

Chapter 15

Energy budget of African Penguin *Spheniscus demersus* chicks

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We used the doubly-labelled water (DLW) technique to measure the pre fledging energetics of African Penguins *Spheniscus demersus* on Robben Island, South Africa. We also measured growth rates of chicks, finding a median Gompertz growth coefficient of 0.0460. These enabled us to devise an energy budget with two main components, the energy metabolized and the energy deposited as tissue. The relationship between daily en-

ergy expenditure and chick mass was estimated from 19 experiments and found to be best modelled by a modified power curve. Total metabolizable energy was estimated to be 88.5MJ, and the peak daily metabolizable energy requirement was estimated to be 1787kJ/day, at age 53 days; 90% of this value was reached at age 36 days, and energy demand remained fairly constant until fledging at average age 68 days.

Keywords: African Penguin, pre fledglings energetics, energy budget, doubly-labelled water technique

As described by Visser *et al.* (2007), a knowledge of energy budgets for chicks between hatching and fledging provides a valuable tool for understanding energy demands during reproduction, and for comparing the consequences of different breeding strategies, or the consequences of breeding under various environmental conditions. This short note extends this knowledge to include the African Penguin *Spheniscus demersus*.

The African Penguin has three discrete breeding areas: the offshore islands of Nelson Mandela Bay, Eastern Cape, South Africa, the offshore islands and four mainland sites in the Western Cape, and in southern Namibia, on the offshore islands and at caves and cliffs along the Namib Desert coastline which are inaccessible to terrestrial predators (Crawford & Whittington 1997).

Clutch size is either one egg or two. The incubation period averages 38 days. If two eggs are laid, hatching is usually asynchronous. During the chick-raising period, adults forage at sea with Sardine *Sardinops sagax* and Anchovy *Engraulis encrasicolus* as the preferred prey. The pre fledging period varies considerably, between 64 and 105 days (Hockey *et al.* 2005). Chicks are altricial, and are fed by both parents. Either one or two chicks fledge; breeding success is influenced by food availability (Crawford *et al.* 2006). The general development of chicks was described by Seddon & van Heezik (1993).

This study was conducted at Robben Island, South Africa (33°47'S, 18°21'E), between March and September 2004. This colony lies in the central core of the breeding range. Over the five-year period 2001–2005, 2004 was a year of below-average breeding success (Barham *et al.* 2007).

Study nests were located prior to hatching. Chicks were weighed with a pesola spring balance; if two chicks were present, the A and B chicks were readily distinguishable by size. The chicks were weighed mostly at four- or five-day intervals until fledging. The hatching day was designated as day 0.

We fitted Gompertz growth curves of the form $M(t) = A \exp(-b \times \exp(-K_G t))$, where K_G is Gompertz growth coefficient; we estimated this using the method described in Underhill (in press) with the asymptote A set at 3 500 g, the average adult mass, and $b = -\log(H/A)$ where H is the observed hatchling mass, and used the median as indicative of the average pattern of growth.

We used the Doubly Labelled Water (DLW) method to measure the daily energy expenditure of free-living chicks of varying masses between hatching and fledging (Speakman 1997). The sampling protocol followed that used by Visser *et al.* (2007), except that the final blood sample was taken after 48 hours (instead of 24).

The analytical procedure applied was that detailed by Visser & chekerman (1999). As in Visser *et al.* (2007), the body water pool was estimated using the "plateau method" (Speakman 1997, Visser *et al.* 2000). Rates of CO₂ production were calculated using equation 7.17 of Speakman (1997), converted to a daily rate. This was transformed to daily energy expenditure (DEE, kJ/d) using a factor of 27.3 kJ/l based on a protein-rich diet (Gessaman & Nagy 1988). We fitted the modified power curve of Tjørve *et al.* (in press) to relate the DEE of a chick to its mass.

