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Estimated Feeding Rates and Energy Requirements of Gentoo Penguins, *Pygoscelis papua*, at Macquarie Island

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Summary. Water and sodium turnovers of 6–7 week old gentoo penguin chicks and breeding adults were measured using isotopically labelled water and sodium. Influx rates for chicks averaged 188 $ml \cdot kg^{-1} \cdot day^{-1}$ and 13.9 $mmol \cdot kg^{-1} \cdot day^{-1}$ for water and sodium, respectively. Chicks consumed an estimated 228 $g \cdot kg^{-1} \cdot day^{-1}$ fresh food or 886 kJ kg^{-1} day. These values correspond to 761 $g \cdot day^{-1}$ or 2945 $kJ \cdot day^{-1}$ for a gentoo chick mid-way through the growth period. Flux rates for adults attending chicks ranged from 199 to 428 $ml \cdot kg^{-1} \cdot day^{-1}$ for water and from 15 to 36 $mmol \cdot kg^{-1} \cdot day^{-1}$ for sodium.

Introduction

Quantitative assessments of the feeding rates and energy requirements of penguins are important if we are to understand their role in the marine environment. Since the recent development of isotope turnover techniques (e.g., Nagy 1975), feeding rates and energy requirements have been estimated for king (*Aptenodytes patagonicus*) (Kooyman et al. 1982), gentoo (*Pygoscelis papua*) (Davis et al. 1983), macaroni (*Eudyptes chrysolophus*) (Davis et al. 1983), jackass (*Spheniscus demersus*) (Nagy et al. 1984) and little penguins (*Eudyptula minor*) (Costa et al. 1986). However, the estimates for king, gentoo and macaroni penguins, all of which breed at numerous sub-Antarctic islands, are for birds at South Georgia only, where their diet and foraging behaviour may differ from those of birds breeding at islands elsewhere in the Southern Ocean.

Our aims in this study were to determine feeding rates and energy requirements of gentoo penguin chicks and the adults feeding them at Macquarie Island, in the Australian sector of the Southern Ocean, using isotopically labelled water and sodium. These isotopes, when used together, provide independent estimates of food consumption and allow the effect of seawater intake by foraging adults on the flux rates of each isotope to be estimated. There are neither published accounts for the use of $^{22}NaCl$ in estimating sodium influx and feeding rates of penguins nor studies of the use of isotopically labelled water in estimating water influx, feeding rates and energy intake of gentoo penguin chicks.

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Materials and Methods

Study Area and Birds

Macquarie Island (54° 30′S; 158° 55′E) lies about 1000 km south of the island of Tasmania in the zone of sub-Antarctic surface waters. The climate is cold, wet and windy. During the study, air temperatures at Macquarie Island ranged from −2.8° to 14.4 °C. The temperature of the ocean around Macquarie Island during summer is about 5 °C.

About 4700 pairs of gentoo penguins breed in numerous small colonies around the coast of Macquarie Island (Robertson 1986). Gentoo penguins at Macquarie Island generally lay two eggs and hatch two chicks, but usually fledge only one chick. Hatching begins in mid October, chicks form creches at about five weeks of age in mid November and fledge at about three months of age in late December.

Field Procedures

The study was conducted between 29 November and 7 December 1984, when most chicks were 6–7 weeks of age, or about 58% of adult weight. Seven adults and six chicks from the same colony were weighed, marked with colour-coded flipper bands and given separate intraperitoneal injections of 1 ml of tritiated water containing 185 MBq tritium, and 185 kBq of $^{22}NaCl$ in 0.5 ml volume.

Adults were restrained in a wire netting enclosure for 6 h to allow the isotopes to equilibrate with body water and exchangeable sodium pools. Chicks were returned to the creche during the equilibration period. After isotope equilibration blood samples of about 1 ml were taken from the brachial veins and the birds were then released. The birds were recaptured, bled and weighed between three and eight days after release.

Blood samples were allowed to clot before centrifugation and removal of serum. Red cell fractions and serum were stored frozen until analysed in the laboratory.

