ENERGETICS OF BLACK-LEGGED KITTIWAKE

*Rissa tridactyla* CHICKS

GEIR WING GABRIELSEN\(^1,2\), MARCEL KLAASSEN\(^1,3,4\) & FRIDTJOF MEHLUM\(^1\)

**ABSTRACT**

We compiled the energy budgets of Black-legged Kittiwake *Rissa tridactyla* chicks in Kongsfjorden, Svalbard (79°N, 12°E), utilising (1) deuterium turnover rates to estimate food intake, (2) the doubly labelled water (D\(_2\)18O) method in conjunction with mass gain measurements and carcass analysis to determine energy requirements, and (3) laboratory assessed components of the nestling energy budget and production cost from mass gain measurements and carcass analysis. While (1) and (2) gave similar results we found that (3) underestimated the total energy expenditure by 13-21%. This is explained by (3) neglecting the activity costs. During the first 15-16 days after hatching Kittiwake chicks are regularly brooded by the parents, resulting in a saving of 19% of the metabolisable energy intake of the chick for this period. Beyond 16 days chicks live within the zone of thermal neutrality. The resting metabolic rate and the energy deposited as tissue (inclusive tissue synthesis) constituted 53% and 24% respectively, of the total energy budget over the entire nestling period. After 16 days, activity of the chicks increased considerably, making up 22% of the total metabolisable energy intake. The main daily proportion of energy delivered to each chick raised is 33% of the energy required by a pair of adult Kittiwakes. The parental investment in the inshore feeding Kittiwake is relatively high, in particular for pairs raising two chicks, when compared with offshore feeders.

\(^1\)Norwegian Polar Research Institute, P.O. Box 158, N-1330 Oslo Lufthavn, Norway; \(^2\)present address: Norwegian Institute for Nature Research, c/o Tromsø museum, University of Tromsø, N-9000 Tromsø, Norway; \(^3\)DLO Institute for Forestry and Nature Research (IBN-DLO), P.O. Box 9201, 6800 HB Arnhem, The Netherlands; \(^4\)present address: Max-Planck-Institut für Verhaltensphysiologie, D-W-8138 Andechs, Germany.

**INTRODUCTION**

In order to determine the impact of birds on the energy flow through marine ecosystems it is important to examine the energy requirements of the birds throughout their entire life cycle. In the Barents Sea area, the Black-legged Kittiwake *Rissa tridactyla* is one of the most numerous seabird species (Lovenskiold 1964), with an estimated 500,000 pairs annually breeding in the area (Gabrielsen et al. 1992). In an earlier investigation (Gabrielsen et al. 1987) we measured the energy requirements of adult Kittiwakes during the chick-rearing period. In the present paper we present data on the energy requirements of Kittiwake chicks up until fledging, here taken as 35 days after hatching (Barrett & Runde 1980), and the allocation of these energy requirements to different components of the energy budget.

Several methods have been used to assess the energy requirements of chicks, including the measurement of components of the energy budget in the laboratory, together with growth rate measurements and carcass analysis (Ricklefs 1974, Ricklefs et al. 1980). Only recently has the doubly labelled water method for measuring total energy expenditure (as CO\(_2\) production: Lifson & McClintock 1966, Nagy 1980) been used in the compilation of chick energy budgets (Fiala & Congdon 1983, Williams & Nagy 1985, Williams & Prints 1986, Klaassen et al. 1989, Weathers et al. 1990, Weathers & Sullivan 1991, Konarzewski et al. 1992). However, although the doubly labelled water method is gaining in popularity,
only one validation of this method has so far been undertaken in chicks (Klaassen et al. 1989).

The method of estimating food intake from water intake, measured via deuterium or tritium turnover (Shoemaker et al. 1976), has yet to be assessed when used to measure chick energy requirements. In theory, this method can be used for Kittiwake chicks as they have no access to free water for the maintenance of their water balance. The only water they receive is through the food they are given at the nest by their parents. The three methods were used by us simultaneously to compile the energy budget of Kittiwake chicks. These methods were compared in order to obtain the best possible estimate of Kittiwake chick energy requirements. To this end we measured growth in the field and recorded the parental behaviour at the nest. In addition, we measured daily energy expenditure using doubly labelled water and we estimated daily gross energy intake from deuterium turnover, both in the field and in laboratory validation experiments. In the laboratory we also measured the metabolism of fasted chicks in relation to ambient temperature.

METHODS

During July-August 1986 and 1987 Kittiwake chicks were studied in the Krykkje-fjellet, Kongsfjorden, Svalbard (79°N, 12°E), where annually 300-600 pairs of Kittiwakes breed.