We decomposed the energy budget into two main components. The metabolisable energy intake (MEI, kJ/d) is the

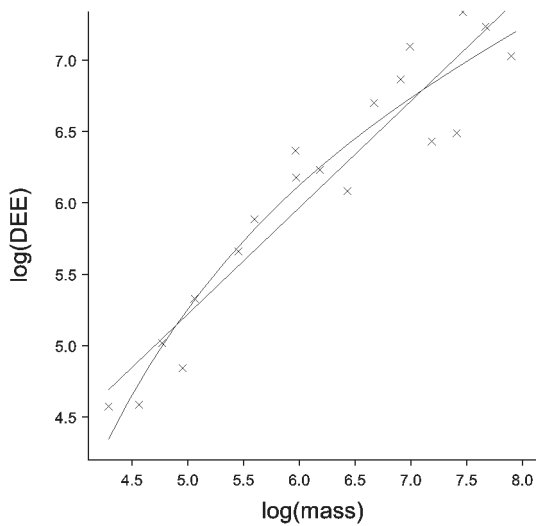


Figure 1: The relationship between body mass and daily energy expenditure in African Penguin chicks. The straight line represents the linear regression relating $\log(\text{DDE})$ to $\log(\text{mass})$ (ie the standard power curve), the curved line represents the modified power curve

sum of DDE (which was measured with the DLW method), and the amount of tissue energy accumulated (E_{tis} , kJ/d) (which was estimated from the growth curve): $\text{MEI} = \text{DDE} + E_{\text{tis}}$. Daily energy expenditure comprises energy consumed through basal metabolism, temperature regulation, behaviour (including movement), heat increment of feeding and biosynthesis (Klaassen *et al.* 1989, Drent *et al.* 1992, Gabrielsen *et al.* 1992).

E_{tis} was estimated from the growth model and the likely mass-specific energy content of the tissue. Mass-specific energy density (ED, kJ/g) has not been determined for the African Penguin so we used the equation for the similar-sized Chinstrap Penguin *Pygoscelis antarctica*:

$$\text{ED} = 3.18 + 7.08M/A$$

where ED is the estimated energy density at mass M and A is the asymptotic mass (Myrcha & Kaminski 1982, Visser 2001). ED at age t was estimated from this relation by using the Gompertz growth curve to estimate the mass on day t , $M(t)$, so that the energy accumulated as tissue on day t was estimated as:

$$E_{\text{tis}}(t) = M(t)(3.18 + 7.08M(t)/A) - M(t-1)(3.18 + 7.08M(t-1)/A)$$

The Gompertz growth coefficient was estimated for 104 chicks for which repeated measurements of mass were available. The median of the Gompertz growth coefficients was 0.0460 (lower and upper quartiles 0.0406 and 0.0506). The estimated mass at hatching was 72 g. Using the method of Underhill (in press), the Gompertz growth curve used to model the growth of African Penguin chicks was estimated to be:

$$M(t) = 3550 \exp(-3.884 \times \exp(-0.0460 t))$$

where $M(t)$ is the estimated mass on day t . The observed median fledging period was 68 days, so that the modelled mass at fledging was 2.95kg, close to the observed mean fledging mass of 2.83kg.

DDE experiments were successfully concluded on 19 chicks (Fig. 1). The relationship between $\log \text{DDE}$ (kJ/d) and