Laboratory Procedures

Water was extracted from the red-cell fraction by vacuum sublimation (Vaughan and Boling 1961). Aliquots containing 0.1 ml sub-samples of extracted water were added to 3 ml of PCS (Beckman) scintillation cocktail and measured for tritium activity in a Beckman LS 2800 liquid scintillation spectrometer. The serum samples were bleached with concentrated hydrogen peroxide, dried and mixed with 3 ml PCS cocktail and assayed for ^{22}Na activity in the spectrometer. Serum sodium concentrations were determined by atomic absorption spectrophotometry. Standard solutions containing 1 ml of each isotope diluted (1 in 1000) in distilled water were counted in the same manner as the samples to enable calculations of initial total body water and exchangeable sodium pools.

The equations of Lifson and McClintock (1966) and Green et al. (1985) were used to calculate flux rates of water and sodium, respectively. Assumptions associated with these techniques are outlined by Lifson and McClintock (1966) and Nagy and Costa (1980) for tritium, and by Green et al. (1985) for sodium. It was assumed that changes in body mass and pool sizes were linear during the sampling period.

Estimating Water, Sodium and Energy Content of the Diet

Stomach contents of 50 adult gentoo penguins were collected as part of a diet study using the wet-offloading technique of Wilson (1984). Birds were captured as they returned to the colony to feed chicks ranging in age from 1–8 weeks. Stomach contents were preserved in 70% alcohol and returned to the laboratory for identification of species. One hundred gram sub-samples were taken from the stomach contents of ten randomly selected birds and oven-dried at 60 °C to constant weight. Caloric content was determined from these sub-samples by combusting them in a Gallenkamp ballistic bomb calorimeter using benzoic acid as a standard.

The stomach sub-samples contained fish, principally *Zanchlorynchus spinifer*, but not squid, which is known to comprise about 10% of the diet usually (Hindell, in press; Robertson and Williams, in preparation). The caloric content of squid in the general diet was thus assumed to be 4.64 $kJ \cdot g^{-1}$ wet weight (Clarke and Prince 1980) and the energy content of the diet was estimated by averaging the caloric content of fish and squid in proportion to their occurrence in the diet.

Because the stomach samples of the penguins were irrigated with fresh water during sampling, water and sodium content of the diet was derived from freshly caught Antarctic cod (*Paranotothenia magellanica*), which occurs commonly in the diet of gentoo penguins at Macquarie Island (Hindell, in press), and from samples of squid (*Nototodarus gouldi*) caught in Bass Strait, 1000 km north of Macquarie Island. This species of squid does not occur in the diet of gentoo penguins at Macquarie Island. Water content of fresh fish and squid was determined by mass change after drying at 60 °C. Sodium content of 0.5 g sub-samples of fish and squid was determined by atomic absorption spectrophotometry after digesting them in 10 ml concentrated nitric acid and subsequent dilution with de-ionised water.

An estimate of the water, sodium and energy content of the diet is shown in Table 1. A diet mix of 90% fish and 10% squid was assumed (Robertson and Williams, in preparation) which would provide 735 $ml \cdot kg^{-1}$ free water and 60.1 $mmol \cdot kg^{-1}$ sodium. Assuming that metabolic water provides a further 100 $ml \cdot kg^{-1}$ food (Schmidt-Nielsen 1975), the total water derived from food is 835 $ml \cdot kg^{-1}$.

Estimating Food and Energy Intake

Chicks. Two independent estimates of food consumption for gentoo chicks were made from water and sodium influx rates. Assuming that ingestion of seawater or fresh water is negligible and the total available water in food (free and metabolic) represents 83.5% of the fresh weight of the food, then:

$$\text{food intake } (g \cdot kg^{-1} \cdot day^{-1}) = \frac{H_2O \text{ influx } (ml \cdot kg^{-1} \cdot day^{-1})}{0.835} .$$

Assuming a dietary sodium content of 60.1 $mmol \cdot kg^{-1}$ (Table 1), then:

$$\text{food intake } (g \cdot kg^{-1} \cdot day^{-1}) = \frac{Na \text{ influx } (mmol \cdot kg^{-1} \cdot day^{-1})}{0.0601} .$$

Adults. Since adult penguins spend much of their time foraging at sea it is probable that some seawater is ingested, thereby providing erroneous estimates of food consumption rates.