When compiling the energy budgets of Kittiwake chicks several components were distinguished as outlined below. Of the gross energy intake of a bird (GEI) only a fraction (Q) is metabolisable energy (ME), the rest leaving the bird in the form of pellets or faeces:

\[ ME = GEI \cdot Q \]  

(1)

The metabolisable energy can be used for both anaerobic (energy accumulated in body tissue, \( E_{\text{tis}} \)) and catabolic purposes (daily energy expenditure, \( DEE \)):

\[ ME = DEE + E_{\text{tis}} \]  

(2)

The daily energy expenditure consists of the resting metabolic cost (\( RMR \)), the cost for body tissue synthesis (\( E_{\text{syn}} \)), the cost for thermoregulation (\( E_{\text{tr}} \)) and activity costs (\( E_{\text{act}} \)):

\[ DEE = RMR + E_{\text{syn}} + E_{\text{tr}} + E_{\text{act}} \]  

(3)

Growth

The colony was visited regularly so that the date of hatching of the chicks was known with an accuracy of one day. Each bird was individually marked and weighed to the nearest gram with a Pesola spring balance. Chicks were subsequently weighed at least once every second day, at around noon.

Body composition

Twenty-nine chicks ranging in age from 0-30 days were collected in the Krykkje-fjellet colony in 1984 and 1986. After collection, the carcasses were weighed and deep frozen until analysed. The carcasses were analysed for water, lipid and non-lipid dry matter (for details see Taylor & Konarzewski 1989) by Janek Taylor & Marek Konarzewski (Department of Biology, University of Warsaw, Poland). Energy equivalents of 38 kJ.g\(^{-1}\) lipid and 20 kJ.g\(^{-1}\) non-lipid dry matter (Ricklefs 1974) were used to determine the energy density of each individual. Protein content was calculated from non-lipid dry mass by subtracting the ash content for which 13% of the non-lipid dry mass was used (Ricklefs 1974).

Indirect calorimetry

The metabolic rate measurements of chicks were made in the Research Station of the Norwegian Polar Research Institute in Ny-Ålesund, 8 km from the colony. Metabolic rates were measured as \( O_2 \) consumption, occasionally with simultaneous measurements of \( CO_2 \) production, as described by Gabrielsen et al. (1988). Metabolic measurements were made on 27 chicks that had fasted for at least 4 hours, at temperatures ranging from 5 to 32°C. Several trials with chicks of all age classes, at varying ambient temperatures, were conducted in order to assess the change in lower critical temperature with body mass. Based on these trials chicks with
a body mass of up to 100 g were assumed to be within their thermal neutral zone at ambient temperatures between 28 and 32°C. For chicks with a body mass higher than 100 g we assumed that this was the case at temperatures between 19 and 26°C. All measurements were done under continuous light conditions, since at Krykkje-fjellet the birds experience 24 hours of daylight. The air flow rate varied from 1 to 4 l.min⁻¹, depending on the size of the bird. Determinations of metabolic rate were based on periods of at least five minutes in which the O₂ consumption was stable. When calculating energy expenditure from O₂ consumption a conversion coefficient of 20.0 kJ.l⁻¹ of dried O₂ at standard temperature and pressure (STPD, 0°C, 760 mm Hg) was used. Resting metabolic rate (RMR) was defined as the metabolic rate of fasted chicks within the thermal neutral zone. Thermal conductance (TC) was measured in fasted chicks at ambient temperatures below the thermal neutral zone (between 3.5 and 9°C) and was calculated as:

\[ TC = H \cdot (T_B - T_A) \cdot 10^{-3} \text{J.g}^{-1}\text{.day}^{-1}\text{.°C}^{-1} \]  

where \( H \) = metabolic rate below thermoneutrality (J.g⁻¹.day⁻¹), \( T_B \) = body temperature (°C), \( T_A \) = ambient temperature in the chamber (°C). \( T_A \) and \( T_B \) were measured using thin copper/constantan thermocouples connected to a Fluke (2168 A) meter. Body temperatures were measured during 15 trials using a thermocouple that was inserted 3 cm into the cloaca of the chick.

**Behavioural observations**

Observations of the colony were made on three days during the study period. Each observation period lasted 3 to 4 hours. Eighteen different nests with chicks of known age were watched, totalling 127 nest hours. The time the parents were incubating, brooding, standing, changing or feeding at the nest were registered.

**Weather**

Weather conditions including ambient temperature, wind and precipitation were recorded three times a day at the meteorological station in Ny-Ålesund.