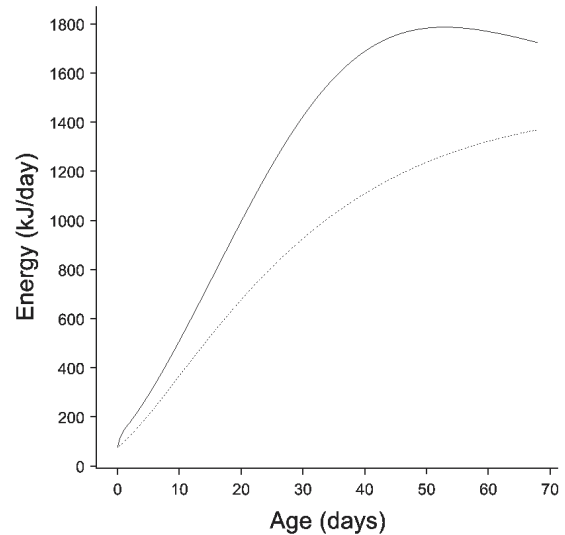


Figure 2: The daily energy budget for African Penguin chicks from hatching to fledging. The metabolisable energy intake (MEI, kJ/day, solid line) is the sum of the energy used for gain in tissue energy (E_{tis}) and the daily energy expenditure (DDE, kJ/day, dotted line)

\log body mass (M , g) was best described by the modified power curve:

$$\log_e(\text{DDE}) = 4.097 + 0.400 \log_e M - 24.992 \log_e M/M$$

with $R^2 = 0.92$; the standard errors of the coefficients are 0.21 ($P = 0.004$), 0.163 ($P = 0.026$) and 11.0 ($P = 0.038$) respectively. The equation is rewritten as:

$$\text{DDE} = 60.16 M^{0.400-24.992/M}$$

The largest daily MEI (Peak-DME, kJ/d) was calculated to be 1787 kJ/d at 53 days. Daily MEI reached 90% of the peak value at age 36 days (Fig. 2) when the average chick weighed 1.67 kg.

Weathers (1992) derived a relationship between Peak-DME and the fledging mass and incubation period, based on the energy budgets for 30 bird species. The equation is $\text{Peak DME} = 11.69 M_{\text{fl}}^{0.9082} T_{\text{fl}}^{-0.428}$ where M_{fl} is the estimated mass at fledging (for the African Penguin, 2.952 kg) and T_{fl} is the fledging period (68 days). Using this equation, the predicted peak is 2 706kJ, so that the observed Peak-DME is 34% below the predicted value.

The sum of the daily MEI values between hatching and fledging at 68 days yields Total MEI (kJ). This was calculated to be 88.5 MJ, which represents the total amount of metabolisable energy needed for successfully raising a chick. Assuming a digestion efficiency of 76% (Cooper 1977), an estimate of the total energy intake is 116.5 MJ. If the diet consisted entirely of Sardine *Sardinops sagax* (8.59 kJ/g wet mass, Batchelor & Ross 1984) the amount of food the parents have to provide to a chick between hatching and fledging would be 13.6 kg, and if the diet consisted of Anchovy *Engraulis encrasicolus* (6.74 kJ/g wet mass Batchelor & Ross 1984), the amount of food would be 17.3 kg.

Weathers (1992) derived a relationship between Total MEI and the fledging mass and incubation period: $\text{Total MEI} = 6.65 M_{\text{fl}}^{0.852} T_{\text{fl}}^{0.71}$. From this equation, the predicted Total MEI of an African Penguin chick from hatching to fledging is 121.6 MJ. Our observed value is 27% below the predicted value.

The sum of the daily gains in tissue energy during growth was calculated to be 26.8 MJ, which represented 30.2% of the Total-MEI. This is slightly above the average value of 27% reported by Drent *et al.* (1992), based on a review of 14 gull and tern species.

Cooper (1977) estimated that the total food intake between hatching and the age of 70 days was 22.5 kg of anchovy, based on weighing food intake of captive chicks. Using a factor of 8.21 kJ/g wet mass, he estimated the total energy intake to be 186.3 MJ, and using an assimilation of efficiency of 76%, that the TME was 140.3 MJ. However, using the value of 6.74 kJ/g wet mass (Batchelor & Ross 1984), the total energy intake obtained by Cooper (1977) is revised to be 146.3 MJ, and the TME to be 111.2 MJ, 27% above our estimate of 88.5 MJ. However, Cooper (1977) commented that the food intake of captive chicks was larger than that of naturally reared chicks; this would bring Cooper's (1977) estimate close to ours.

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