It is possible to partition the water and sodium influxes into intake via food and that derived from the ingestion of seawater. If it is assumed that no sea water is ingested and that all of the water influx is derived from food, proximate estimates of food consumption rates can be calculated, using the value for total available water in the diet i.e. 835 ml/kg food. The difference between this approximation of Na influx from food and the measured influx must have accrued from sea water ingestion. The volume of seawater that would account for the discrepancy can be calculated (seawater contains 470 mmol/l) and subsequently used to correct the estimate of water obtained from the food. By the third iteration of this corrective calculation the respective estimates of dietary water and sodium influx, food consumption and water and sodium derived from seawater are effectively balanced.

The energy intake of gentoo penguins were estimated from the energy content of their food and their daily rates of food consumption. Fish obtained from the stomach contents of adult gentoos has a caloric content of 18.33 $kJ \cdot g^{-1}$ dry matter and it was assumed that squid in the diet contributed 20.17 $kJ \cdot g^{-1}$ dry matter (Table 1). Assuming an assimilation efficiency of 75.3% for fish (Cooper 1977) and 81.3% for squid (Adams 1984), these values represent assimilated energies of 13.8 $kJ \cdot g^{-1}$ and 16.4 $kJ \cdot g^{-1}$ dry matter, respectively. Thus the assimilated energy in a diet of 90% fish and 10% squid would be about 14.1 $kJ \cdot g^{-1}$ dry matter. Correcting this value for dietary water intake (Table 1) yields an assimilated energy intake of 3.74 $kJ \cdot g^{-1}$ of fresh food.

All values are reported as means ±1 SD.

Table 1. Estimates of water, sodium and caloric content of fish (*Paranotothenia magellanica*), squid (*Nototodarus gouldi*) and of fish from stomach sub-samples of adult Gentoo penguins. Dietary water and sodium content are estimated for a diet of 90% fish and 10% squid

Food	Free water		Caloric content ($kJ \cdot g^{-1}$ dry)
	(%)	($mmol \cdot kg^{-1}$)	
Stomach sub-samples ($n = 10$)			18.33±2.5
Fish ($n = 5$)	73.1±2.3	54.6±7.6	
Squid ($n = 15$)	77.0±1.2	110.0±11.7	20.17[a]
Diet mix (90%/10%)	73.5	60.1	18.51

[a] Calculated from a caloric value of 4.64 $kJ \cdot g^{-1}$ wet weight (Clarke and Prince 1980) and 77% water content

Results

Chicks

All six chicks injected with isotopes were recaptured and blood samples taken. One chick showed no change in body weight during the sampling period but all others showed weight gains of up to 15%. The mean body water pool was 73.7%±3.4% of body weight and the mean exchangeable sodium pool was 55.6±2.6 $mmol \cdot kg^{-1}$ body weight. The mean influx rates for water and sodium were 188.3±30.6 $ml \cdot kg^{-1} \cdot day^{-1}$ and 13.9±2.3 $mmol \cdot kg^{-1} \cdot day^{-1}$, respectively (Table 2).

The rate of change of body weight in gentoo penguin chicks was significantly correlated ($r = 0.83$; $P < 0.05$)

Table 2. Body weight, sampling duration, % body weight change, % body water and water and sodium influx rates for chick and adult Gentoo penguins

