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Water Flux and Estimated Metabolism of Free-Ranging Gentoo and Macaroni Penguins at South Georgia

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Summary. Water turnover rates were measured in gentoo and macaroni penguins breeding sympatrically on South Georgia Island. At the time of this study, adult male macaronis were attending the nest while female macaronis and both sexes of adult gentoos were making regular foraging trips to sea and returning to feed their chicks. Both species feed principally on krill, *Euphausia superba,* although gentoos also feed on fish. The average water turnover rate in 2 fasting male macaronis was 12.5 ml · kg^{-1} · day^{-1} with a half-time for water turnover of 36 days. The mean water flux rate in feeding birds was 155 ml · kg^{-1} · day^{-1} in gentoos and 184 ml · kg^{-1} · day^{-1} in macaronis. The half-times for water turnover were 2.8 days, and 2.6 days, respectively. The average metabolic rate of fasting macaronis calculated from water turnover rates was 5.6 W · kg^{-1} or 1.8 × the standard metabolic rate (SMR). In order to calculate prey consumption and average daily metabolic rate (ADMR) from water flux rates in feeding birds, it was assumed that a) the only sources of water are from metabolism and performed water in the diet and b) the composition of the diet is known. Based on the type of prey consumed, the calculated ADMR was 7.1 W · kg^{-1} or 2.6 × SMR (n = 5) for gentoos and 9.1 W · kg^{-1} or 2.9 × SMR (n = 3) for macaronis. The ADMR of female macaronis making regular trips to sea was 1.6 × greater than the fasting metabolism of males brooding the chick.

Introduction

Penguins comprise 75 – 85% of the bird biomass in the Southern Ocean (Mougin and Prevost 1980; Croxall 1984) and represent a major consumer of antarctic marine living resources. During the summer breeding season on South Georgia Island, seabirds are estimated to consume 2 million tonnes of food, of which about 1.8 million tonnes is krill, *Euphausia superba* (Dana) (Croxall and Prince 1982). Consumption by penguins accounts for about 80% of the overall intake and 85% of the krill. As a result, penguins are considerably more important krill consumers than seals or whales in the waters around South Georgia.

The two most common species of penguins on South Georgia are gentoo penguins, *Pygoscelis papua,* and macaroni penguins, *Eudyptes chrysolophus.* Although the breeding season for these two sympatric species overlaps, they are ecologically separated in their nesting sites and foraging behavior (Croxall and Prince 1980a). Gentoos appear to forage closer to shore on large krill (5.4 cm), and immature notothenid fish, particularly *Notothenia rossii* (15 – 25 cm). An average trip at sea lasts about 10 h. Macaronis spend about 30 h at sea on a single trip and take both large (5.3 cm) and small (2.0 cm) krill. Croxall and Prince (1980a) suggested that macaronis may forage up to 50 km offshore where small krill have been seen to concentrate in waters at the edge of the South Georgia continental shelf. The average daily metabolic rate (ADMR) for these two species may reflect differences in prey and foraging ranges.

Despite a growing scientific and commercial interest in krill (Biomass 1977, 1981), the role and impact of its principal predators, and particularly the energy flux between trophic levels in the Antarctic marine food chain, have received much less attention. Recent models of the food consumption and ADMR of penguins are based on time-energy budgets involving field or laboratory measurements of fasting metabolism and allometric extrapolations from other avian species for the energetic cost of brooding and foraging (Croxall and Prince 1982). The purpose of this study was to determine whether more direct estimates of food consumption and ADMR could be obtained from water turnover measurements lasting 1 – 3 weeks in 2 species of penguins which exhibit different parental care and feeding cycles.

Materials and Methods

Birds and Environment

Field work was conducted from 14 January to 19 February 1979, on Bird Island, South Georgia (54° S, 36° W), South Atlantic. The climate is cold, wet, and cloudy with strong winds and little seasonal variation (Richards and Tickell 1968). The mean air temperature in January and February is +4 °C with a maximum of +9 °C and a minimum of −2 °C. Average monthly rainfall at this time of year is 8 – 15 cm. The ocean temperature is about +2 °C reflecting South Georgia's position 250 km south of the Antarctic Convergence.