**Food samples**

A total of 20 food samples were obtained from spontaneously regurgitating adults (4) and chicks (16) upon capture in the colony. The food samples consisted exclusively of polar cod *Boreogadus saida*, krill *Thysanoessa inermis* and the crustacean *Parathemisto libellula*. Chemical composition (fat and protein) and energy content were determined by the lipid extraction method (Folch *et al.* 1957), the Kjeldahl method and bomb calorimetry, respectively. Chicks used in the validation study were fed polar cod, which were analysed for their energy content using the methods described above. Values for protein and lipid content, necessary for the calculation of food intake from deuterium turnover (see Equations 7, 8), were not estimated. These values were taken from the measurements of food samples collected in the field.

**Doubly labelled water experiments**

Field A total of 36 chicks varying in age from 0 to 35 days were injected intraperitonially with 0.09 to 0.27 ml (depending on the size of the bird) of 30 atom % D₂O and 60 atom % H₂¹⁸O. Blood samples were taken before injection, 1 h after injection (equilibration completed) and 12 h and 24 h after equilibration. During each sampling, up to eight 15 µl microcapillary tubes were filled with blood taken from a wing vein. The whole procedure of catching, weighing, marking, bleeding and replacing the chick in the nest took 10 minutes. Blood samples were stored at 5°C until analysis by Isotope Ratio Mass Spectrometry (Masman & Klaassen 1987) at the Center of Isotope Research (CIO) in Groningen, The Netherlands.

Laboratory validation Six chicks varying in age from 2 to 34 days were subjected to validation of the doubly labelled water method via experiments following the same procedure as in the field. Between the blood sampling procedures we measured the O₂ consumption and the CO₂ production using the same experimental design described above. During the validation experiments the chicks were fed polar cod three times during each of the two 12 h experimental periods. No drinking water was pro-
vided. Five of the six chicks were simultaneously used for the validation of water influx rate. The food administered to the chicks during the validation period was weighed to the nearest gram using a Mettler (PE 16) balance.

**Calculations**

Water influx rate and CO\(_2\) production were calculated assuming linear mass changes and using the Equations 15 and 21 given in Lifson & McClintock (1966) after the equations were adapted for physical fractionation effects (Lifson & Lee 1961, Lifson & McClintock 1966). Body water, needed in the calculation of CO\(_2\) production, was calculated on the basis of the results from the body composition analysis. We calculated CO\(_2\) production and water influx for the interval between first and second, and between second and third sample after injection. Enrichment values were only used in the calculations if not clearly out of range due to a faulty analysis. When enough filled microcapillary tubes were available, duplicates were made of each sample for the doubly labelled water enrichment measurements. When the analyses deviated by more than 10%, more tubes were analysed in order to determine which analysis should be ignored. This procedure yielded two to eight usable CO\(_2\) production and water influx rate estimates per animal over each of the 12 h intervals, of which the mean and standard error were taken. CO\(_2\) production was converted to daily energy expenditure using an equivalent of 25 kJ·l\(^{-1}\) CO\(_2\). Only measurements of daily energy expenditure for individuals with an arbitrary chosen standard error around the mean of less than 50 kJ·day\(^{-1}\) (10% of the average metabolisable energy, of 511 kJ·day\(^{-1}\), see Results) were used in further analyses (53 out of 72 for field estimates and 9 of 12 validation experiments).

Gross energy intake can be calculated when the water influx rate, the composition of food eaten and the composition of the accumulated tissue of the young during the chick stage are known. Water influx \(W_f\) (ml·day\(^{-1}\)) is the sum of metabolic water production \(W_m\) (ml·day\(^{-1}\)) and water in the food \(W_f\) (ml·day\(^{-1}\)), assuming the animals do not drink water or exchange much vapour across lungs and skin:

\[
W_i = W_m + W_f \text{ (ml·day}^{-1})
\]  
(5)

The amount of water in the food equals the fraction of water in the food \((F_w)\) times the fresh mass of the food \((M_f)\):

\[
W_f = M_f \cdot F_w \text{ (ml·day}^{-1})
\]  
(6)

The metabolic water production can be derived from the fractions of lipid \((F_l)\) and protein \((F_p)\) in the food when the metabolic water yield of each of these tissues is known \((H_l, \text{ ml·g}^{-1}, \text{ and } H_p, \text{ ml·g}^{-1}, \text{ respectively})\). Of the food eaten by growing chicks, part of the nutrient is catabolised and part is deposited in the body tissue yielding no metabolic water. Thus calculation of metabolic water production from lipid and protein content of food should be corrected for the change in the amounts of lipid \((\delta M_l, \text{ g·day}^{-1})\) and protein \((\delta M_p, \text{ g·day}^{-1})\) in the body tissue:

\[
W_m = M_f \cdot (F_l \cdot H_l + F_p \cdot H_p) - (\delta M_l \cdot H_l + \delta M_p \cdot H_p) \text{ (ml·day}^{-1})
\]  
(7)