Gentoo penguin	Mean body weight (kg)	Sampling duration (days)	Body weight change ($\% \cdot day^{-1}$)	Body water (%)	Mean water influx rate ($ml \cdot kg^{-1} \cdot day^{-1}$)	Mean Na influx rate ($mmol \cdot kg^{-1} \cdot day^{-1}$)
Chick 1	3.33	7.2	1.06	79.4	188.3	14.06
Chick 2	3.20	7.2	0.87	72.4	181.2	13.64
Chick 3	3.06	7.2	0.0	73.0	140.1	9.03
Chick 4	3.20	7.2	2.12	75.5	224.6	15.57
Chick 5	3.92	8.3	1.27	68.6	177.9	15.01
Chick 6	3.28	7.2	0.98	73.5	217.8	15.85
Mean	3.33	7.4	1.05	73.7	188.3	13.86
SD	0.30	0.5	0.68	3.6	30.6	2.51
Adult 1[a]	5.80			78.4		
Adult 2[a]	6.00			68.5		
Adult 3	5.15	3.2	−1.49	75.1	199.4	17.5
Adult 4	5.80	4.0	5.75	70.1	247.1	15.2
Adult 5	5.87	5.3	1.16	80.4	428.1	35.9
Adult 6[a]	5.45			78.9		
Adult 7[a]	6.25			81.5		
Mean	5.76		1.8	76.1	291.6	22.9
SD	0.36		3.7	5.1	120.3	11.3

[a] Birds not recaptured after initial collection of blood samples
SD = standard deviation

with the rate of water influx, but not with the rate of sodium influx (r = 0.79; $P < 0.1$). Possibly the chicks ingested varying, small amounts of seawater when being fed by their parents. Even so the rates of water influx and sodium influx were significantly correlated (r = 0.89; $P < 0.025$), indicating an underlying conformity in the rates of turnover of both water and sodium.

The mean estimated rates of food consumption derived from water and sodium influxes were 226±37 and 230±42 $g \cdot kg^{-1}$, respectively. The five chicks that registered weight gains during the seven-day sampling period averaged 51 g (range: 39–83 g) gain in body weight for each kilogram of food consumed.

Adults

The mean total body water of seven adults was 76.1%±5.1% of the body weight, and the mean exchangeable sodium pool was 37.6±6.6 $mmol \cdot kg^{-1}$. Only three of the seven adults were recaptured. These showed water influx rates ranging from 199 to 428 $ml \cdot kg^{-1} \cdot day^{-1}$ and sodium influx rates ranging from 15.2 to 35.9 $mmol \cdot kg^{-1} \cdot day^{-1}$ (Table 2).

Iterative partitioning of water and sodium influxes provided estimated food consumption rates of 239 and 513 $g \cdot kg^{-1} \cdot day^{-1}$ for adults 3 and 5, respectively. The food consumption rate, derived by averaging water and sodium fluxes for adult 4 (see below), was 274 $g \cdot kg^{-1} \cdot day^{-1}$. These estimates correspond to assimilated energy intakes of 890, 1000 and 1900 $kJ \cdot kg^{-1} \cdot day^{-1}$ for adults 3, 4 and 5, respectively.

Discussion

The mass-specific body water pools were similar for chicks and adults, but the estimates for the latter were significantly higher (ANOVA: $F_{1,10} = 19.57$; $P < 0.0025$) than those of gentoo penguins feeding chicks at South Georgia (Davis et al. 1983). Since the body weights for adults between study areas were similar, the difference in percentage of body water possibly reflects a difference in amount of body fat in birds between study areas, the South Georgian birds being fatter. However, Davis et al. (1983) only allowed 1 h for equilibration of tritiated water injections and this may be too brief a time for complete isotope equilibration.

The two estimates of food consumption by chicks derived from water and sodium fluxes were within 2% of each other, therefore we considered the iterative correction procedure for the chick data was unnecessary. Averaging the estimates (water and sodium) for each chick yields a food consumption of 228±38 $g \cdot kg^{-1} \cdot day^{-1}$ fresh food, equivalent to an assimilated energy intake of 853±143 $kJ \cdot kg^{-1} \cdot day^{-1}$.

The approximate amount of food consumed by gentoo penguin chicks in the period from hatching to fledging can be calculated as follows. Hatchlings weigh about 100 g and increase in weight over the next 70 days or so to about 5.7 kg at Macquarie Island, after which body weight stabilises until fledging 15 days later (Reilly and Kerle 1981). During the weight increment phase growth is approximately linear in gentoo chicks (Volkman and Trivelpiece 1980; Reilly and Kerle 1981) and the average rate of weight increase is therefore about 80 $g \cdot day^{-1}$ at Macquarie Island.