Between 3000 – 6000 pairs of gentoos and about 175,000 pairs of macaronis breed annually in the summer at Bird Island (Croxall and Prince 1980b). Gentoo penguins breed in numerous small colonies, lay two eggs and, at South Georgia, frequently raise two chicks. Macaroni penguins breed in a few vast colonies, lay two eggs of very unequal size, and never hatch more than one chick. At the start of this study, gentoo penguin chicks were about 41 days old, had been in creches for 14 days, and both parents were making regular foraging trips. Macaroni penguin chicks were about 18 days old and just beginning to form small creches. For about the first 10 days after creche formation, the male macaroni, which has just completed a 35-day fast attending the nest, takes only a small part in feeding the chick, but thereafter both parents share in feeding the chick (Croxall 1984).

Administration of Tritiated Water (HTO) and Blood Sampling

Adult birds returning from sea were allowed to feed their chicks before capture. Each bird was weighed in a sack with a Chatillon spring scale (range 0 – 10 kg). One ml HTO (~0.3 mCi) in normal saline was injected into a brachial vein or intraperitoneally with a 1cc tuberculin syringe. The precise specific activity was determined on aliquots of HTO taken back to San Diego. The bird was held in a box for 90 min to allow equilibration of HTO with total body water (TBW). A 3 ml blood sample was then taken from the contralateral brachial vein and stored in a 5 ml vacutainer. A number was painted on the bird's chest with black aniline dye prior to release. Daily observations were made in the rookeries to relocate, sample, and weigh injected birds. If the weight of a recaptured bird had changed by more than 10%, the TBW was re-measured with a second injection of HTO.

Analytical Techniques

Water was distilled from blood samples by evaporative-freeze capture under vacuum (Turner et al. 1960). Each sample was distilled to dryness to avoid possible fractionation effects. Aliquots were analyzed for tritium activity in duplicate on a Beckman LS 8000 liquid scintillation counter after standing in the dark for 24 h.

Calculations

The theoretical basis and derivation of equations used to calculate TBW and water flux rates have been reviewed by Nagy and Costa (1980). Degen et al. (1981) further verified the use of HTO for measuring water flux rates in birds. The following equations were used:

1) TBW (ml) = N_0

$$N_0 = CPM_{(inj)}/SA_{(t=0)}$$

a) $CPM_{(inj)}$ = activity (mCi) of HTO injected
b) $SA_{(t=0)}$ = specific activity (mCi · ml^{-1}) of HTO in blood water after a 90 min equilibration period

2) Fractional clearance rate (k, day^{-1}) and half-time ($t_{1/2}$, day) for TBW turnover

$$k = \ln (SA_0/SA_t) \cdot \Delta t^{-1}$$

$$t_{1/2} = (\ln 2)/k$$

a) SA_0 and SA_t = specific activity of HTO in blood water at times t_1 and t_2
b) $\Delta t = t_2 - t_1$

2) Water flux rate, r_w, for constant body mass (BW) and TBW. Body mass changes of less than ±10% were considered constant.

$$r_w \text{ (ml/day/kg)} = k \times TBW \div BW$$

3) Water influx, $r_{w,in}$, and efflux, $r_{w,out}$, for changes in body mass greater than ±10%.

$$r_{w,out} = \frac{(N_t - N_0) \cdot \ln (SA_0 \cdot N_0/SA_t \cdot N_t)}{\ln (N_t/N_0) \cdot \Delta t}$$

$$r_{w,in} = r_{w,out} + \frac{N_t - N_0}{\Delta t}$$

a) N_0 and N_t = TBW (HTO space) measured initially and after recapture with a second injection of HTO.
b) SA_0 and SA_t = specific activity of HTO in blood water initially (t_1) and after recapture (t_2).
c) Δt = time between blood samples.

Results

Five of 6 gentoos and 4 of 8 macaronis injected with HTO were recovered and blood samples taken. The decline in specific activity of HTO in the blood under free-ranging conditions is shown in Fig. 1. Two of the birds, macaronis 6 and 9, remained in the rookery and fasted for 2.7 and 5.9 days, respectively, before departing for sea.