The change in the amount of lipid and protein in the body tissue of experimental chicks was calculated from the total body mass change and the data on body composition (see Equations 10, 11 and 12 in Results). Combining the Equations 5, 6 and 7, and solving for food intake yields:

\[
M_f = (W_i + \delta M_l \cdot H_l + \delta M_p \cdot H_p) \cdot (F_w + F_l \cdot H_l + F_p \cdot H_p)^{-1} \text{ (g·day}^{-1})
\]  
(8)

Food intake was converted to gross energy intake using the energy densities of the food. We used the values 1.070 and 0.392 ml H\(_2\)O·g\(^{-1}\) dry matter oxidized for the metabolic water yield of lipid and protein respectively (Nagy 1983). Gross energy intake was calculated over the same intervals as daily energy expenditure using available estimates of D-enrichments for each blood sampling. Gross energy intake values were used in further analyses only if
RESULTS

A logistic equation (Ricklefs 1967) was fitted to the increase of body mass \( (M, \text{g}) \) with age \( (t, \text{days}) \) using body masses of chicks of which we were sure that they had not died of starvation (Fig. 1).

\[
M = 410 \cdot (1 + 8.2 \cdot e^{-0.163t})^{-1}
\]  
(9)

Body composition analyses of chicks yielded equations, necessary in the calculation of daily energy expenditure and food intake from doubly labelled water turnover, for water content \( (B_w, \% \text{ of fresh mass}) \), lipid content \( (B_f, \% \text{ of dry mass}) \) and protein content \( (B_p, \% \text{ of dry mass}) \) as a function of body mass \( (M) \):

\[
B_w = 81.14 - 0.039 \cdot M \quad (r = -0.965, P < 0.001) \quad (10)
\]

\[
B_f = 15.09 + 0.040 \cdot M \quad (r = 0.817, P < 0.001) \quad (11)
\]

\[
B_p = 73.87 - 0.035 \cdot M \quad (r = -0.817, P < 0.001) \quad (12)
\]

In addition the body composition analyses resulted in an equation relating energy content of body tissue \( (E_t, \text{kJ.g}^{-1} \text{ fresh mass}) \) to body mass:

\[
E_t = 4.24 + 0.011 \cdot M \quad (r = 0.970, P < 0.001) \quad (13)
\]

Equations 9 and 13 enable us to calculate the daily cost of tissue deposition \( (E_{tis}, \text{kJ.day}^{-1}) \) over the entire developmental period (Fig. 2, upper graph). Assuming a synthesis efficiency of 75% (Ricklefs 1974), the cost of biosynthesis was calculated from the daily cost of tissue deposition by multiplying this cost by 0.33.

The daily resting metabolic rate and thermo-regulatory cost of the chicks throughout development in the colony (Fig. 2, second graph from top) were calculated using data on the operative temperature, body mass growth (Equation 9), resting metabolic rate (Equation 14), thermal conductance (Equation 15), and observations of adult behaviour (Fig. 5). Combination of this information allows us to calculate the energy saved by a chick as a consequence of parental brooding behaviour (Fig. 2, second graph from top).

Daily energy expenditure \( (DEE) \) and gross energy intake \( (GEI) \) increased with age up to approximately 23 days, after which age both parameters slightly decreased and stabilised (Fig. 2, two lower graphs).

Mass-specific resting metabolic rate \( (RMR) \) is described by the parabolic equation (Fig. 3):

\[
RMR = 547 + 6.1 \cdot M - 0.013 \cdot M^2 \quad (\text{J.g}^{-1} \cdot \text{day}^{-1}) \quad (r = 0.901, N = 56, P < 0.001)
\]  
(14)

Mean body temperature \( (T_p) \) of chicks during metabolic measurements was 39.2°C (\( SD = 0.4, N = 15 \)). This average value was used in the calculation of thermal conductance \( (TC, \text{Equation 4}) \). Thermal conductance of starved chicks is described by the equation (Fig. 4):

\[
TC = 1358 \cdot M^{0.651} \quad (\text{J.g}^{-1} \cdot \text{day}^{-1} \cdot ^\circ\text{C}) \quad (r = 0.917, N = 27, P < 0.001)
\]  
(15)
The respiratory quotient ($RQ$) value of starved chicks was $0.71$ ($SD = 0.21$, $N = 52$), indicating that fat was the major fuel during the indirect calorimetric measurements of starved chicks.

