in about 80% less time. However, adults fatten in summer when constant daylight permits diving throughout the day, whereas chicks are raised during the winter, spring and early summer, when the short day lengths places limits on daily hunting time (Robertson 1994), food yields less energy (Robertson *et al.* 1994) and may be more difficult to access due to the fast-ice cover of the continental shelf. At Auster in winter and spring adults appeared to have difficulty gathering the extra food they needed for the chick, even though the chick requirements were relatively small compared to their own. This is indicated by the retarded growth of the chick during the first 50 days of life (partly due to the chick's inability to thermoregulate; see Mougin 1966), long and repeated fasts between meals (Robertson 1994), high incidence of starvation-related mortality (c. 40% at both Auster and Taylor Glacier, Robertson 1992) and the low mass of the fledglings (40–50% of adult mass). This suggests that chick provisioning is a major energetic cost to adults and that adults compromise their chick's development, and even their survival, to reduce the burden on themselves (see Drent & Daan 1980, Ricklefs 1983). Further study involving isotope dilution measurements of FMR and determinations of foraging proficiency (on a much finer scale than presented here), conducted simultaneously with studies of chick provisioning rates and prey availability, are required to determine the additional energetic cost of parenting and to place in perspective, in terms of time and energy utilization, the period of chick care in the annual energetic cycle of emperor penguins.

Population requirements

The daily estimates of food consumption by adults for the three seasons examined can be used to calculate the total

mass of food consumed by adults at Auster and Taylor Glacier while rearing chicks. The following assumptions are necessary:

- 1) Chick rearing commenced with the first foraging bout of the winter males (there are no data on the feeding rates of females in winter prior to their return to the colony to brood the chick).
- 2) The foraging performances of males and females during relief from brooding was similar.
- 3) In the last 100 days of chick rearing, when both adults were free to commute between colony and ice edge, adults shared the feeding duties equally, made a total of six or seven feeding trips and spent nine days at the colony fasting (deduced from attendance patterns of adults at Auster in 1993 [R. Kirkwood, unpublished data], and Mougín 1966).
- 4) Adult feeding rates, foraging trip durations and time spent fasting with the chick were similar for both colonies.

The relevant data are shown in Table IV. In the absence of more detailed information on temporal changes in feeding rates the three seasons were considered of equal duration and feeding rates were assumed to be constant within each season. Since this approach may introduce a bias of unknown direction and magnitude the estimates in Table IV should be considered as a first approximation of the food masses consumed by penguins. Feeding rates were based on the time spent away from the colony because this makes no assumptions about the time the penguins actually spent at sea (as opposed to commuting to and from the ice edge). During chick rearing each adult emperor consumed an estimated 482 kg of food, assimilated about 440 kg themselves and fed the remainder (about 42 kg, Robertson 1994) to their chick. This amounts to an average daily food intake of 2.84 kg, or the equivalent of about 12% of adult mass for each day during the 155 day chick rearing period. The chick ration represented

only about 9.5% of adult maintenance requirements over this period. Estimates for the breeding populations at Auster and Taylor Glacier were 10 700 t and 2800 t respectively, which includes food intended for chicks (648 and 178 t respectively, Robertson 1994). Removing the chick ration leaves an adult maintenance requirement of 9967 and 2622 t, respectively, for the breeding populations at Auster and Taylor Glacier during the five month period of chick care. Assuming the adults' diet mix was similar to that of the chicks (Robertson *et al.* 1994), adults at Auster would have consumed about 5500 t of fish (principally blunt scaly head, Antarctic silverfish, *Gymnodraco acuticeps* and paralepidids) and about 4450 t of squid (*Alluroteuthis antarcticus*, *Psychroteuthis glacialis* and *Histeoteuthis* sp.) for self-maintenance (krill was also consumed but was unquantifiable in the diet samples). The corresponding estimates for adults at Taylor Glacier would be about 805 t of fish (Channichthyids, blunt scaly head and *Pagothenia borchgrevinkii*) and about 1820 t of squid (*Alluroteuthis antarcticus* and *Psychroteuthis glacialis*).

The significance of these prey consumption levels must be taken at face value, because there is no information on the size and productivity of the resource systems that supply these demands. However, some of the fish species taken by the emperors have also been exploited periodically since 1985 by commercial fishing vessels operating over and adjacent to the continental shelf region of the Mawson Coast (Kailola *et al.* 1993 and references therein), including in the waters frequented by the birds from Auster. Catches in summer of up to 1816 t of channichthyids, 966 t of Antarctic silverfish and 148 t of blunt scaly head have been reported, and are not insubstantial when considering the birds' requirements. Were the fishery to develop further strict management protocols, supported by the appropriate scientific information, would need to be established to ensure potential harvest rates would not be detrimental to the emperor penguins breeding along the Mawson Coast.

Table IV. Provisional estimate of food consumption by 11 000 breeding pairs of emperor penguins at Auster colony during the period of chick production in 1988. Foraging statistics relate to one member of a breeding pair and food consumption estimates include the food ration intended for the chicks (see text).

Season	Season duration (days)	Foraging statistics			Food consumption		
		Time at colony (days)	^a Away (days)	^b Food intake (kg d ⁻¹)	Per adult (kg)	Per couple (kg)	Population (t)
Winter	55	27.5	27.5	2.1	58	116	1300
Spring	50	5	45	3.6	166	332	3700
Summer	50	4	46	5.6	258	516	5700
Total					482	964	10 700

^aTotal time spent away from the colony on foraging trips.

^bEstimated from Table III.

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