Mean TBW represented 62 – 65% of the body weight for both species (Table 1). The mean water flux rate for

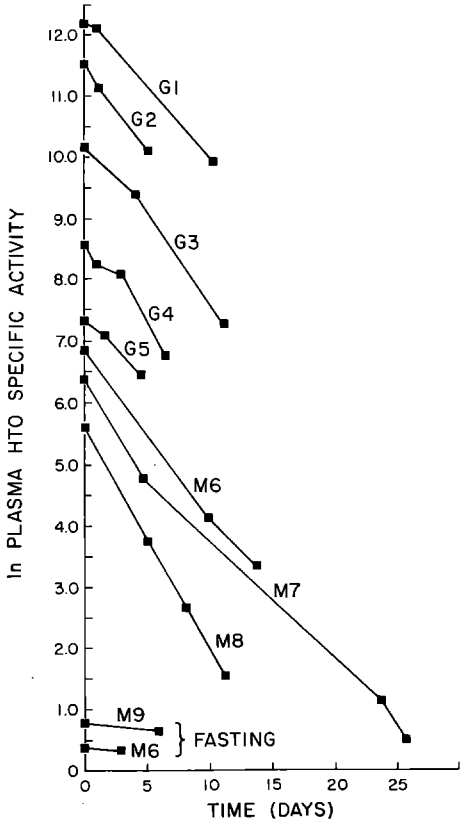

Fig. 1. Natural logarithm of plasma water specific activity, cpm · ml^{-1}, as a function of time after systemic injection of HTO. Lines are identified by species (*G* gentoo and *M* macaroni) and number. All samples were run in duplicate

Table 1. Body mass, number of days monitored, TBW, % body water, $t\frac{1}{2}$ for body water turnover, and mean water flux rates for 5 gentoo and 4 macaroni penguins

Species	Mean Wt (kg)	No days monitored	TBW (L)	% body water	$t\frac{1}{2}$ body water turnover (days)	Mean water flux rate, r_w (ml/kg/day)
Gentoo 1	8.2	10.3	4.8	59	3.1	132
Gentoo 2	6.2	5.1	3.5	56	2.5	158
Gentoo 3	6.3	10.9	3.9	62	2.5	171
Gentoo 4	5.1	6.5	3.4	67	2.5	181
Gentoo 5	5.1	4.5	3.5	69	3.5	134
Mean	6.2		3.8	62	2.8	155
(SD) (n = 5)	1.3		0.6	5.2	0.5	22
Macaroni 6	3.9	13.8	2.4	62	2.8	156
Macaroni 7	3.6	25.7	2.3	64	3.0	145
Macaroni 8	3.3	11.3	2.3	70	1.9	252
Mean	3.6		2.3	65	2.6	184
(SD) (n = 3)	0.3		0.1	4.2	0.6	59
Macaroni 6 (fasting)	3.7	2.9	2.3	63	36.7	12
Macaroni 9 (fasting)	3.8	5.9	2.4	63	3.0	13

birds making regular trips to sea was 155 ± 22 ml · kg^{-1} · day^{-1} for gentoos and 184 ± 59 ml · kg^{-1} · day^{-1} for macaronis (Table 1). Half-times for body water turnover were 2.8 and 2.6 days, respectively. The average weight change for all foraging birds excluding gentoos 1 and 3 was −0.72% ± 3.8 (n = 17). It was assumed that these birds were in metabolic and fluid homeostasis. Gentoos 1 and 3 lost 10% and 15% of their initial body weight, respectively, and were reinjected with HTO to measure changes in TBW. There was no significant change in the TBW of gentoo 1 so that water influx equaled water efflux. Part of the weight lost by gentoo 3 resulted from a 6% decrease in TBW. As a result, water efflux exceeded influx by 7%.

Macaronis 6 and 9 were fasting males brooding their chicks while the females foraged at sea, a normal part of the reproductive cycle for this species. The TBW and percent body water did not differ between the fasting and foraging birds, although water flux rate was 93% less in the fasting birds. Two days after blood sampling, macaroni 9 left the rookery and was not seen for 11 days. During this time its body weight increased 32%. Unfortunately, the food consumption and ADMR while at sea could not be determined because the final blood sample was accidently destroyed before it could be analyzed.