Ambient temperature in Ny-Ålesund during the experimental period was stable and ranged between $3.3$ and $6.7^\circ C$ (mean $4.7^\circ C$). Mean daily precipitation was $1.0$ mm (range $0$ to $14$ mm). The col-
ony was in the shade for most of the day and was only exposed to the sun at ‘night’, resulting in a low solar heat gain. Measurements of the operative temperature for adult Kittiwakes in the same colony in 1989 (G.W. Gabrielsen) yielded an average of 6°C which value we have adopted here for unbrooded chicks.

During the entire nestling period the nest was attended by at least one parent for 96% of the time (Fig. 5). Just after hatching parents brooded the chick for 90% of the time. This proportion gradually decreased with age, and chicks older than 20 days were brooded only incidentally. We assumed that brooded chicks did not thermoregulate.

Water, fat, protein and energy densities of the food samples did not differ significantly among prey species (one-way ANOVA, $P > 0.05$) so that only the overall mean (% of the fresh mass) is given: water content 79.8% ($SD = 3.9, N = 20$), fat 3.4% ($SD = 1.4, N = 10$), protein 12.5% ($SD = 3.2, N = 9$) and ash 4.3% ($SD = 1.1, N = 9$). Energy content amounted to 20.3 kJ·g$^{-1}$ (dry mass, $SD = 2.5, N = 20$). Water and energy content of polar cod provided to the chicks in the doubly labelled water validation experiments were determined to be 83.7% (fresh mass) and 20.2 kJ·g$^{-1}$ (dry mass), respectively.

When comparing doubly labelled water estimates of daily energy expenditure with values obtained by indirect calorimetry, no significant difference between the sample means was found (Table 1, paired $t$-test, $T(8) = 0.85, P = 0.42$). Values for single samples, however, varied from -24% up to 107%. In contrast, single estimates of gross energy intake from D turnover experiments were in close agreement with the daily gross intake values found by weighing of the food ingested (-34% up to 25%, Table 1). The sample means of these two data sets did not differ significantly either (Table 1, paired $t$-test, $T(9) = 0.14, P = 0.86$).

Daily net energy requirement, i.e. metabolisable energy intake, was compiled using three methods:

1. by multiplying the daily gross energy intake ($GEI$, Fig 2, lower graph) with the assimilation efficiency (0.8, B. Brekke),
2. by adding together the daily energy expenditure ($DEE$, Fig. 2, second graph from bottom) and energy accumulated in body tissue ($E_{tiss}$, Fig. 2, upper graph), and
3. by assuming the activity costs to be negligible and adding together the resting metabolic rate ($RMR$, Fig. 2, second graph from top), thermoregulatory cost ($E_r$, Fig. 2, second graph from top), energy accumulated in body tissue ($E_{tiss}$, Fig. 2, upper graph) and the synthesis of this tissue ($E_{syn}$, Fig. 2, upper graph). The total metabolisable energy requirements using these three methods is compared in Figure 6. For daily energy expenditure and gross energy intake the seven point running mean lines were used so that the comparison is limited to a chick age of 2 to 28 days. The second method resulted in a 9% lower result than the first method. Considering the scatter in the daily energy expenditure and gross energy intake values, this might be considered as a close fit. The third method had a 21% lower result than the first method and a 13% lower result than the second one, but here activity costs are excluded. This clearly prevents a reliable estimate of true energy requirement through the third method.
Table 1. Comparison of methods used in validation experiments of Kittiwake chicks. Daily energy expenditure measured with doubly labelled water and indirect calorimetry. Gross energy intake measured by D turnover rate and from measurement of ingested food.