Assuming that chicks are fed at the same mass-specific rate during the growth phase, i.e. 22.8% of body mass$\cdot$day^{-1}, the total food consumption of each chick is approximately described by the expression:

$$\text{Food intake (g)} = \sum_{n=1}^{70} 0.23\ (100+80n)\ .$$

The estimate of total food intake during the first 70 days of growth is therefore about 46 kg for each chick. The chicks are fed at maintenance rates only for the remaining period prior to fledging, and in the present study one chick that showed no weight gain had a maintenance food consumption rate of 168 g$\cdot$kg$^{-1}\cdot$day^{-1}. The final period of chick development would therefore require 12.7 kg of food (5.4 kg$\times$0.168$\times$15 days). Thus the approximate total food requirement for a gentoo chick from hatching to fledging is 60 kg.

During this study about 4000 gentoo chicks fledged (Robertson 1986). Since most mortality in gentoo chicks occurs between hatching and creche formation at about five weeks of age (Van Zinderen Bakker 1971; Trivelpiece et al. 1987), it is reasonable to assume that most of the 6–7 week old chicks studied here fledged, and that the total amount of food consumed by gentoo chicks on Macquarie Island is approximately 240 tonnes in a single breeding season.

The mean body mass increase relative to the mass of food consumed in the growth phase is about 12% in gentoo chicks, similar to values calculated for Jackass penguin chicks (*Spheniscus demersus*) by Cooper (1977) which range from 13.7% to 8.4%.

The iterative partitioning procedure showed that seawater ingestion accounted for only 4.1% and 3.1% of the total water influxes, and 27% and 20% of the total sodium influxes of adults 3 and 5, respectively. The iterative procedure, however, yielded an anomalous result for adult 4 due to the disparate flux rates for water and sodium. This could arise if adult 4 drank fresh water during the release period. Because of this anomaly, food consumption by adult 4 was determined by averaging the estimates derived from both water and sodium fluxes.

The influx rates and estimated food intake of adult 5 were about double those of adults 3 and 4. This adult had the longest release-to-recapture interval (40% and 25% longer than adults 3 and 4, respectively) and presumably made more foraging trips and had the opportunity to eat more than the other two adults.

Adults 3, 4 and 5 consumed 239, 274 and 513 g fresh food$\cdot$kg$^{-1}\cdot$day^{-1} which is equivalent to about 1.23, 1.6 and 3.0 kg$\cdot$day^{-1}, respectively. Since gentoo penguin chicks are fed by both parents, these adults fed their chicks about 380 g food$\cdot$day^{-1} (i.e. 760 g$\cdot$chick^{-1} $\cdot$day$^{-1}\div$2). Subtracting this amount from their daily food consumption leaves adults 3, 4 and 5 with about 850, 1220 and 2600 g fresh food$\cdot$day^{-1} and about 3200, 4600 and 9700 kJ$\cdot$day^{-1} assimilated energy for maintenance and activity.

By comparison, adult gentoo penguins at South Georgia (where the energy content of the diet is higher than that of gentoos at Macquarie Island) consumed 1.1 kg$\cdot$day^{-1} (estimated from Davis et al. 1983), which is similar to the amount of food consumed by adult 3. In a diet study at Macquarie Island the mass of stomach contents of 26 water-offloaded gentoo penguins feeding chicks two weeks older than those studied here averaged 492 g and ranged from 58–1230 g (Robertson and Williams, in preparation). The estimates from Macquarie Island, could possibly be doubled, because at this stage of the breeding cycle adults were making two foraging trips each day. The estimated amount of food consumed by adults 3, 4 and 5, while reflecting the variability expected from a small sample size, seem reasonable when compared with the values that would be expected if the water-offloaded birds were feeding twice daily.

In this study we sampled gentoo chicks for one week only of an approximate 12-week growth period and obtained only limited data for adults. Additional research incorporating isotopically labelled water techniques and based on a larger sample size of adults is needed throughout the entire fledging period to adequately assess the feeding rates and energy requirements of adults and the total energy and food cost of chick production.

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