Discussion

Water Balance

The TBW of gentoo and macaroni penguins lies in the range of 62 − 70% for normally hydrated birds of all sizes (Skadhauge 1981). The average daily water intake equaled 25% of the TBW in gentoos and 28% in macaronis. This is similar to water flux rate of 23% in the domestic duck weighing 3 kg (Thomas and Phillips 1975) but 2 − 3 × greater than in domestic fowl (Chapman and Mihai 1972). The average water flux in free-ranging king penguins, *Aptenodytes patagonicus,* feeding at sea on squid was 29% of the TBW/day (Kooyman et al. 1982). However, the measurements on king penguins were restricted to their time at sea and are not directly comparable to the present measurements on gentoos and macaronis which cover time spent at sea and on shore.

Although the TBW was normal in the two male macaronis near the end of their 35 day brooding fast, the water flux rate was only one-fourteenth that of the foraging birds. During this time, males do not feed but are able to remain in water balance by relying on metabolic water and by minimizing evaporative and excretory water loss (Schmidt-Nielsen and Sladen 1958; Murrish 1973). The half-time for water turnover of 33 − 37 days emphasizes the degree to which body water was conserved. The longest half-time for water turnover reported for a mammal was 54 days in fasting elephant seal pups, *Mirounga angustirostris* (Ortiz et al. 1978).

Possible errors in the measurement of water flux with HTO have been discussed elsewhere (Lifson and McClintock 1966; Nagy and Costa 1980). In the present study, the principal source of error is the exchange of inspired water vapor for HTO along the respiratory surfaces. This error was calculated from estimates of ventilation (Lifson and McClintock 1966) to overestimate water flux by 10% in fasting penguins and 5% in feeding penguins assuming 1) a fasting or average daily metabolic rate and 6% oxygen extraction efficiency 2) 20 kJ · L O_2^{-1} and 3) an ambient temperature of 4 °C and relative humidity of 80%. Overestimates of water flux will produce equivalent errors in the estimated metabolism of fasting and feeding penguins.

Fasting Metabolic Rate

The fasting metabolism of macaronis 6 and 9 while on the rookery brooding their chicks can be calculated from

water flux if 1) metabolic water production from the catabolism of fuel reserves was the only source of water entering the body pool and 2) the birds remained in water balance (Nagy 1975; Nagy and Costa 1980). The very low water turnover rates (Table 1) indicate that the macaronis did not drink during their fast, and their normal TBW (63% of BW) suggests that they were normally hydrated. The calculated metabolic rate is independent of whether fat or protein was the primary fuel because the ratio of oxidative energy production to metabolic water formation is identical for fat or protein in uricotelic animals (e.g. 0.445 W · day · ml H_2O^{-1}) (Schmidt-Nielsen 1979). The average metabolic rate, MR (W · kg^{-1}) = r_w × 0.445 W · day · ml H_2O^{-1} where r_w equals the fasting water turnover rate in ml H_2O · day^{-1} · kg^{-1}. The mean fasting metabolic rate for the two macaronis with a mean mass of 3.8 kg and water flux of 12.5 ml · day^{-1} · kg^{-1} (Table 1) was 5.6 W · kg^{-1} or 1.8 × the predicted standard metabolic rate (SMR) (Aschoff and Pohl 1970). Similar estimates based on weight loss over an 18 – 39 day period ranged from 4.0 – 6.6 W · kg^{-1} ($n = 5$) depending on the assumed composition of the mass lost (e.g. 56% fat and 9% protein or 90% fat) (Croxall 1982). However, the estimated metabolic rate based on weight loss is sensitive to small errors in the amount of tissue protein catabolized because protein loss releases intracellular water to be used in urine formation of lost by evaporation. For each gram of protein catabolized, 2.3 g of intracellular water is released assuming 1) lean tissue is 30% protein and 70% water and 2) the birds remain normally hydrated. The release of preformed intracellular water provides no energy to the animal and reduces the fraction of weight loss attributable to fat catabolism. In contrast, the proportion of fat and protein catabolized is not critical to metabolic estimates based on water turnover because 1) the calculation is based on de novo water production from catabolism within the prelabeled body water pool and 2) the oxidative water production is identical for fat and protein in birds.