<table>
<thead>
<tr>
<th>Nr</th>
<th>Age (days)</th>
<th>Change M (g)</th>
<th>M2 (g-day⁻¹)</th>
<th>DEE ± SE³ (kJ·day⁻¹)</th>
<th>True DEE⁴ (kJ·day⁻¹) (kJ·day⁻¹)(%)</th>
<th>Difference (kJ·day⁻¹) (kJ·day⁻¹)(%)</th>
<th>GEI ± SE⁵ (kJ·day⁻¹)</th>
<th>True GEI⁶ (kJ·day⁻¹)</th>
<th>Difference (kJ·day⁻¹)(%)</th>
<th>N7</th>
</tr>
</thead>
<tbody>
<tr>
<td>41a</td>
<td>2</td>
<td>47</td>
<td>12.1</td>
<td>79 ± 8</td>
<td>40</td>
<td>-39 99</td>
<td>121 ± 3</td>
<td>146</td>
<td>25 -17 6</td>
<td></td>
</tr>
<tr>
<td>41a*</td>
<td>2</td>
<td>53</td>
<td>0.0</td>
<td>77 ± 11</td>
<td>52</td>
<td>-25 48</td>
<td>172 ± 14</td>
<td>138</td>
<td>-34 25 4</td>
<td></td>
</tr>
<tr>
<td>19s</td>
<td>6</td>
<td>95</td>
<td>27.9</td>
<td>203 ± 3</td>
<td>98</td>
<td>-105 107</td>
<td>287 ± 1</td>
<td>289</td>
<td>3 -1 4</td>
<td></td>
</tr>
<tr>
<td>19s*</td>
<td>6</td>
<td>108</td>
<td>7.2</td>
<td>121 ± 6</td>
<td>104</td>
<td>-17 17</td>
<td>259 ± 2</td>
<td>224</td>
<td>-34 15 4</td>
<td></td>
</tr>
<tr>
<td>18a</td>
<td>13</td>
<td>186</td>
<td>6.0</td>
<td>161 ± 47</td>
<td>212</td>
<td>51 -24</td>
<td>300 ± 5</td>
<td>310</td>
<td>11 -3 4</td>
<td></td>
</tr>
<tr>
<td>18a*</td>
<td>13</td>
<td>189</td>
<td>-13.5</td>
<td></td>
<td></td>
<td>280 ± 8</td>
<td>248</td>
<td>-95 19 4</td>
<td>10 2</td>
<td></td>
</tr>
<tr>
<td>24a</td>
<td>15</td>
<td>171</td>
<td>53.5</td>
<td>291 ± 22</td>
<td>358</td>
<td>67 -19</td>
<td>598 ± 1</td>
<td>503</td>
<td>-95 19 4</td>
<td></td>
</tr>
<tr>
<td>24a*</td>
<td>15</td>
<td>199</td>
<td>36.3</td>
<td>348 ± 6</td>
<td>398</td>
<td>50 -13</td>
<td>742 ± 1</td>
<td>678</td>
<td>-65 10 2</td>
<td></td>
</tr>
<tr>
<td>15a</td>
<td>22</td>
<td>277</td>
<td>37.5</td>
<td></td>
<td></td>
<td>625 ± 6</td>
<td>653</td>
<td>28 -4 4</td>
<td>10 2</td>
<td></td>
</tr>
<tr>
<td>15a*</td>
<td>22</td>
<td>296</td>
<td>20.3</td>
<td></td>
<td></td>
<td>463 ± 9</td>
<td>698</td>
<td>234 -34 4</td>
<td>10 2</td>
<td></td>
</tr>
<tr>
<td>22b</td>
<td>34</td>
<td>400</td>
<td>9.7</td>
<td>439 ± 4</td>
<td>380</td>
<td>-59 15</td>
<td>417 ± 5</td>
<td>4</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>22b*</td>
<td>34</td>
<td>405</td>
<td>46.7</td>
<td></td>
<td></td>
<td>518 ± 10</td>
<td>436</td>
<td>-82 19 701 ± 4</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td>248</td>
<td>231</td>
<td>-18 28</td>
<td>414 389</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>SD</td>
<td></td>
<td></td>
<td>151</td>
<td>153</td>
<td>58 46</td>
<td>201 211</td>
<td>85</td>
<td>17</td>
<td>10 2</td>
<td></td>
</tr>
<tr>
<td>N</td>
<td></td>
<td></td>
<td>9</td>
<td>9</td>
<td>9 12</td>
<td>10 10</td>
<td></td>
<td></td>
<td>10 10</td>
<td></td>
</tr>
</tbody>
</table>

1asterisk indicates second part of experiment; 2body mass at start of experiment; 3estimated from doubly labelled water turnover; 4indirect calorimetry; 5from D turnover rate; 6from weighing of ingested food; 7sample size of DEE and GEI analysis with doubly labelled water and D turnover experiments, respectively.

**DISCUSSION**

Considerable variations in the estimates of the daily energy expenditure are found in doubly labelled water experiments with adult birds, although the mean error in validation experiments is seldom more than 8% to both sides (e.g. Nagy 1980, Masman 1986, and others that used the same analysis method as we). Williams & Nagy (1985) argued that severe errors might result from the use of doubly labelled water in rapidly growing animals such as chicks. Hitherto only one validation study in chicks is available and showed that the use of doubly labelled water in Arctic Tern Sterna paradisaea chicks resulted in an underestimation of the daily energy expenditure of 2-26% (Klaassen et al. 1989). This underestimation could be the result of an irreversible incorporation of D in the growing body tissues (Williams & Nagy 1985). However, in
our results the daily energy expenditure as measured with the doubly labelled water method overestimates as well as underestimates the actual daily energy expenditure (Table 1). Moreover, in our study irreversible incorporation of D in the body tissue is unlikely to have happened to any great extent as the gross energy intake estimates from D turnover rate are rather accurate (Table 1). The relative errors in the doubly labelled water estimates were extremely high in young chicks. However, the absolute errors were insignificant compared to the total energy budget for development, as at very young age the energy requirements are low. Clearly, much is still to be learned about the source of the errors obtained in the doubly labelled water experiments. It is, however, clear that in experiments with doubly labelled water measurements which last only a relatively short period of time as in our experiments (12 hours), only a large data set can provide reliable information on the daily energy expenditure of Kittiwake chicks throughout development.

Our validation of gross energy intake from D turnover rate could possibly have been improved by keeping the chicks in the laboratory on a regular feeding schedule before validation. The validation data from this study might be affected by individual differences in pre-experimental feeding circumstances. Nevertheless, measurements of gross energy intake from D turnover rate seem to be rather accurate and might be a promising alternative for cases where chicks depend exclusively on water intake through the food.

In order to compute the total metabolisable energy intake over the entire chick period (0-35 days), we used an assimilation efficiency of 0.8 (B. Brekke) and estimates of gross energy intake from D turnover. To do this, we had to conduct a minor extrapolation of our seven point running lines of the gross energy intake (Fig. 2, lower graph), which cover only age 2 to 33 days. The total metabolisable energy intake for development amounted to 18.4 MJ. Using the data of resting metabolism, thermoregulation, tissue deposition and tissue synthesis plotted in Figure 2, the proportional allocation of metabolisable energy to these processes and to activity (which is the remainder) could be calculated (Fig. 7). The allocation pattern of metabolisable energy strongly resembled the pattern found in laboratory-raised chicks (Drent et al. 1992), mainly due to the low thermoregulatory costs of Kittiwake chicks. Both in laboratory-raised chicks (Drent & Klaassen 1989, Drent et al. 1992) and in field studies with tern chicks (Klaassen et al. 1989) a considerable proportion of the energy expenditure is allocated to activity. This might seem strange for nestlings. However, although the chicks are restricted to the nest, preening and wing flapping are noticeable outlets of energy expenditure.

Our estimate of the thermoregulatory costs is weakened by the lack of thermal conductance estimates below a body mass of 177 g (Fig. 4), which corresponds to an age of 11 days. For young age classes we therefore had to extrapolate our thermal conductance estimates. However, compared with measurements of the thermal conductance in Kittiwake hatchlings by Bech et al. (1984) our equation overestimates the thermal conductance by only 14%.

Fig. 7. Total energy requirements of free-living Kittiwake chicks in Krykkje-fjellet colony at Svalbard, from hatching until fledging (0-35 days). Proportional allocation (in %) of metabolisable energy intake in Kittiwake chicks over the total nestling period (18.4 MJ) to resting metabolism (RMR), thermoregulation (Erot), tissue deposition (Etis), tissue synthesis (Esyn) and activity (Eact) is indicated.
At a body mass of 253 g, which corresponds to an age of 16 days, the thermoregulatory cost equalled zero when a lower critical temperature of 6°C was reached. Beyond 16 days, there were no thermoregulatory costs. Adult Kittiwakes have a lower critical temperature of 4.5°C (Gabrielsen et al. 1988). That chicks, approximately 100 g lighter than adults, have such a low lower critical temperature is mainly due to the high mass specific resting metabolic rate at that point of development (Ricklefs 1974). However, after the age of 16 days, adults spent some time in brooding (Fig. 5). It is suggested that at that age the main aim of the behaviour is mainly to protect the chick, which has a non-waterproof plumage, against rain. In cold areas brooding may also led to a better energy budget for the parents. Moreover, adults have to stay somewhere at the nest when attending their young. Although not strictly necessary it is likely that they continue to remain in brooding posture as long as the chick is small enough and will not suffer from overheating by this parental behaviour. The energy saved by brooding was 1.2 MJ, or 6% of the total metabolisable energy intake over the entire developmental period. The saving amounts to 19% of that intake when calculated up to an age of 16 days, the period during which the chick has to thermoregulate when not brooded (see above). In Arctic Tern chicks studied in the same area 10% of the total metabolisable energy required for development was saved on the total energy expenditure by parental brooding (Klaassen et al. 1989). The higher value in the Arctic Tern probably results from differences in size, and therefore the vulnerability for cold, between the two species.