ADMR in Feeding Birds

Estimates of prey consumption based on water flux rates require that: 1) the only sources of water are from metabolism and preformed water in the diet, and 2) the composition and water content of the diet are known (Shoemaker et al. 1976). If these conditions are satisfied, then:

$$r_F = \frac{r_w}{P_w + E_F \cdot E_m \cdot M_w}$$

where r_F is the number of grams of dry food (F) consumed per kg of body weight/day, r_w is the total water turnover in ml/kg/day, P_w is the amount of preformed water/g of F, E_F is the number of kilojoules of energy/g of F, E_m is the metabolizable energy coefficient and equals the number of kilojoules metabolized per kilojoule ingested, and M_w is the water produced/kilojoule of F metabolized. The feeding rate (r_F) is converted to energy metabolized (in watts/kg) by

$$ADMR = r_F \cdot E_F \cdot E_m \cdot k$$

where k is a constant that converts the units to W · kg^{-1} ($k = 1.157 \cdot 10^{-8}$ W · day · kJ^{-1}). Values used to calculate prey consumption and ADMR for gentoos and macaronis are shown in Table 2. Croxall and Prince (1980a) found that macaronis feed exclusively on krill while the average diet of gentoos is composed of 67% krill and 33% fish. The nutritional value of gravid female krill is 42% greater than that of male krill because of a higher lipid content (Clarke 1980). This difference will significantly alter the calculated ADMR depending upon which sex is predominant in the diet. Analysis of stomach contents (Croxall, unpublished) has shown that approximately equal numbers of male and female krill were taken by gentoos and macaronis on South Georgia. This is similar to the ratio observed by Volkman et al. (1980) for Adelie penguins, *Pygoscelis adeliae,* and gentoos on King George Island, although chinstrap penguins, *Pygoscelis antarctica,* consumed more male than female krill. ADMR was calculated assuming that equal numbers of male and female krill were consumed with a maximum and minimum range based on diets composed exclusively of either male or female krill. This range of ADMR should cover seasonal changes in the sex ratio or nutritional value of ingested krill. Identification of the fish taken by gentoos is limited to *Notothenia rossii, Notothenia larseni* (Notothenidae) and *Champsocephalus gunnari* (Chaenichthyidae). The composition of these fish was not available, so a similar subantarctic species of nototheniid, *Notothenia coriiceps* (Crawford 1979), was used for biochemical composition and water content (Table 2).

The difference in the fresh weight consumption of either male or female krill estimated from water flux rates was negligible because of their similar water contents (Tables 2 and 3). Gentoos consumed an average of 118 g fresh krill · kg^{-1} · day^{-1} and 61 g fresh fish · kg^{-1} · day^{-1}. Macaronis consumed an average of 210 g fresh krill · kg^{-1} · day^{-1}. The mean ADMR for gentoos was 7.1 W · kg^{-1} with a range of 6.2 W · kg^{-1} on a diet of fish and male krill to 8.0 W · kg^{-1} on a diet of fish and gravid female krill. The mean ADMR of macaronis was 9.1 W · kg^{-1} with a range of 7.5 – 10.6 W · kg^{-1} on a diet of either male or female krill, respectively (Table 3). The higher lipid content of gravid female versus male krill increased the calculated ADMR 29% in gentoos and 41% in macaronis. The ratio of ADMR/SMR was 2.6 (range 2.3 – 2.9) for gentoos and 2.9 (range 2.4 – 3.4) for macaronis depending on whether male or female krill were used in the calculation. The ADMR of female macaronis foraging at sea was 1.6× greater than the fasting metabolism of males brooding the chick.