The energy requirements of Kittiwake chicks can be compared with measurements of parental energy requirement. On Hopen Island (76°N, 25°E) the energy requirement of an adult Kittiwake averaged 795 kJ·day⁻¹ (Gabrielsen et al. 1987). The proportion of energy delivered through the adults per chick raised (0 to 35 days) is thus 33% of the energy required by a pair of adults. This value is close to the value obtained in the Black Guillemot Cepphus grylle (32%, G.W. Gabrielsen), but is twice as high as in the Little Auk Alle alle (15%, Konarzewski et al. 1992). The similarities in parental investment in Kittiwake and Black Guillemot and the difference in the investment of the two species with that in the Little Auk might be linked to the species’ foraging behaviour. Both Kittiwake and Black Guillemot are inshore feeders whereas the Little Auk is an offshore feeder. Low parental investment values were also found in other offshore feeding alcids (Roby & Ricklefs 1986). The use of allometric relations for assessing the energy requirements of offspring (e.g. Walsberg 1983) is weakened by the fact that they do not take into account species-specific biological phenomena, such as differences in feeding habit. Thus one should be wary on applying these methods when sensitive analyses of the food requirement are needed.

Gabrielsen et al. (1987) estimated the average food consumption of a couple of breeding Kittiwakes at 315 g fresh capelin Mallotus villosus per day. Using the parental investment efficiency of 33% (see above) the average food consumption of a couple with one chick would be 419 g capelin per day. However Kittiwakes at Svalbard typically start with two chicks in the nest of which only one chick usually survives. Assuming a constant mortality rate throughout the developmental period the average family food consumption would amount to 462 g capelin per day. For the Hopen colony, the 3000 breeding pairs would therefore consume about 1358 kg capelin per day, which is 10% above the figure earlier given for that colony by Gabrielsen et al. (1987).

ACKNOWLEDGEMENTS

We thank the staff at Ny-Ålesund for their assistance and accommodation during the summers of 1986 and 1987, Ole Jørgen Lønne, Department of Zoology and Marine Biology, University of Tromsø, for analysing the food samples, Dirkjan Masman for his help in analysing the DLW samples, and Rob Barrett, Kjel Einar Erikstad, Kenneth A. Nagy and Janek Taylor for their helpful comments on an earlier version of the manuscript. The study was supported by the Norwegian Research Program for Marine Arctic Ecology (PRO-MARE) of the Norwegian Research Council for Sciences and the Humanities. This
REFERENCES


**SAMENVATTING**

Om de invloed van vogels op de energiestroom door het mariene ecosysteem te meten, is het nodig een goede schatting te hebben van hun dagelijkse energiebehoefte. Op Spitsbergen is op drie verschillende manieren de energiebehoefte van kuikens van Drieteenmeeuwen...

De eerste twee methoden gaven overeenkomstige resultaten, terwijl de derde methode 13-21% lager uitviel. De derde methode gaat echter voorbij aan de activiteitskosten die, ondanks het feit dat het om nestblijvers gaat, klaarblijkelijk toch aanzienlijk zijn. Tot de kuikens 16 dagen oud zijn, worden ze geregeld bebroed. Dit leidt voor de kuikens tot een besparing van de energie-uitgave van 19% over deze periode. Hierna nemen de activiteitskosten aanzienlijk toe. De totale netto-opname over de gehele nestperiode (35 dagen) was 18.4 MJ. Hiervan maakten de kosten (percentages afgerond) van het rustmetabolisme 53% uit, de weefselkosten 18%, de synthesekosten 6%, de activiteitskosten 22% en de thermoregulatiekosten 2%. De totale netto-energieopname van een opgroeid kuiken bedraagt 33% van de energie die beide ouders nodig hebben. Dit percentage komt overeen met dat wat bij de Zwarte Zeekoet Cepphus grylle, een andere typische kustvogel (inshore feeder), gevonden is en is tweemaal zo hoog als het percentage bij de Kleine Alk Alle alle, een vogel die ver op zee foerageert (offshore feeder). Een paartje broedende Drieteenmeeuwen eet per dag gemiddeld 315 g lodde Mallotus villosus, een voor deze meeuwen in dit gebied karakteristieke prooi-soort. Rekeninghoudend met het gemiddelde aantal jongen in het nest en hun sterftekans voor het uitvliegen, komt de gemiddelde voedselconsumptie van een gezin Drieteenmeeuwen in de kuikenperiode op 462 g lodde per dag neer. Voor de 3000 paar tellende kolonie op het eiland Hopen houdt dit een totale loddeconsumptie van 1.4 ton per dag in.