Table 2. Composition of male and female *Euphausia superba, Notothenia coriiceps* and the parameters used to calculate prey consumption and ADMR from water turnover rates; proximate biochemical composition of *E. superba* and *N. coriiceps* from Clarke (1980) and Crawford (1979); preformed water (P_w) in food equals the water content divided by the dry weight; caloric content of food (E_f) calculated assuming carbohydrate = 17.2 kJ · g^{-1}, lipid = 39.4 kJ · g^{-1}, and protein = 18.4 kJ · g^{-1} for uricotelic animals; metabolic water production (M_w) calculated assuming carbohydrate metabolism produces 3.1 × 10^{-2} g H_2O · kJ^{-1}, lipid produces 2.6 × 10^{-2} g H_2O · kJ^{-1}, and protein produces 2.6 × 10^{-2} g H_2O · kJ^{-1}; metabolizable energy coefficient for penguins from Costa (pers. comm.)

Species	*Euphausia superba* (male)	*Euphausia superba* (gravid female)	*Notothenia coriiceps*
Composition (%)			
Water	80.1	76	78
Protein	10.4	10.6	17.1
Lipid	2.4	6.3	0.97
Carbohydrate	0.34	0.64	0.28
Chitin	2.1	1.9	NA
Ash	4.1	2.8	3.6
Preformed water (P_w) (g H_2O/g dry food)	4.0	3.17	3.55
Caloric content, E_f (kJ/g dry food)	19.28	22.73	16.28
Metabolic water, M_w (g H_2O/kJ metabolized) × 10^{-2}	2.64	2.64	2.64
Metabolizable energy coefficient, E_m (J metabolized/J food)	0.8	0.8	0.8

It was assumed that all of the foraging birds were in metabolic homeostasis. We think this is a valid assumption based on the small weight change (−0.72% ± 3.8) for all of the birds studied except gentoos 1 and 3. These latter two birds lost 10% and 15% of their body weight, respectively, over a 10 day period. The calculated water flux rates used to estimate prey consumption and ADMR were appropriately corrected for changes in body weight and TBW according to Nagy and Costa (1980). However, whether the weight loss represented a real decrease in the bird's tissue mass is uncertain. Every attempt was made to capture and weigh the birds after they had fed their chicks. However, it was not possible to be certain that their stomachs were completely empty, and part of their mass may have been undigested food. As a result, an apparent increase or decrease in body weight might simply reflect differences in the amount of food remaining in the stomach. Despite these uncertainties, the estimated prey consumption for the 5 gentoos and 3 macaronis is reasonably consistent.

A significant error in the calculated ADMR would result if the birds lost weight due to fat catabolism. The utilization of stored fat in small amounts would increase the bird's actual metabolism without a large change in body weight. For example, a 3% weight loss due to fat metabolism in a 6.2 kg gentoo would underestimate ADMR by 20% over a 10 day period. Conversely, deposition of fat while feeding would cause an overestimate of ADMR. However, short term cyclical changes in the storage and utilization of fat while at sea and on shore would be averaged during a 5–20 day study period so long as there was an overall stability of body weight and composition. There was no reason to believe that foraging birds were not in metabolic homeostasis, and the small average weight change during the study period supports this assumption.

An important consideration for birds feeding at sea is the ingestion of sea water. The deliberate or incidental ingestion of sea water could not be quantified in this study, and it was assumed that all preformed water came from food. The estimated food consumption and ADMR calculated from water flux rates is, therefore, a maximum estimate. The actual food consumption and

Table 3. Prey consumption and ADMR of free-ranging gentoo and macaroni penguins. Values for ADMR assume that equal numbers of male and female krill were consumed with a minimum and maximum range (parenthesis) based on diets composed exclusively of either male or female krill. The allometric coefficient for the mass dependent metabolism (0.729) and the estimated SMR from Aschoff and Pohl (1970)

Species	Male or female krill (g fresh/kg · day)	Fish (g fresh/kg · day)	ADMR (W/kg)	ADMR ($W/kg^{.729}$)	SMR (W/kg)	ADMR/SMR
Gentoo 1	100	51	6.1 (5.3–6.8)	10.8 (9.4–12.0)	2.5	2.4 (2.1–2.7)
Gentoo 2	120	61	7.2 (6.3–8.1)	11.8 (10.3–13.3)	2.7	2.7 (2.3–3.0)
Gentoo 3	130	67	7.8 (6.8–8.8)	12.8 (11.2–14.5)	2.7	3.0 (2.6–3.3)
Gentoo 4	138	71	8.3 (7.2–9.3)	12.9 (11.2–14.5)	2.8	2.9 (2.5–3.3)
Gentoo 5	102	52	6.1 (5.3–6.9)	9.5 (8.2–10.7)	2.8	2.2 (1.9–2.4)
Mean	118	61	7.1	11.6	2.7	2.6
SD	17	9	0.99	1.4	0.1	0.34
Macaroni 6	178	NA	7.7 (6.3–9.0)	11.1 (9.1–13.0)	3.1	2.5 (2.1–2.9)
Macaroni 7	165	NA	7.2 (5.9–8.4)	10.2 (8.3–11.9)	3.1	2.3 (1.9–2.7)
Macaroni 8	287	NA	12.4 (10.2–14.5)	17.1 (14.1–20.0)	3.2	3.9 (3.2–4.5)
Mean	210	NA	9.1	12.8	3.1	2.9
SD	67	NA	2.9	3.8	0.1	0.84

ADMR would be less than calculated if significant sea water were ingested. However, previous studies of California sea lions, *Zalophus californianus,* and harbor seals, *Phoca vitulina,* concluded that sea water ingestion was less than 10% of water intake and occurred accidently while swallowing food underwater (Pilson 1970; Depocas et al. 1971).

There were no significant differences in the ADMR of gentoos and macaronis when scaled allometrically using the coefficient of Aschoff and Pohl (1970), nor in the ratio of ADMR/SMR (Table 3). This suggests that despite pronounced differences in the duration of individual foraging trips to sea, the energy expended per day by adults of the two species is approximately equivalent.

The estimated ADMR of king penguins, *Aptenodytes patagonicus,* at South Georgia based on an equal division of time in the rookery and foraging at sea was 10.4 $W \cdot kg^{-0.729}$ or 2.4 × SMR (Kooyman et al. 1982). Both values are very similar to those of gentoos and macaronis (Table 3). Previous estimates of ADMR in birds weighing 5 – 406 g range from 2.2 – 5.9 × SMR based on the following methods 1) pellet analysis, 2) crop content, 3) time-activity budgets combined with laboratory data, 4) observations of feeding rate and excretion rate and 5) doubly labeled water (King 1974; Hails and Bryant 1979). Our values for gentoo and macaroni penguins are at the low end of this range, but there are too few measurements to say whether the ADMR of aquatic birds such as penguins is less than flying birds. Underwater swimming is certainly a less expensive form of locomotion than flying (Schmidt-Nielsen 1972), but most data for swimming are derived from studies on fish. Although penguins are hydrodynamically shaped to minimize drag (Nachtigall and Bilo 1980), measurements of swimming metabolism have not been made.

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References

Aschoff J, Pohl H (1970) Rhythmic variations in energy metabolism. Fed Proc 29:1541 – 1551

Biomass (1977) Biological investigations of marine Antarctic systems and stocks, vol I. Research proposals. Scientific Committee on Antarctic Research. Scott Polar Research Institute, Cambridge, 79 pp

Biomass (1981) Biological investigations of marine Antarctic systems and stocks. vol II. Selected contributions to the Woods Hole Conference on Living Resources of the Southern Ocean. Scientific Committee on Antarctic Research. Scott Polar Research Institute, Cambridge, 155 pp

Chapman TE, Mihai D (1972) Influences of sex and egg production on water turnover in chickens. Poult Sci 51:1252 – 1256

Clark A (1980) The biochemical composition of krill, *Euphausia superba* (Dana) from South Georgia. J Exp Mar Biol Ecol 43:221 – 236

Crawford RE (1979) Effect of starvation and experimental feeding on the proximate composition and caloric content of an antarctic teleost, *Notothenia coriiceps neglecta.* Comp Biochem Physiol A62: 321 – 326

Croxall JP (1982) Energy costs of incubation and moult in petrels and penguins. J Anim Ecol 51:177 – 194

Croxall JP (1984) Seabird ecology. In: Laws RM (ed) Ecology of the Antarctic. Academic Press, London New York

Croxall JP, Prince PA (1980a) The food of gentoo penguins, *Pygoscelis papua,* and macaroni penguins, *Eudyptes chrysolophus,* at South Georgia. Ibis 122:245 – 253

Croxall JP, Prince PA (1980b) Food, feeding ecology, and ecological segregation of seabirds at South Georgia. Biol J Linn Soc 14:103 – 131

Croxall JP, Prince PA (1982) A preliminary assessment of the impact of seabirds on marine resources at South Georgia. Com Nat Franc Recherch Antarct 51:501 – 509

Degen AA, Pinshow B, Alkon PU, Aron H (1981) Tritiated water for estimating total body water and water turnover rate in birds. J Appl Physiol: Resp Environ Exercise Physiol 51:1183 – 1188

Depocas F, Hart JS, Fisher HD (1971) Sea water drinking and water flux in starved and fed harbor seals, *Phoca vitulina.* Can J Physiol 49:53 – 62

Hails CJ, Bryant DM (1979) Reproductive energetics of a free-living bird. J Anim Ecol 48:471 – 482

King JR (1974) Seasonal allocation of time and energy resources in birds. In: Paynter RA (ed) Avian energetics. Nuttall Ornithological Club, Massachusetts, pp 23 – 40

Kooyman GL, Davis RW, Croxall JP, Costa DP (1982) Diving depths and energy requirements of king penguins. Science 217:726 – 727

Lifson N, McClintock R (1966) Theory of use of the turnover rates of body water for measuring energy and material balance. J Theor Biol 12:46 – 74

Mougin JL, Prevost J (1980) Evolution annuelle des effectifs et des biomasses des oiseaux antarctiques. Rev Ecol (Terre et Vie) 34:101 – 133

Murrish DE (1973) Respiratory heat and water exchange in penguins. Respir Physiol 19:262 – 270

Nachtigall W, Bilo D (1980) Stromungsanpassung des Pinguins beim Schwimmen unter Wasser. J Comp Physiol A 137:17 – 26

Nagy KA (1975) Water and energy budgets of free-living animals: measurement using isotopically labeled water. In: Hadley NF (ed) Environmental physiology of desert organisms. Halsted Press, Pennsylvania, pp 227 – 245

Nagy KA, Costa DP (1980) Water flux in animals: analysis of potential errors in the tritiated water method. Am J Physiol 238:454 – 465

Ortiz CL, Costa DP, Le Boeuf BJ (1978) Water and energy flux in elephant seal pups fasting under natural conditions. Physiol Zool 51:166 – 178

Pilson MEQ (1970) Water balance in California sea lions. Physiol Zool 43:257 – 268

Richards PA, Tickell WLN (1968) Comparison between the weather at Bird Island and King Edward Point, South Georgia. Br Antarct Surv Bull 15:63 – 69

Schmidt-Nielsen K, Sladen WJL (1958) Nasal salt secretion in the Humboldt penguin. Nature 181:1217 – 1218

Schmidt-Nielsen K (1972) Locomotion: energy cost of swimming, flying and running. Science 177:222 – 228

Schmidt-Nielsen K (1979) Animal physiology: adaptation and environment. Cambridge University Press, Cambridge London, p 319

Shoemaker VH, Nagy KA, Costa WR (1976) Energy utilization and temperature regulation by jackrabbits *(Lepus californicus)* in the Mojave desert. Physiol Zool 49:364 – 375

Skadhauge E (1981) Osmoregulation in birds. Springer, New York, pp 6 – 7

Thomas DH, Phillips JA (1975) Studies in avian adrenal steroid function. 2. Chronic adrenalectomy and the turnover of ^3H_2O in domestic ducks. Gen Comp Endocrinol 26:404 – 411

Turner MD, Neely WA, Hardy JD (1960) Rapid determination of deuterium oxide in biological fluids. J Appl Physiol 15:309 – 310

Volkman NH, Presler P, Trivelpiece W (1980) Diets of pygoscelid penguins at King George Island, Antarctica. Condor 82:373 – 378